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Social Learning in Animals: Sex Differences and Neurobiological Analysis

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CHOLERIS, E. AND M. KAVALIERS. *Social learning in animals: Sex differences and neurobiological analysis.* PHARMACHOL BIOCHEM BEHAV **64**(4) 767–776, 1999.—Social learning where an "individual's behavior is influenced by observation of, or interaction with, another animal or its products" has been extensively documented in a broad variety of species, including humans. Social learning occurs within the complex framework of an animal's social interactions that are markedly affected by factors such as dominance hierarchies, family bonds, age, and sex of the interacting individuals. Moreover, it is clear that social learning is influenced not only by important sexually dimorphic social constraints but also that it involves attention, motivational, and perceptual mechanisms, all of which exhibit substantial male–female differences. Although sex differences have been demonstrated in a wide range of cognitive and behavioral processes, investigations of male–female differences in social learning and its neurobiological substrates have been largely neglected. As such, sex differences in social learning and its neurobiological substrates merit increased attention. This review briefly considers various aspects of the study of social learning in mammals, and indicates where male–female differences have either been described, neglected and, or could have a potential impact. It also describes the results of neurobiological investigations of social learning and considers the relevance of these findings to other sexually dimorphic cognitive processes. © 1999 Elsevier Science Inc.

Observational learning Social learning Individual learning Imitation Social constraints Social facilitation male–female differences Gender differences

THE experimental paradigms used in many investigations of learning and memory involve an animal having to "solve" a task through individual learning. Although mammals are usually quite skilled and develop the appropriate behaviors and responses necessary to master the situation, individual learning can be time consuming, and may place an animal in potentially nonadaptive situations. For example, during taste aversion learning an animal must first ingest small quantities of a toxic food, then experience a gastrointestinal malaise, and finally, learn to avoid the food that made it ill [e.g., (25–28,33,129,157)]. There are obvious risks involved with this food-related learning, as well as other types of individual learning. Social learning, on the other hand, allows an individual animal to "exploit the expertise of others" (127), thus, circumventing the disadvantages associated with individual learning. If another individual has already acquired vital skills, such as the selection of the appropriate diet or the location of food sources or shelters to escape from predators, an animal that can effectively socially acquire such knowledge will be in an advantageous situation (132). Social learning also plays a vital role in the acquisition of knowledge by adult and juvenile humans (24,132). However, despite these advances in our understanding of social learning as a biologically significant phenomenon, social learning is only rarely considered in investigations of the neurobiological bases of cognition in either males or females [e.g., (148)].

Social learning, where an "individual's behavior is influenced by observation of, or interaction with, another animal or its products" [e.g., breath or odor (76)] has been investigated in a variety of species of vertebrates. The studies range: from the social transmission of mate choice (46), feeding sites (90,94,95), and information about potential social opponents (79,113) in fishes; songs (149), mate preferences [e.g., (52,53, 150)], and identity (45) or location of food (9,45) in birds; fear of predators in birds and monkeys (38,104); food preferences [e.g., rats, *Rattus norvegicus* (69); mice, *Mus domesticus* (142); gerbils, *Meriones unguiculatus*: (141); sheep (105); rabbits (10); hyenas (157); birds (111)]; food-processing behaviors [rats (91,139); monkeys (40,83); apes (152)]; to the acquisition of complex language in apes (50,51) and humans (132).

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Surprisingly few studies of social learning have, however, considered the roles played by the sex of the animals. In the most recent comprehensive book published to date reviewing social learning (77), out of the 17 chapters, only three marginally addressed the question of the sex of the individual. In eight recent review articles on social learning only one (16) mentions the gender-biased social acquisition of information that was shown in a half-century old study of Japanese macaques (83,84). Of the approximately 105 articles examined in our survey of social learning only 12 showed any evaluation of the factor of sex. The vast majority of studies involved either only males or only females [e.g., (92,93,136)] and in those studies where subjects of both sexes were used, the factor of sex was often not mentioned in the statistical analysis of results [e.g., (69,103)]. In the latter cases the reader is left with the question of whether a sex differences was not reported because it was either not found or not looked for. This lack of consideration of sex differences in social learning was reiterated in a recent study by Laland and Reader (94) that examined male–female differences in foraging innovation and their social transmission in guppies, *Poecilia reticulata*. The authors specifically noted the lack of experimental studies that focus on sex, age, or dominance rank differences.

There are well-established male–female differences in a range of reproductive and nonreproductive behaviors [e.g., social behavior, social recognition, aggression, activity patterns, motivation, anxiety, and fear-associated behaviors, etc. (5,110)]. These male–female differences are shaped by natural selection and constrained by factors such as; life history and ecology, physiology, including reproductive condition and endocrine status (5,110). For example, in many territorial species of rodents reproductive males display more exploratory behavior and greater activity levels than reproductive females [gerbils (1,3)]; meadow voles, *Microtus pennsylvanicus* (70); deer mice, *Peromyscus maniculatus* (134)]. This behavioral/ecological difference has been invoked as an underlying basis for the evolution of sex differences in spatial abilities (54,55,70,85,131). Similarly, males and females have been shown to differ in their motivational tendencies, and displays of anxiety and fear-related responses in various learning tasks [e.g., (23,25–28,33,55,80,85,96,102,106,116,129,130,147,153,154)]. In addition, males and females also normally occupy different positions within a social hierarchy and/or play very different roles within a social group. Moreover, the differing reproductive and parental investment patterns of males and females impose different costs on individual learning. This imposes different social constraints on the two sexes, facilitating the emergence of sex differences in various behaviors that can influence cognitive functions. Social relationships have been shown to be an important constraint in channeling food-related social learning in gerbils (141), mice (32), rats (35), cats (29), monkeys (78,84), and other primates (37). It is, thus, reasonable to hypothesize that, in at least some situations, the social acquisition of information would be influenced by the sex of the interacting animals.

The present review on sex differences in social learning, or rather the lack thereof, is a “call” for studies to investigate this important issue. Toward this end we will first provide a review of various studies on social learning in mammals that have, either directly investigated, or that can more indirectly provide evidence regarding the role of gender in this learning paradigm. Second, we will consider the results of neurobiological investigations of the mechanisms that may underlie social learning in male and female rodents. We will combine these descriptions with speculations that may provide insights into potentially fertile future research directions.

THE ROLE OF GENDER IN SOCIAL LEARNING

Social learning in males and females has been investigated in several different experimental paradigms. The research with mammals considered here has concentrated on three major paradigms; social learning of food preferences, observational learning of a number of tasks by rodents, and social learning by primates. The social recognition paradigm, where an animal is tested for the memory of a conspecific after separations of various duration, has also received analysis and has been termed by some authors as a form of sexually dimorphic social learning (11,12). However, it is not considered to represent social learning according to the definition applied in this review (76) and, as such, will not be directly considered here.

Social Learning of Food Preferences

When a naive animal, or observer, interacts with a recently fed conspecific, a demonstrator, the observer subsequently exhibits a preference for the food of the demonstrator (Fig. 1). This phenomenon has been investigated in several species of rodents including; rats (58,136), Belding’s ground squirrels, *Spermophilus beldingi* (115), spiny mice, *Acomys cahirinus* (103), house mice (142), and Mongolian gerbils (141). One of the most critical moments for the development of an animal’s diet selection is during the transition from maternal food dependence to independent feeding. As such, many studies have focused on the social acquisition of food preferences by weanling animals from either their mother or other adults in the colony. Young animals can extract information about the mother’s diet as early as in utero (74), and subsequently, from the taste of the milk (63,67,100). As the young animals develop they can obtain dietary information by following the mother or other adults to feeding sites (57,61,143) and eating where olfactory cues from either the mother or other conspecifics are present (62,144,145). In these studies the demonstrator is typically the mother and the observers are groups of weanling pups [e.g., (143)]. In most of these studies the sex of the pups has either been not reported [e.g., (137)] or the groups were composed by both males and females [e.g. (115)] with no statistical analyses of the effects of gender being provided [e.g., (103,143)]. As sex differences in individual learning are often only evident in adults when activational effects of gonadal hormones are expressed (153,154), the presence of a sex difference in learning in prereproductive animals may have been considered to be unlikely. As such, the authors may simply not have evaluated the effects of the factor of sex in the analysis. Alternatively, they may have performed the analysis and, having found no sex differences, not reported the results.

There are, however, indications of sex and dominance-related differences in play, exploration, and related social behaviors as well as attention to maternal cues in young animals (5,110). In addition, there have been speculations that the mother may, in certain situations, differentially attend to the offspring [e.g., (98)]. As well, the possible impact of various other prenatal factors on social learning needs to be considered. In this regard, prenatal exposure to aluminum lactate (71) and a dietary deficiency (148) have been shown to influence social learning in mice, with the results of the latter study suggesting no apparent sex difference in the responses. The effects of ontogenetic factors on the social learning of food preferences and other behaviors require further investigation before any conclusions regarding possible sex differences can be drawn.

Adult rats, mice, and gerbils were shown to socially learn a food preference from other adults [see (65,142) and (141), re-

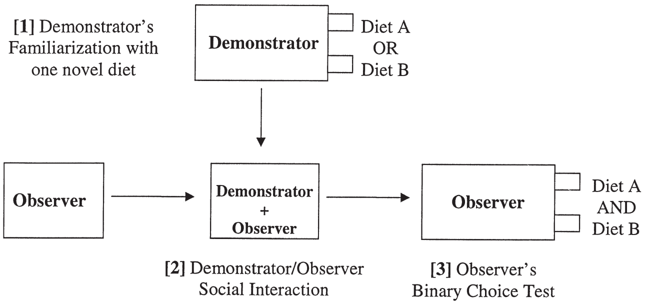

FIG. 1. Experimental procedures for the study of the social learning of food preferences. [1] The demonstrator is presented with a novel diet (A or B) and then is [2] allowed to interact with an observer that is naive to the diet fed to the demonstrator. [3] At the end of the interaction with the demonstrator the observer, alone, is given a choice test where it can choose between two novel diets (A and B), one of which is the same eaten by its demonstrator. When social learning occurs, in phase 3 the observer will exhibit a clear preference for the diet whose odor it could smell in the demonstrator's mouth during the social interaction in phase 2.

spectively], or, in the case of mice, even from their weanling offspring (32). In almost all of these studies same sex demonstrator/observer pairs were utilized, with only males or only females being tested [e.g. only females (59,66,142); only males (60,92,93,112,136)]. To the best of our knowledge, social transmission of food preferences in both male–male and female–female observer/demonstrator pairs within a same experiment has been infrequently examined, and when it has been examined there has been no mention in the statistical analysis of the factor of "sex" [e.g., (64,68,69)]. In one study with the C57BL/6 strain of mice (86) and in another with C57BL/6J × DBA/2J (B6D2F$_1$) hybrid mice (148) the results of the statistical analysis revealed no significant differences in social learning between demonstrator/observer pairs composed either of two males or two females. Similarly, in a study of the social transmission of food preferences between either male or female Mongolian gerbils there was no significant effect of sex (141). In addition, in mixed-sex demonstrator/observer pairs male and female gerbils equally acquired diet preferences from their respective partners (141). This same study, however, also revealed an important social constraint on the social learning of food preferences in gerbils. In order for the observer gerbil to acquire the food-related information, the demonstrator had to be either a familiar and/or a related individual. A male or a female observer would not learn from a totally strange same-sex conspecific. Results of a subsequent study revealed that administration of the anxiolytic, chlordiazepoxide, allowed the social transmission of food preferences to occur even between same-sex strange gerbils, with males being more sensitive than females to the effects of the anxiolytic (34). This raises the possibility of an underlying sex difference in social learning that was not detected in the original experimental procedures used [(34), for more details see the next section]. It also suggests that laboratory experimental conditions that provide optimal conditions for the social transmission of food preferences to occur may mask underlying sex differences that can emerge during the suboptimal conditions that are more likely present in nature.

Results of further studies showed that observer gerbils would acquire a food preference from a strange demonstrator if the intensity of the food-related information present in the demonstrator's breath was increased (56). Although the factor of "sex" was not discussed in that study, there are data suggesting a possible underlying sex difference with only males responding to the augmented odor cues (30). A similar odor–concentration effect on socially transmitted food preferences was found in a study with male and female rats in which again no analysis of the factor of sex was reported (133).

Taken together, these studies on social learning of food preferences suggest that in mice and gerbils females can learn from other females, and males can learn from other males with no apparent overall differences in acquisition between the sexes. The results of the studies with Mongolian gerbils do, however, also suggest that when a constraint appears in the social learning paradigm sex differences in response to manipulations reinstating learning become evident (30,34). However, whether this male–female difference arises from sex differences in the actual process of learning and, or reflects sex differences in anxiety, motivational, and attention-related factors remains to be investigated. This parallels the situation seen in studies of sex differences in spatial learning by rats and other rodents where sex differences in acquisition, performance, and motivational factors have been shown [e.g., (54,55,116,126,131)]. A direct analysis of the role played by the sex of the interacting animals and the effects of biological constraints is necessary before any conclusion regarding possible sex differences in the social learning of rats can be drawn.

Observational Learning in Rodents

In the typical laboratory observational learning paradigm a trained demonstrator performs a task in the presence of a conspecific observer. The observer has no opportunity to perform the task, and, depending on the experimental procedure, may or may not be exposed to the reinforcement that is intrinsic to the task [e.g., (88)]. When the observers are subsequently presented with the task, they perform it better than conspecifics that, either had no access to a demonstrator, or were exposed to a nontrained animal that was not performing the task [e.g., (87,128)]. To date, observational learning in rodents has been investigated primarily in rats and mice, often with either only male [e.g., (71,75,87,88,91,128)] or female (151) demonstrator/observer pairs being utilized. In some cases, the sex of the demonstrator and observer was not reported [e.g., (42)] or, when both male–male and female–female demonstrator/observer pairs were employed, no statistical analysis of the factor of "sex" were provided [e.g., (97,123) in golden hamsters]. In one study with adult B6D2F$_1$ mice, trained female demonstrators performed a task in front of either a male or female observer (36). The task consisted of opening a pendulum door to access an area of food with the demonstrator being trained to push the door either to the right or to the left. The results of this study showed that observer mice of both sexes performed significantly better, pushing the door to either direction and entering the food area faster than control mice that were not preexposed to a demonstrator. Interestingly, only male mice acquired the "laterality" of the task and pushed the door in the same direction as did the demonstrator. Results of other well-known studies on observational imitation learning in male rats have shown a similar laterality in a paradigm where the observer learns to push a joystick in the same direction as that of the demonstrator [e.g., (75)].

In conclusion, studies of observational learning in rodents have often neglected the analysis of the factor of "sex." Results of one study with mice suggest interesting gender-biased differences in the kind of information, laterality, that is acquired during observation of the demonstrator's behavior. This is consistent with the sex differences in bilateral asymmetries that are evident in a variety of species including laboratory rats (22). These sex differences in behavioral asymmetry appear to be related to differences in mesostriatal dopamine activity, as well as being influenced by gonadal steroid hormones. This suggests that the studies with male rats that revealed a laterality in the acquisition of a joystick task [e.g., (75)] be extended to females. This would show whether the sex differences observed in mice are of a general nature and can be extended to other species of rodents.

Social Learning in Primates

Various types of social learning ranging from a socially mediated attraction of the observer's attention towards a specific stimulus [which, in turns, increases the probability of individual learning occurrence], to the imitation of action and goals of the demonstrator's behavior, are common among primates.

A series of observations of various groups of Japanese macaques (*Macaca fuscata*) living on islands in Japan revealed several socially transmitted local habits [e.g., (84)]. Observations conducted over several decades have allowed the identification of the origins and analysis of the subsequent propagation of a number of novel behaviors within various distinct social groups or troops of macaques (83). This has provided primatologists with important insights into the mode of propagation of a novel behavior from its discovery until it is established as a social group-typical "cultural" feature. Innovative behaviors such as potato washing or separation of wheat from sand by throwing it in the water were typically "invented" by a young juvenile individual, which, in the case of the two above-mentioned behaviors, was the same female, Imo'. Imo's mother, male and female playmates, and subsequently their mothers where then shown to display this behavior. During the initial phase the new behavior spread to most of the juveniles and many of the adult females, but not to any of the adolescent and adult males, which tended to stay apart from the females and juveniles. Thus, during this first phase, sex, age, and kinship were important factors in channeling socially mediated learning. During the second phase, once Imo' and her playmates grew up and had their own offspring, the behavior was transmitted from the knowledgeable mother to her juveniles of both sexes. At this stage, several years after its discovery, the occurrence of the behavior was widespread within the group and independent of sex, age, and kinship (83). Several other behaviors have followed a similar route of transmission from an "inventive" juvenile to becoming established as a feature that is characteristic of a specific social group. It is commonly suggested that one of the functions of juvenile play and exploration is to facilitate the emergence of new behavior (99). Interestingly, however, in one case when a novel behavior was "invented" by an adult male and subsequently acquired by the dominant male, its transmission through the group was faster and did not depend upon age, sex, and kinship (84).

The majority of studies on social learning in primates deal with the issue of whether monkeys and apes are capable of imitating the demonstrator's behavior and/or its goals [e.g., the second half of the book edited by Heyes and Galef (77)]. The issue is not whether the animals can or cannot learn socially a new behavior, but rather it is how this social acquisition occurs and the extent to which cognition is involved [e.g., (39)]. This issue is beyond the scope of this review. Rather, we will consider several purported cases of imitation in relation to possible sex differences in social learning.

Studies with apes typically involve one or few individuals [e.g., (39)], and an analysis of sex differences is often impossible. However, in one case where two chimpanzees (*Pan troglodytes*) were taught to reproduce human gestures at the command "do this!" the male performed better than the female [100 vs. 80% accuracy (39)]. In another study where the social transmission of tool use was investigated in 15 chimpanzees, the sex of the animals was not reported (109). This study, like others with chimpanzees, included a group of young human children, the primate species clearly capable of imitation, as a "positive control." In that and other studies where social learning was investigated in both chimpanzees and children, the groups were typically composed of males and females. However, in the analyses the factor of "sex" was not reported [e.g., (19,109,140,152)].

When male and female capuchin monkeys (*Cebus apella*) were tested on an imitation task previously employed with chimpanzees (39), the analysis on the factor sex was also not reported (40). However, in a study with marmosets (*Callithrix jachus*), which included males and females, no significant sex differences in social learning were found (18).

In conclusion, results of pioneering studies with Japanese macaques on the transmission of novel behaviors suggested the existence of social constraints on the channeling of socially mediated learning in primates. Such constraints appear to be related to the specific behavioral roles played by individuals of different ages and genders within the social group [e.g., (83,84)]. However, in the more recent primate literature ethological analysis of social learning tend to be neglected, and there is minimal consideration of the roles played by gender, age, social status, etc., in the social transmission of behavior.

NEUROBIOLOGICAL ANALYSIS OF SOCIAL LEARNING

Neuroanatomical Studies

Social learning of food preferences has been utilized for the investigation of the neurobiological mechanisms associated with cognition. The experimental procedure used in this social learning paradigm typically follows the three steps shown in Fig. 1. First the demonstrator is presented with a novel diet. Second the demonstrator is allowed to interact with an observer that is naive to the diet fed to the demonstrator. Third after the interaction with the demonstrator, the isolated observer is given a choice test where it can choose between two novel diets, one of which is the same as that eaten by the demonstrator. When social learning occurs, during phase 3, the observer will exhibit a clear preference for the diet whose odor was smelled in the demonstrator's mouth during the social interaction in phase 2 (66).

This learning paradigm permits the investigation of the neurobiological substrates associated with both the acquisition and retention of social learning. Manipulations of the observer before the social interaction with the demonstrator and, thus, before learning occurs, allow the investigation of the motivational/neurobiological mechanisms involved in the social acquisition of the food preference. On the other hand, manipulations of the postsocial interaction phase, once learning has occurred, can provide insights into the mechanisms that are associated with memory, retention, and recall of social learning. Both of these approaches have been utilized in pharmacological and neuroanatomical studies of the social learning of food preferences in rats, mice, and gerbils and will be briefly considered here [e.g., (31,34,135,155)].

Two studies have investigated the roles played by the hippocampal and dorsomedial thalamic regions in social learning and retrograde memory (19,155). Winocur (155) tested observer male rats with lesioned dorsal hippocampal and dorsomedial thalamic regions. The observers underwent the binary choice test (phase 3) either immediately after the social interaction with the demonstrator or at different postinteraction intervals. He found that the rats with hippocampal or dorsomedial lesions acquired the food preference as well as control rats. However, while at 8 days after the social interaction rats with the dorsomedial thalamic lesions remembered the acquired food preference equivalently to that of control animals, rats with dorsal hippocampal lesions showed a rapid forgetting and retained the information for only 1–2 days (155). In a second experiment Winocur (155) investigated the effects of the same two lesions given either immediately or at 2, 5, or 10 days postlearning, after the observer/demonstrator interaction. He found that, while the control rats displayed normal forgetting rates, the thalamic group showed no recall when the lesion was made immediately after learning, but normal recall when the lesion had been made with some postinteraction delay. In contrast, the hippocampal-lesioned group displayed no recall when lesioned immediately after learning, and showed a gradual improvement in recall when surgery was delayed. Similarly, Bunsey and Eichenbaum (19) showed that male rats whose hippocampal region had been lesioned before learning normally acquired and briefly retained a food preference, but were severely impaired in their long-term retention. In addition, when the lesions were localized to a specific hippocampal region (hippocampus proper, dentate gyrus, and subiculum), neither short- nor long-term memory was impaired, suggesting that the whole hippocampus is necessary for the retention of long-term memory of a socially acquired food preference.

These findings of a temporally graded retrograde amnesia in social learning in hippocampal-lesioned rats are consistent with the effects of hippocampal lesions on contextual fear conditioning and spatial learning in rats (7,21). In this regard, sex differences have been reported in hippocampal involvement in spatial and nonspatial learning paradigms in rats (101,131). These findings from spatial learning and fear conditioning suggest that it would be of value to extend the examinations of the role of the hippocampus in the social learning of food preferences to females. In female rats, there are reported to be estrogen- and progesterone-induced changes in hippocampal circuitry that have been correlated with alterations in spatial performance (153,154,156). Intriguingly, social learning of food preferences by female rats has been shown to be a function of parity (i.e., number of prior litters) (49) and, by implication, also of hormonal status (146). Although this raises some interesting possibilities regarding the possible influences of reproductive state on social learning, further investigations of the effects of hormonal status on social learning are necessary before any conclusions can be drawn.

Other brain regions such as the parietal and prefrontal cortex have also been implicated in the mediation of learning. In rats, there are sex differences in the effects of frontal lesions in a variety of learning tasks, with females displaying greater reduction in performance than males (89). It would be of interest to determine the role of the prefrontal and parietal cortex in the mediation of nonspatial tasks such as social learning, and whether or not this involvement is sexually dimorphic.

Studies with targeted mouse mutants (“knock-out” mice) are being increasingly used to examine the neurobiological mechanisms underlying memory. Recently social learning of food preferences was examined in mutant mice lacking cAMP-responsive element-binding protein (CREB), a transcription factor the activity of which is regulated by increases in the intracellular levels of cAMP and calcium (86). It was found that in the CREB mutant mice both males and female displayed deficits in their long-term, but not short-term, memory of food preferences as well as fear conditioning. Although this study did not focus on social learning, as such the authors also reported that there were no sex differences in social learning in the hybrid wild-type mice. It should, however, also be noted that they also failed to find any sex differences in a spatial learning paradigm in which sex differences have been consistently reported in various other strains and species [e.g., (54,70,89,116,126,153)]. The results of these investigations suggest other directions by which social learning and its underlying neural mechanisms can be explored. These studies also show the potential use of the social learning paradigm to dissect the effects of various environmental, physiological, and genetic factors on cognitive processes.

Pharmacological Studies

N-Methyl-D-aspartate (NMDA) receptor mechanisms are involved in the mediation of both spatial and nonspatial learning and memory. For example, blockade of NMDA receptors has been shown to disrupt spatial memory formation, the acquisition of conditioned taste aversion, and acquisition of conditioned fear (21,72,81). Preliminary evidence has been presented suggesting that NMDA mechanisms may also be involved in the social learning of food preferences. Administration of low doses of the noncompetitive NMDA antagonist, MK-801, to a female observer rat immediately after social interaction with a demonstrator seemed to impair the social acquisition of a food preference, while high doses of MK-801, likely through nonspecific effects, apparently induced a taste aversion (108). This study needs to be replicated with a more specific NMDA antagonist that is administered before and after the social interaction before any definite conclusions can be made regarding the roles of NMDA receptor mechanisms in the mediation of the social learning of food preferences.

Results of recent studies have provided evidence for the involvement of NMDA receptor mechanisms in the mediation of the social learning of aversive responses to biting flies, a natural stimulus commonly encountered by animals (82). Brief single exposure to biting flies (stable flies, *Stomoxys calcitrans*) induces opioid-mediated analgesia and avoidance responses in rodents (80). Male mice further displayed an analgesic response when exposed 24 h later to biting flies that were altered to be incapable of biting (81). This “one-trial” conditioned analgesia was shown to be acquired through social learning without direct individual aversive experience with the biting flies. Mice (observers), while witnessing other mice (demonstrators) being attacked by biting flies but themselves were not bitten, displayed analgesic responses during observation (82). The observers further displayed a conditioned analgesia upon subsequent (24 hour) exposure to altered biting flies. The initial analgesic responses were likely elicited by the stress-related cues emitted by the attacked demonstrators, whereas the subsequent responses to the altered flies can be interpreted as involving socially mediated observational learning. It was further shown that this conditioned analgesia was absent in observer mice that were administered the specific competitive NMDA antagonist, NPC

1626, prior to their exposure to the demonstrator (82). These findings support NMDA involvement in the mediation of socially mediated rapid aversive learning as well as nonaversive (food preference) learning.

Sex differences have been reported in NMDA involvement in a number of neurobiological processes [e.g., (80,101)]. However, whether or not there are sex differences in NMDA involvement in the mediation of social learning remains to be determined.

The neurohypophyseal hormones, vasopressin and oxytocin, and their metabolites, have also been implicated in various cognitive and memory processes (6,17,124), including that of social recognition in male rats (11,13,14,41,44,47,48,117–122) and male mice (15). This involvement in the mediation of both social behaviors and learning suggests vasopressin and oxytocin as ideal candidates for the modulation of social learning. Strupp and colleagues (20,135) have examined the effects of prechoice test (before phase 3) administration of a vasopressin metabolite, AVP_{4-9}, on the social learning of food preferences in female rats. Choice tests carried out at various postinteraction (postlearning) times revealed a biphasic response to AVP. AVP_{4-9}-treated rats displayed significant impairments in recall at postinjection time intervals when recall in controls was excellent, and conversely, an improvement of recall at time periods that were associated with poor retention in the controls. The authors suggested that the exogenous peptide interacted with endogenous changes associated with "accessibility of memory" (20). Popik and Van Ree (118) examined the effects of either the vasopressin-related peptide, desglycinamide[Arg8]-vasopressin (DGAVP), or oxytocin administered immediately after social interactions in male rats. Their results revealed that both peptides had facilitatory effects on social learning 2 h after the demonstrator/observer interaction.

The first of the preceding two series of studies were carried out with female rats, and the last two used males. However, a study directly comparing of the effects of vasopressin and oxytocin on social learning of food preferences in males and females is missing. Moreover, the use of different vasopressin metabolites as well as other methodological differences (the use of solid vs. liquid diets and/or different flavors), makes it impossible to directly compare the results obtained from the male and female rats. However, sex differences have been demonstrated in vasopressin immunoreactive fibers in various limbic regions that have been associated with the expression of emotional behaviors (43). As well, results of a number of studies have indicated sex differences in the effects of vasopressin on behavior (4,73). Indeed, Bluthe and colleagues have reported that although androgen dependent vasopressinergic neurons are involved in social recognition in male rats (12), social recognition does not appear to involve vasopressinergic neurotransmission in female rats (11). Thus, sex differences in the modulatory effects of vasopressin and oxytocin on social learning appear possible. Further studies are necessary to address this question.

The involvement of motivational factors in the social learning of food preferences was further investigated in another series of pharmacological studies (31,34). As indicated, results of investigations with Mongolian gerbils revealed social constraints on the passage of diet-related information between same-sex individuals. The interacting animals had to be either familiar or genetically related, though not necessarily familiar, for social learning to occur (141). A male or a female gerbil would not acquire a food preference from a completely strange (nonfamiliar and nonrelated) same-sex conspecific (141). It was hypothesized that this constraint was based on the social structure of gerbils. In seminatural conditions, as well as in the wild, gerbils live in family-based groups with a dominant reproductive pair aggressively excluding nonresident intruders (1,3,138). Likewise, in the laboratory, unfamiliar same-sex gerbils display very high aggressive behavior (2,12). This suggested that reductions in anxiety/aggressiveness might facilitate social learning between unfamiliar and unrelated individuals. It was subsequently shown that administration of the benzodiazepine anxiolytic, chlordiazepoxide (CDP), before the demonstrator/observer interaction, reinstated social learning in male and female gerbils (34) most likely by reducing the anxiety-related responses associated with aggressive interactions (125).

It was found that two doses of CDP (2.5 and 5.0 mg/kg) affected social learning in males, while in females only the higher dose of 5.0 mg/kg was effective (34). This apparent differential sensitivity of male and female gerbils to the effects of chlordiazepoxide on social learning may arise from a number of factors. For instance, the female gerbils may either display a higher level of anxiety/fear than males during the social interaction and, or as suggested in studies of spatial learning in rats (116) anxiety may have a greater impact on learning in females than males.

These results indicate that socially related emotional responses affect socially mediated food preferences and, that at least in gerbils, this effect is different in males and females. This proposal is further supported by the results of a recent study examining the effects of acute corticosterone administration on the social learning of food preferences in male and female Swiss CD1 (31). The results of that study revealed parallel sex differences in the facilitatory effects of presocial interaction administration of corticosteroine on social learning of food preferences, with males responding to a lower dose than females. These studies further emphasize the likelihood of underlying sex differences in social learning.

The effects of CDP on social learning in gerbils are also consistent with the involvement of vasopressin and oxytocin in the mediation of anxiety-related responses (8,47) and the facilitatory effects of vasopressin metabolites on the social learning of food preferences in male rats. They are also consistent with the suggestions of possible sex differences in the effects of vasopressin on social recognition (11–13). It should, however, be noted that in those studies the drug treatment was after and not before the social interaction.

A variety of other neuromodulatory systems, including that of the endogenous peptides, are also involved in the mediation of social interactions and potentially social anxiety (23,114). Recent results showed that the opioid antagonist, naltrexone, given prior to the social interaction, decreased social behaviors and attenuated the social transmission of food preferences in female mice (107). This adds further support to the involvement of anxiety in the mediation of social learning. In view of the evidence for sex differences in stress related responses (c.f. effects of corticosterone on social learning; (31)] and opioid systems [e.g., (80)] it would be of interest to compare the effects of naltrexone and other opioid antagonists on social learning in males and females.

CONCLUSIONS

Although sex differences have been demonstrated in a wide range of cognitive and behavioral processes, investigations of male–female differences in social learning remain largely neglected. Social learning varies in a biologically meaningful way as a function of social constraints (social, characteristics, social setting) and the type of information that may be transferred. Social transmission and acquisition of information involves sexually dimorphic motivation, perception, attention, and social structures and neurobiological mechanisms. Whether or not these entail adaptive specializations is an open question. For these many reasons male–female differences in social learning and its underlying neurobiological substrates is a problem worthy of further study.

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