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How does incentive motivational theory apply to sexual behavior?

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Introduction

The incentive motivational view of motivation ascribes a primary role to incentive stimuli as the generators of motivational states and elicitors of actions. A central motivational state is said to be set up in the organism as a result of direct interactions with either primary (unconditioned) incentive stimuli or conditioned incentive stimuli, or through thoughts about these stimuli and events. Modifications in the internal environment such as those induced by cyclic changes in endogenous hormones, by deprivation, and by pharmacological agents are thought to alter the behavioral effectiveness of unconditioned and conditioned incentive stimulus events by altering both their salience and the quality and magnitude of the central motivational states they generate. The induction of an incentive motivational state, in turn, further enhances the salience and behavioral effectiveness of these and related stimulus events [see 1-5] providing a mechanism for the maintenance of goal-directed behavior. Although the evidence to support this view of motivation comes from studies using a range of incentive stimuli and motivational systems including food, sweet substances, objects of prey, and the incentive properties of electrical stimulation of the brain, studies of sexual motivation provide in many ways some the most compelling evidence for this view.

Primary or Unconditioned Incentive Stimuli

By definition, unconditioned positive incentive stimuli are those stimuli which, for a given species, have a high probability of eliciting an emotional or motivational state, approach behavior, and engagement with the incentive and related stimuli. The effectiveness of such stimuli depends on the current hormonal and neurochemical state of the organism, and, in that sense, they do not elicit motivation or behaviors unconditionally. The creation of the motivational 'state' by these stimuli occurs through their actions on modulatory neurochemical systems such as the monoamine, neuropeptidergic, and neuroendocrine systems and on secretion of hormones from the endocrine glands. Some of these actions may occur in sequence, others concurrently.

Conditioned Incentive Stimuli

Conditioned incentive stimuli are those that through pairing with unconditioned incentive stimuli come to be able to elicit, by themselves, aspects of the motivational state elicited previously by the unconditioned incentive

stimuli. Knowledge about the functioning of these stimuli is important for an understanding of how motivated behavior can be initiated in anticipation of and in the absence of unconditioned incentive stimuli.

General and Specific Effects of Incentive Stimuli

An incentive stimulus can through its actions enhance its own effectiveness. Furthermore, the evidence indicates that the motivational states created through the interaction with an incentive stimulus may enhance the effectiveness of other stimuli and facilitate behaviors other than those normally elicited by these particular incentive stimuli. For example the neuroendocrine changes accompanying the presentation of stimuli capable of eliciting sexual behaviors may facilitate the effectiveness of stimuli that elicit aggression. The problem that has faced the motivational theorist, as well as the researcher interested in a particular motivational system such as that underlying sexual behaviors, has been to identify the degree to which motivational states are specific to one class of motivated behaviors and the degree to which there is a common basis with others. It can be noted, that there has been a tendency to consider important only those contributions to a motivational state that can be shown to be specific, and to consider unimportant those that are common to others. It can be argued, however, that the common aspects may be as critical to our understanding of the neural basis of any particular appetitive motivational state as are the specific aspects, for the general may modulate the specific.

It can be shown as well that conditioned incentive stimuli and the states they generate can affect the impact of unconditioned stimuli. It has been argued by Hollis [6], for example, that the primary function of conditioned stimuli is to prepare the organism to deal with oncoming unconditioned stimuli. Conditioned stimuli based on pairing with one set of unconditioned stimuli can also affect the response to other apparently unrelated stimuli. An example from a study in adult male rats will serve to make the point. We gave male rats injections of morphine (10 mg/kg, i.p.) paired with a distinctive test chamber following a procedure we knew led both to a conditioned preference for that environment (conditioned place preference, CPP) and conditioned control of the expression of the heightened activity effects of morphine that develop with repeated exposure (sensitization). A second group received morphine in the home-cage and saline in the test chamber, and a third saline in both environments. After several pairings, all animals were tested for sexual behavior with a receptive female in the test chambers. Sexual behavior was facilitated in those animals that had previously received morphine in the test environment; both gonadally intact and castrated males displayed more frequent female-directed behavior (pursuit, anogenital exploration, and partial mounts), and intact males mounted and intromitted with shorter latencies than animals in the other groups [7]. Thus conditioned activation based on pairing an environment with a drug known to have appetitive motivational effects, facilitated the response to the unconditioned stimulus effects of the receptive female.

Appetitive Motivational and Copulatory Components of Sexual Behavior

The idea that it is possible to differentiate a sexual motivational or arousal component of sexual behavior from a copulatory performance component was clearly laid out by Beach in 1956 [8]. Studies in the male rat have provided the clearest evidence for the dissociability of the neural pathways underlying the activation of appetitive motivational components of sexual behavior and those underlying copulatory performance. It has been shown for example that lesions of the medial preoptic area of the hypothalamus (MPOA) that reduce mounting, intromission and ejaculation, leaving appetitive sexual responses intact. Under these circumstances males show normal attraction to the estrous female, they engage in precopulatory activities such as anogenital sniffing, nuzzling, and following, but do not engage in copulatory acts. These males develop conditioned place preferences for chambers paired with estrous females and will engage in learned instrumental behaviors for access to the female. On the other hand, lesions of the mesolimbic dopamine (DA) system or pharmacological blockade of transmission in this system reduce the initiation of interactions with the female and the acquisition and maintenance of appetitive responses based on interactions with the female without interfering with copulatory behaviors once they are initiated [for a review see 9]. Everitt has argued that these are parallel systems that become engaged in sequence only fortuitously because of the fact that appetitive behaviors are initiated through the actions of distal stimuli and the copulatory ones through the actions of proximal tactile stimuli. It may well be, however, that although the two aspects of behavior can be elicited independently, in the normal course of events appetitive arousing stimuli have impact on those systems responsible for copulation by facilitating activity in those circuits that are directly affected by specific stimulus events [for a recent analysis of this issue see 10], or by initiating hormonal events that serve to maintain and sustain behavior.

Unconditioned Incentive Stimuli for Sexual Arousal

Let us consider now the unconditioned stimuli that arouse sexual appetite in the male rat and the nature of their impact. For the male rat the odors from the estrous female, the visual stimuli arising from her movements, and ultrasonic calls appear to act as the primary incentive stimuli for appetitive responses. DA activity measured in the nucleus accumbens septi (NAS) by microdialysis or voltammetry rises sharply when males are given access to a receptive female or allowed to both see and smell a female through a wire-mesh screen [11-13]. A similar response is seen when males are given access to bedding from estrous females, but not that from ovariectomized females or males [14]. Interestingly, this response sensitizes with repeated presentations, becoming larger and peaking earlier in time. It is significant that the response can be blocked by prior treatment with the opioid receptor antagonist, naloxone, and that such treatment appears to attenuate the response to bedding on subsequent presentations without naloxone. This finding is consistent with the evidence that injections of morphine into the VTA, known to increase firing in A10 dopamine cells, facilitate precopulatory behaviors and mating in male rats that have been surgically castrated and maintained on low levels of testosterone [15]. It has also been found, in the anesthetized male rat, that air impregnated with estrous female bedding odors can activate the DA signal in the NAS and that this effect can be mimicked by K+ to the vomeronasal nerve layer of the

accessory olfactory bulb (AOB) [16]. These studies show that sexually relevant olfactory stimuli have access to the mesolimbic DA system, possibly via the amygdala, and may involve the activation of opioid systems in the VTA. AOB information is conveyed to the amygdala, and recent studies have shown lesions of the olfactory peducle interfere with c-fos expression in the amygdala following anogenital sniffing of the estrous female [17].

Activation of the mesolimbic DA system is an effect common to all positive incentive stimuli studied and cannot, therefore, be considered specific to sexually relevant stimuli [18-20]. This does not imply, however, that under normal circumstances the activation of this system is not critical for the occurrence of sexual interactions. Male rats whose mesolimbic DA systems have been compromised by lesions require the female rat to engage in highly stimulating sex-eliciting or proceptive behaviors in order to initiated sexual interactions [21]. It is interesting in light of the effects of sexually relevant olfactory cues on DA levels, therefore, that anosmic male rats do not initiate sexual behavior with motionless females, though normal animals are perfectly capable of doing so [22]. A recent study on DA transmission in the NAS in female rats in response to male bedding demonstrates as well that hormonal state of the animal may gate responsiveness of the system to different incentive stimuli. Normally cycling females were tested for their response to bedding from intact males and to food at diestrus, proestrus and estrus. The DA signal rose maximally in response to bedding at estrus and not at all at diestrus, whereas the response to food was maximal at proestrus and much attenuated at estrus [23].

Sexually relevant olfactory stimuli have another set of effects that can be considered to be more specifically related to sexual motivation. LH levels have been found to increase in male rats exposed to the odors of estrous females [24]. When males are allowed access to the female, LH rises within 5-15 minutes of her presentation. This rise in LH is followed by increases in testosterone (T) and in prolactin (PRL) levels in those males that mate. All of these effects are greater in sexually experienced males. Interestingly, the rise in LH upon presentation of the female is seen in males with lesions of the MPOA even though these animals do not copulate [25]. On the other hand, normal intact males that do not mate, though free to do so, (so-called 'spontaneous noncopulators' that seem to suffer from general arousal deficits and low interest in their environments [26]) do not show increases in any of these hormones when presented with an estrous female [27]. The importance of sexually relevant odors for these rises in LH and the fact that they can be seen in response to females following lesions of the MPOA may be explained by the recently discovered LHRH neurons in the terminal nerve of the AOB [28]. Interestingly, odors from an estrous female are not sufficient to induce penile erections in experienced male rats, though distal stimuli in the absence of contact are [29], a finding that suggests differential effects of these stimuli on separate mechanisms underlying sexual arousal.

Non-Specific Unconditioned Stimuli and Sexual Arousal

A series of studies carried out in the late 1960s and early 70s demonstrated that brief intermittent electric shocks to the flanks or tail facilitate

copulation [e.g., 30,31] and, in inexperienced male rats, the initiation of sexual behavior [32-34]. Sexually naive males or spontaneously noncopulating males rapidly initiate sexual interactions and copulation when given shocks in the presence of an estrous female. Such shocks also reduce the intervals between intromissions and the latencies to resume sexual activity following ejaculation. It is now known that brief shocks of this nature and tail pinches activate the mesolimbic DA system neurons [e.g., 35] in addition to noradrenergic and other systems. Such stimulation also facilitates eating and ingestive behaviors in the presence of appropriate stimuli. It is likely, therefore, that this nonspecific activation acts to increase the effectiveness of the incentive stimuli in the environment, in this case the sexually relevant stimuli arising from the female, and to prime the circuitry mediating copulatory behaviors. Brief shocks have also been found to widen the range of stimuli (to include other males and a stuffed toy animal) that will elicit sexual behaviors from males [32]. Furthermore, once copulation has occurred in previously noncopulating males, the behavior is maintained on subsequent tests suggesting that stimuli from the female previously unable to arouse sexual interest acquire incentive salience through their pairing with the shock induced arousal and the subsequent sexual interactions. In fact, Sachs and Barfield [31] have suggested that shock acts to decrease intervals between intromissions and to shorten the inactive period post-ejaculatory by lowering the threshold for effective stimuli from the female during the relative refractory period.

Flank shock and tail pinch have been shown to facilitate sexual behavior in male rats after olfactory bulbectomy [36,37]. Bulbectomized males are reported to show both initiation and copulatory deficits including long intromission latencies and failure to ejaculate, deficits that exceed those due to damage to the olfactory epithelium. These males can be induced to engage in normal copulatory activity when presentation of the female is paired with shock or tail pinch. However, unlike intact males that maintain copulatory behavior from test session to test session once it has been induced by shock, bulbectomized males required shock induction at each test. These results would seem to suggest that bulbectomy interferes not only with those circuits through which sexually relevant olfactory stimuli induce arousal, but also with the circuits that mediate other sensory information to this system or with the actions of gonadal hormones that modulate these systems. Failure of bulbectomized animals to mate is not due to inadequate levels of gonadotropins or T [e.g., 38], but androgen receptor binding is reduced in both amygdala and hypothalamus in these animals [39].

Conditioned Incentive Stimuli and Sexual Arousal

Conditioned preferences for places previously paired with access to an estrous female are easily established in male rats [40,41], and it has been shown in numerous experiments that sexual behavior in male rats is facilitated in environments previously associated with sexual activity. Furthermore, a specific role for conditioned incentive stimuli in this effect (as opposed to habituation to a novel environment) has been demonstrated. For example, Zamble and colleagues [42] showed that presentation of a stimulus previously paired with unconditioned stimuli for sexual arousal (sights and smells of a receptive female, see [43])

decreases the time to ejaculation and speeds the rate of intromission. Interestingly, this effect is similar to the facilitating effect of electric shock on copulation. In addition, these researchers showed that a second stimulus paired only with the conditioned incentive stimulus acquired second-order conditioned effects capable of facilitating copulation in a similar manner.

Several possible mechanisms may be operating to mediate these effects. Once established CPPs based on access to a receptive female are disrupted by naloxone [41] and by castration [40]. Conditioned stimuli repeatedly paired with copulation in male rats lead to increases in serum levels of LH and T equal to those seen in males after presentation of a receptive female [44]. These hormonal changes may serve to both heighten the effectiveness of natural incentive stimuli and increase persistence of behavior. Mitchell has recently found that the DA levels in the NAS in response to bedding from estrous females increases markedly following a single sexual experience given to sexually naive animals, whereas there is no change in the response to food (personal communication). Neurons in the NAS of male rats show enhanced responding to novel odors previously paired with sexually receptive females [45]. Thus both neuronal and hormonal events capable of being elicited by unconditioned stimuli can come to be elicited by conditioned stimuli previously paired with them. It is interesting that stimuli previously paired with electric shocks can act as conditioned stimuli to facilitate the initiation of sexual behavior in normally unresponsive male rats [33]. Furthermore, once animals have begun to copulate in the presence of these stimuli, copulation continues to be facilitated in their absence. This findings suggests that stimuli from the female acquire the capacity to activate sexual motivation through their pairing with the arousal induced by the conditioned stimuli and the subsequent sexual interactions. The ability of conditioned stimuli to facilitate approach and to maintain responding to conditioned stimuli appears to be transmitted via the basolateral amygdala, an area of the limbic forebrain with access to the terminal regions of the DA system in the NAS [9]. Whether this region mediates the effects of conditioned stimuli on hormonal responses and activity in the DA system is not known.

Testosterone and Sexual Arousal

An incentive theory of motivation considers that modifications in the internal environment, such as those induced by changes in endogenous hormones, have their effects on behavior by altering the impact on the organism of unconditioned and conditioned incentive stimulus events. Here we shall consider only one of these modifications, changes in circulating testosterone (T). The role of T in arousal and maintenance of sexual behavior in male mammals has been widely studied. It is well known that in many mammals sexual behaviors are reduced and eventually eliminated after castration. Let us consider some of the ways in which changes in T might affect sexual arousal. T appears to facilitate the behavioral effectiveness of both natural incentive stimuli and conditioned incentive stimuli. It is interesting to note that a certain level of T is necessary for sexually stimulated release of LH and PRL [46] and presumably T (in the intact male rat), suggesting a feed-forward effect whereby adequate levels of T promote higher levels of T in response to sexually related stimuli. T has been shown to alter an animal's response priority to competing

incentive stimuli. Male rats given access to a highly palatable sweet solution and to an estrous female markedly reduce drinking in the presence of circulating T, whereas castration led to increased drinking over time [47].

Conditioned place preferences in male rats based on access to sexually receptive female are quickly abolished following castration [40]. In humans low T levels are associated with low levels of sexual interest and reduced sexual thoughts and fantasy [48-50]. Castration reduces the concentrations of DA and its metabolites in the NAS [51,52], an effect that can be prevented with treatment with T. This reduced DA activity might account for the virtual inhibition of sexual behavior and CPPs in male rats treated with the opioid antagonist, naloxone, shortly after castration [53]. Reductions in DA activity induced both by castration and naloxone should in turn lead to reduced effectiveness of incentive stimuli and reduced maintenance or persistence of sexually related thoughts and behaviors. Interestingly, animals given repeated opportunities to copulate following castration showed little change in dopamine activity suggesting that frequent exposure to a sexually receptive female might help maintain mesolimbic DA levels [54]. In addition, highly arousing stimulation such a flank shock known to increase mesolimbic DA activity has been shown to induce copulation in castrated male rats, but like in olfactory bulbectomized animals, and unlike in spontaneously non-copulating animals, the effects on copulation do not persist following termination of the stimulation [55].

Finally, a recent study has shown that a rapid increase in T level can, in itself, promote the development of a conditioned place preference in rats, suggesting that T can induce a positive affective state [56] that can become associated with previously neutral stimuli. This finding is interesting in view of the evidence that T may enhance not only sexual motivation, but also general well-being in females [57]. Furthermore, increased levels of T have been shown to be associated with winning in tennis, and tennis players with the highest prematch T levels have been found to have the most positive improvement in mood before matches [58], an effect that might facilitate subsequent play in the feed-forward manner discussed above. Quite an opposite effect might be expected to result from the dramatic fall in T levels following physical defeat or severe stress [59]. Low levels of T would be expected to reduce the effectiveness of the sexual incentive stimuli normally capable of inducing increases in the levels of sexually related hormones [45], which in turn would serve to maintain the ineffectiveness of these stimuli on behavior and possibly. through time, reduce their impact even further.

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Discussion - HOW DOES INCENTIVE MOTIVATIONAL THEORY APPLY TO SEXUAL BEHAVIOR?

W. Everaerd

I would like to know to what extent the data that you presented about increase in dopamine activity in the nucleus accumbens in male rats given access to a receptive female represents a specific response. Could motor activity play any role in this effect?

J. Stewart

No. The increase is not seen in animals doing vigorous exercise on a running wheel until they are presented with the bedding from an oestrous female. At this point a very steep rise occurs.

J.G. Pfaus

Actually, in this type of study, the dopamine levels continue to increase after the animal stops exercising and simply lays down, apparently ignoring the bedding. I don't think there is a clear correlation with the amount of physical effort the animal has to perform.

W. Everaerd

The incentive motivation theory would predict that when you deprive the animal of sexual stimuli the response will increase. Do you have any data on that?

J. Stewart

No, it would not predict that. It would predict that in the absence of the incentive stimuli the response would not occur.

W. Everaerd

But, for humans it has been predicted that absence of sexual stimuli would increase the activity through abstinence.

J. Stewart

What kind of abstinence? If it is abstinence with the possibility of continuing to think about sex, all right, but if it is abstinence that occurs because subjects are thinking about other things, then I would think that it would have less effect.

B.D. Sachs

It has been shown that the dopamine rise is also found in anaesthetized male rats exposed to estrous female odors. This speaks to the question of how much activity is needed to generate the response, but I wonder what it says about the induction of a central motive state by the olfactory stimuli. Do anaesthetized males have a central motive state, specifically a sexual central motive state at the time that dopamine is increasing in the accumbens?

J. Stewart

I would not argue that the rise in dopamine is the central motive state. I would say that it is one of the contributors to it and that the rising hormones, the changes in peptides, all these other things are contributing to it. But I think that it is a concept that allows you to talk about the specifics of all these events, and at the same time, account for the behavioural changes that occur in response to stimuli.

M. Mas

Concerning the release of dopamine induced by olfactory stimuli in sexually experienced animals, I would like to point that one also gets that response in sexually naive animals. It is an innate response that eventually can be sensitised. With regard to specificity, in our experience, one gets increased dopamine release in the accumbens with many stimuli, but there are important quantitative differences. For example the increases seen associated with movement or with other social interactions are much smaller than those occurring during mating, so the quantitative aspects of these responses should be assessed carefully.

J. Stewart

Yes. I certainly don't want to imply that there is anything specific about this rise

in dopamine but in my view the way to think about it is that the massive rise in dopamine that you see to these primary incentives is going to facilitate responses to everything else that the animal encounters.

J. Bancroft

What would happen if you prevented that, for instance through a specific lesion?

J. Stewart

I have a list of experiments that need to be done. First of all, what is the response in the endocrine system in the male rat if you lesion the midbrain dopamine neurons? There are really a series of things that should be looked at before we could begin to say something about the sequence of events that occurs during this period of establishment of arousal.