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Male risk taking, female odors, and the role of estrogen receptors

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ABSTRACT

Male risk-taking and decision making are affected by sex-related cues, with men making riskier choices and decisions after exposure to either women or stimuli associated with women. In non-human species females and, or their cues can also increase male risk taking. Under the ecologically relevant condition of predation threat, brief exposure of male mice to the odors of a sexually receptive novel female reduces the avoidance of, and aversive responses to, a predator. We briefly review evidence showing that estrogen receptors (ERs), ERα and ERβ, are associated with the mediation of these risk taking responses. We show that ERs influence the production of the female odors that affect male risk taking, with the odors of wild type (ERαWT, ERβWT), oxytocin (OT) wildtype (OTWT), gene-deleted 'knock-out' ERβ (ERβKO), but not ERαKO or oxytocin (OT) OTKO or ovariectomized (OVX) female mice reducing the avoidance responses of male mice to cat odor. We further show that administration of specific ERα and ERβ agonists to OVX females results in their odors increasing male risk taking and boldness towards a predator. We also review evidence that ERs are involved in the mediation of the responses of males to female cues, with ERα being associated with the sexual and both ERβ and ERα with the sexual and social mechanisms underlying the effects of female cues on male risk taking. The implications and relations of these findings with rodents to ERs and the regulation of human risk taking are briefly considered.

1. Introduction

What factors guide an individual's decisions when faced with potential risk? A growing body of evidence suggests that decisions regarding risk and risk taking in males are affected by sexual cues and stimuli. Men are reported to make "poorer" and "riskier" decisions when female related cues or stimuli are present (e.g. [1–4]). These decisions are suggested to facilitate sexually motivated behaviors with men's time perspective being shifted away from the long term consequences of their choices and focused on the immediate that is associated with the availability of a possible sexual partner [1,3,6]. Likewise in non-human species the presence of, either a female or sexual stimuli associated with a female, increases male risk taking in ecologically relevant contexts. For example, in rodents where chemical signals play a key role in social communication, male mice that are exposed to female odor show reduced fear responses and greater risk taking. Brief exposure to the odors of a novel sexually receptive female enhances the risk taking and boldness displayed by male mice towards a predator [7,8].

There is also an expanding interest in the neurobiological mechanisms that underlie social and sexual behaviors and responses [9–12]. Sex steroid hormones are excellent candidates for mediating external and internal information into adaptive behavioral responses to various challenges and opportunities (i.e. mating). There is substantial evidence suggesting that estrogens and estrogen receptors (ERs) have an important role in determining various aspects of social and sexual behavior in males as well in females [11,12] and are likely involved in the mediation of sexually associated risk taking [8]. Here, we first briefly review the effects of female cues on male risk taking, focusing on: (i) the effects of female sexual cues and stimuli on male risk taking in humans and other species and; (ii) the specific effects of exposure to female odors on the responses of male mice to predator threat. Secondly, we consider: (iii) the roles of estrogen receptors (ERα and ERβ) in risk taking, specifically reporting the results of studies showing the involvement of ERα and ERβ in the expression of female odors that influence socio-sexual responses and risk taking in male mice; and finally, (iv) we review the roles of ERs in mediating the risk taking responses elicited in males by exposure to female odor cues.

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2. Sexual cues and male risk taking

Sex-related cues have a significant impact on male behavior. A growing body of literature suggests that sexual motivation and augmented arousal elicited by females or their cues leads males to make riskier decisions and choices (e.g. [3,6,13]). This may be due to a decline and, or shift in men's cognitive performance. For example, men's cognitive performance, as assessed by a working memory task involving word lists, is reduced and more impulsive after a short interaction with a woman, especially if that woman is attractive [14]. Brief exposure of men to photos and videos of women engaged in sexual activity has also been associated with poorer performance on a cognitive go/no-go task [15]. Moreover, there is evidence suggesting that just the mere anticipation of an interaction with a woman that might be an attractive sexual partner and potential mate can reduce men's cognitive performance (Stroop color naming task), leading to riskier and poorer decisions [16].

Face-to-face contact with a fertile woman leads to greater risk taking by men in a gambling scenario [17]. Exposure to sexual photos of women has also been shown to enhance risk taking by men in a monetary reward context [3]. Likewise exposure to erotic images of women leads to men taking riskier economic and financial decisions [14]. However, it should be noted that in the economic and finance literature risk seeking and taking is usually defined in terms of a preference for a higher-variance pay off, whereas clinical and other researchers generally identify risk taking in terms of behaviors that can result in loss or harm to oneself or others. The latter may better capture the ambiguous nature of "real world" risky decision making in which choices are often associated with both rewards and risks of adverse consequences, which may be physically unrelated to one another. For a review of various measures of economic risk taking and their relations to other measures of risk taking see Schonberg et al. [18].

Results of several studies have revealed that the presence of an attractive woman can enhance immediate physical risk taking in young men (e.g. skate-boarding [19], crossing a road in the face of traffic [20], and in a virtual reality scenario crossing an ominous bridge [21]). Riskier sexually related decisions are also evident after exposure to female cues and images [22]. Ariely and Lowenstein [4] found that male heterosexual undergraduate students made a series of riskier judgments and decisions, including several related to HIV-related sexual risk, when sexually motivated and aroused after viewing sexual cartoons as compared to when not aroused (for discussions of the relationship between sexual motivation and arousal see [23–26]).

The enhanced risk taking elicited in men by sexually related cues has in several studies been associated with testosterone [2,27,28]. Slight rises in cortisol, possibly associated with arousal, have also been reported to occur in men and suggested to play a role in human mate responses, though larger rises likely suppress sexual functioning [2,27]. Sexual and erotic thoughts and psychological sexual arousal have been indicated to increase testosterone in men as well as in women [29]. In a classic study, Anonymous [30] reported that his beard growth, a bioassay for testosterone, increased on the days prior to sexual activity with his partner, perhaps due to the anticipation of sex.

Rapid (20–40 min) rises in salivary testosterone and physical risk taking have been documented in young men after non-sexual social interactions with attractive young women [2,19,27]. It is suggested that these rises in testosterone may focus attention on rewards and reduce sensitivity to losses, both of which are likely to enhance risky decision making [31] and likely, also affect economic decision making [9]. It was also found that larger testosterone increases in response to possible interactions with women were seen among men with smaller numbers of CAG codon repeats in exon 1 of the androgen receptor which are associated with a greater expression of the androgen receptor [32,33]. In this regard, the 2D:4D digit ratio, which has been considered as a proxy of prenatal testosterone exposure and possibly influences adult testosterone sensitivity, was also shown to influence the impact of sexual images on men's decisions [5]. There were, however, in most cases substantial inter- and intra-individual variation in these single acute measures of male testosterone levels.

Administration for 7 days of the aromatase (estrogen synthase) inhibitor, letrozole, which reduces the transformation of testosterone into estrogens such as 17β-estradiol, and resulted in elevated levels of testosterone (high end of normal levels), also led to men making riskier decisions under conditions of unknown probabilities (balloon analog risk task) but not in conditions of known probabilities (game of dice task) or when strategic decision making was required (Iowa gambling task with an incremental increase in decision probability) [34]. This was, in part, consistent with the positive correlation of daily natural testosterone levels with risk taking in economic decisions by financial day traders [35], though this was not found in a subsequent study examining the effects of testosterone administration in post-menopausal women [36]. It should be noted that none of the tasks in the aromatase studies involved sexual cues and sexually related decisions. However, importantly, it was suggested that the effects of testosterone on risk taking may also be related to, and, incorporate simultaneous variations in the metabolite of testosterone, estradiol. As subsequently discussed there is evidence that estrogen receptors are involved in the mediation of the effects of exposure to female cues on naturalistic risk taking by male rodents [7,8]. Testosterone could either directly, or indirectly, through aromatization to estradiol and subsequent effects on estrogen receptors, along with modifications in other neurochemical systems (e.g. serotonin, dopamine, glutamate, neuroactive steroid metabolites), affect cognition and anxiety leading to changes in risk taking (e.g. [10–12,37–39]).

This link between exposure to sexual stimuli and increases in testosterone is found in a variety of other non-human species of vertebrates. For example, sexual stimuli have been shown to trigger a rapid (less than 45 min) release of testosterone in male mice and rats (e.g., [37,39–45]), with novel females having particularly potent effects [46]. Sexual behavior per se is not needed for these responses to occur as increases in testosterone are evident in males after exposure to sexually receptive females placed behind transparent barriers (e.g. [37,43]) or to female chemosensory stimuli such as urine or vaginal secretions (e.g. [7,39,43,44,46]).

3. Predator exposure and male risk taking

In non-humans, predation threat has provided an ethologically relevant means for examining risk taking and decision making [47,48]. Anti-predator response patterns are shaped by tradeoffs between the benefits associated with the successful detection and avoidance of predation threat and those associated with a suite of fitness-related response patterns such as foraging, territorial defense, and mating. Results of studies with guppies and other species of fish have provided evidence indicating that the presence of a female is directly associated with a greater risk taking, increasing male boldness in the presence of predators [49]. The behavioral changes evident in males either after exposure to, or in the presence of, a female may involve an overall reduced fearfulness that leads to enhanced responses to potential mating opportunities.

Animals usually respond to the threat of predation risk with a number of defensive behaviors including either immobilization or fleeing and risk assessment (e.g. decision making as to when and how to forage, etc. in the presence of a predator), increased vigilance, and the suppression of non-defensive behaviors [48,50–53]. Results of field, laboratory, and semi-natural studies have shown that rodents display aversive and avoidance responses to either predators, or the odors of predators such as the domestic cat [48]. As found in prior