

Translating the biology of rodents' sex-recognition and mate-recognition to humans': bridging the pheromonal-visual gap

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Abstract

A large part of our understanding of the biological substrates of sex-recognition and mate-recognition is derived by studying animal models. In performing those tasks, rodents rely mostly of pheromones and other olfactory cues, whereas humans rely mostly on visual cues. That may hinder the translation of rodents' biology to humans' biology, especially at the neural-networks level, where those cues traverse different networks in humans and rodents brains. That may be called the "pheromonal-visual gap". A theoretical model presented here addresses those issues. The model merges observations from humans and model-animals, as reported in specific scientific reports, and general biological principles that are accepted by the scientific community. The model suggests that the voices of men and women are the innate cues based on which humans learn to use visual cues in sex-recognition and mate-recognition. Children learn the two tasks in associative learning mechanisms, by being immersed in their community, and observing adult role-models in innocuous, non-sexual scenarios. The model proposes that the human medial-geniculate-nucleus (MGN) is the analog of the rodents' accessory-olfactory-bulb (AOB) and the main-olfactory-bulb (MOB), and that the human MASH pathway (MGN, amygdala, bnST, hypothalamus) is the analog of the rodents' VNOP (Vomeronasal-organ-pathway). Considering the differences in the pathways should facilitate the translation from rodents' brain nuclei and tracks to humans'. Also, the model hypothesizes that innate direct and indirect connections between auditory centers, e.g., MGN, and sex-control centers, e.g., hypothalamus, vary across three groups of children, and those variations determine the individual's mate-recognition that emerges at puberty.

Key words

Sex-recognition; mate-recognition; sexual orientation; puberty; vomeronasal-organ; VNO; learning sexual behavior; Medial-geniculate-nucleus; MGN; MASH

Highlights

- The following is suggested based on the observation that humans rely mostly on visual cues in their sex-recognition and mate-recognition:

- The voices of men and women are innate cues for sex-and mate-recognition based on which visual cues are learned. Those cues are analogs of the rodents' sex pheromones.
- A theoretical model proposes that the human MGN is the analog of the rodents Accessory Olfactory Bulb and Main Olfactory Bulb.
- The model proposes that the human MASH pathway (MGN, amygdala, bnST, hypothalamus) is the analog of the rodents vomeronasal organ pathway.
- Innate human direct and indirect pathways that connect auditory hubs (e.g., MGN) and sex control hubs (e.g., the hypothalamus), vary across three group of children. That determines the various mate-recognitions that emerge at puberty.

Introduction

When we interact with other people, we automatically recognize their sex based on their looks and their voice. Depending on the situation, this sex-recognition process may invoke in us various responses. One possible response is the feelings of sexual attraction to the other person and the physiological processes of the onset of sexual arousal. From that point on, our behavior may evolve in many different ways. That combination of invoked sexual attraction and the onset of sexual arousal is herein termed "mate-recognition". This paper introduces a theoretical model that deals with sex-recognition and mate recognition.

The basic assumptions of the model

- Sex recognition is a component of mate-recognition.
- Sex-recognition and mate-recognition have innate and learned components (nature and nurture).
- The voices of men and women are innate auditory cues of sex-recognition. Together with other innate cues, they are also innate cues of mate-recognition.
- Sex- and mate-recognition evolve by associative learning mechanisms during childhood. Their visual cues are learned based on their direct and indirect associations with men's and women's voice.
- Sex-recognition is expressed first at early childhood, and mate-recognition emerges at puberty.
- During childhood, learning new mate-recognition cues does not activate actual sexual responses, because the system is not functional. At puberty, due to hormonal effects, the system becomes functional and the mate-recognition cues that were learned during childhood can trigger physical sexual responses.

The goals of the model

- To integrate human and animal empirical evidence into a comprehensive model that describes, at the neural networks level, the childhood development of sex-recognition and mate-recognition, and the emergence of mate-recognition at puberty.
- To explain the reliance of sex-recognition and mate-recognition on learned visual cues.

A lot is known about the biology of rodents' sex- and mate-recognition. In rodents, pheromones that encode cues of sexual and reproductive features of potential mates are processed in the vomeronasal pathway (VNOP) that includes the vomeronasal organ (VNO), the auxiliary olfactory bulb (AOB), the medial amygdala (MeA), the bnST (bed nucleus of the Stria Terminalis) and the hypothalamus. The VNOP operates in tandem with the main olfactory bulb (MOB) pathway that handles volatile olfactory information and pheromones. Together with other brain areas, they integrate their inputs with other sensory, emotional, and reward information, and information about past experiences and expected outcomes [1,2,3,4,5,6,7,8,9]. All that processed information affects the resulting behaviors, including sex- and mate-recognition.

Humans on the other hand, rely mostly on visual cues in sex- and mate-recognition. Still, the amygdala, bnST and the hypothalamus play central roles in those tasks also in humans [10,11,12,13,14,15,16].

The fact that humans rely mostly on visual cues whereas rodent rely mostly on pheromonal cues hinders the translation of what is known about rodents biology to humans biology. That may be referred to as "the pheromonal-visual gap". This paper presents a model that could facilitate the bridging of that gap.

Innate sex-recognition cues

The model assumes that the innate cues for sex-recognition must satisfy the following saliency requirements:

1. Specificity. They correctly identify the sex of a target.
2. Robustness. They are easily detectable in environments that have a variety of other cues.
3. Universality. They are present in every community at any time.

In addition, new cues could be acquired based on their direct and indirect associations with the innate cues.

Starting at childhood, humans use visual cues in sex-recognition. However, a quick check reveals that no commonly used visual cue satisfies all those three saliency requirements. For example, clothes and other arbitrary appearance features that distinguish between the sexes do not satisfy the universality requirement. They vary from one society to another and may also change with time. External sex organs that distinguish between the sexes do not satisfy the robustness requirement, because they are covered by clothes, and they are not discernable to young children. Therefore, the visual cues that humans are most often using for sex-recognition are learned.

Human olfactory and tactile cues too do not satisfy all those saliency requirements.

As it turns out, the voices of men and women are sex-recognition cues that satisfy all the saliency requirements. They are produced and detected by innate body systems. They are specific. It is possible to correctly identify the sex of sexually mature humans by their voice. The voices are robust. Human voices are easily detected by infants, children and adults in noisy surroundings that include the speaker and other stimuli. They are universal. Infants and adults can identify the sex of men and women that belong to any group of people on Earth, based only on their voice, e.g., over the phone and in darkness. In addition, children's and adults' brains automatically create a variety of audio-visual associations, including association between the voices of people and their images.

The model's basic assumption is that the voices of men and women are the innate cues based on which children classify adults into two categories: men and women. Men are those humans that broadcast cues that have been associated, directly or indirectly, with men's voice. Women are those humans that broadcast cues that have been associated, directly or indirectly, with women's voice. The skills of sex-recognition and mate-recognition are based on the ability to do that categorization [17,18].

Innate mate-recognition cues

In addition to sex-recognition cues, potential mates broadcast cues about their non-sexual features. Those non-sexual cues are often called emotional cues. If the external conditions are favorable and the combination of sexual cues and emotional cues meets the requirements of the receiver, the receiver will be aroused [17,18,19,20,21].

There are positive emotional cues, that enhance the sexual responses, and negative cues that suppress them. Quite often, the positive emotion is about feeling safe and enjoyment with the target. The negative emotion is about feeling threatened. Those emotions are felt at the courtship phase of sexual interactions, when both parties evaluate whether or not to proceed. Both parties are aware that they are about to enter the safety zone of each other, and that may be risky. The relative proportion of the positive and negative emotions depends on the individuals and on the situation. At a certain proportion, the courtship proceeds. Such emotional situations happen not only in sexual contexts (reviewed in [18]). They happen when there is something positive to gain, and something to lose. For example, in sports, in gambling, in rollercoaster rides, etc. Such activities of calculated risk-taking generate a pleasant excitement, and that maybe why people enjoy doing them. The amygdala is implicated as a hub that handles that kind of situations [18,22]. It weighs the pros and cons and relays its decisions to other brain centers [23,24,25]. Other feelings, such as novelty of stimulus, may also contribute to the mate-recognition's arousal. In addition to those pleasant feelings that may continue also in the following consummatory phases, there is another group of innate pleasant feelings that characterize sexual interactions. Those are the pleasurable sensations that are

triggered by tactile stimulation of erogenous areas. The hypothalamus is one of the hubs that handles that information [26].

Real-life sex- and mate-recognition activities depend on the integration of many types of information that represent the condition of the body, external conditions, past experiences, future expectations, motor and endocrine activities, and learning processes. That information is processed by many brain centers that could be grouped into activity patterns, such as the “sexual-liking-pattern” and the “sexual-wanting-pattern”, identified in fMRI images [10,11,12,13]. The amygdala is part of the sexual-wanting-pattern, and the hypothalamus is part of the sexual-liking-pattern.

A combination of sexual cues and emotional cues that causes sexual attraction and arousal is called herein a “sexiness cue”. The model presented here treats the emotion part of sexiness cues just as a contributing factor, without dealing with its details.

The learning processes

The model assumes that sex-recognition and mate-recognition skills evolve automatically and subconsciously during childhood. The sex-recognition cues are learned first and are implemented starting at early childhood. The mate-recognition cues are learned throughout childhood and emerge at puberty. Adults in the child’s surroundings act as passive innocuous role-models, whose non-sexual activities provide the cues that the child learns. Those assumptions are based on observations that growing up in families with parents of different-sexes, same-sex parents, or single parent families or in abusing circumstances do not influence sexual orientation [27,28]. Apparently, children develop their mate-recognition skills by being immersed in their society and picking up sex-recognition and mate-recognition cues that are broadcasted by role-models around them [17,18]. Children subconsciously spot on their own the role-models from which they subconsciously learn the cues. They spot them based on cues that the role-models broadcast. The brains of the children are innately wired so that when they detect those innate cues in another person, they treat that person as a role-model and learn the other cues from her or him. Children encounter adults that invoke in them various emotions, including feeling safe and feeling threatened at the same time. The children learn the cues that those adults broadcast, such as facial expressions, general demeanor, and tone of voice. Those cues are broadcasted by men and by women. When those cues are broadcasted by a person of the specific sex, they become the cues that would induce sexual arousal. Children also learn by association in non-sexual experiences the emotional meaning of tactile stimuli such as a hug or a push, based on the positive or negative feelings that are associated with them. Before puberty, the sexual responses are not functional, and sexual responses are not activated. At puberty, when the system is functional and those cues are detected in sexual interactions, they trigger the sexual responses.

Materials and Methods

This paper introduces a theoretical model that deals with the development of sex-recognition and mate-recognition during childhood, and with the learning of the visual cues that are used in the performance of those tasks.

The first step of the study was putting together a rough model based on the general assumptions described above. Then, two iterative efforts were carried out: Literature search and updating the assumptions of the model. The literature search was done by Google and PubMed search engines. Experimental findings that might be related to the model's assumptions were collected. Those findings have been reported in papers about sexual and non-sexual behaviors. Then, the model's assumptions were re-evaluated based on the collected experimental findings. Some assumptions were refined, some were dropped, and some new ones were added. Next, the literature was searched again for experimental facts related to the updated model. The model was then re-evaluated and updated, and so on. This literature search is dynamic and is different from those used in preparing meta-analyses reviews. It uses keywords that vary as the model evolves. This entire process is similar to solving a crossword puzzle. Hundreds of papers were explored in this search. Those iterative steps continue till the final version of the model. Reductionist experiments that focus on very specific and limited questions could be performed for further testing the model.

Results

The following is a list of the empirical observations that were found in the literature-search and their implications.

Learning sex-recognition by humans

Observations

Between 33-41 weeks of gestation, fetuses respond differently to mother's voice, father's voice, and voices of male and female strangers [29,30]. The fetus can memorize not only his mother's voice but also more complex acoustic external sounds with a big ability of discrimination [30].

Implications

That suggests that innate brain circuitries can distinguish between auditory cues broadcasted by women and those broadcasted by men and respond differently to the two groups.

Observations

Studies have been conducted to find out which kinds of sound draw the attention of infants and make them focus on the ongoing event: "At birth, infants prefer listening to vocalizations of human and nonhuman primates; within 3 mo, this initially broad listening preference is tuned

specifically to human vocalizations. Moreover, even at this early developmental point, human vocalizations evoke more than listening preferences alone: they engender in infants a heightened focus on the objects in their visual environment and promote the formation of object categories, a fundamental cognitive capacity. This initially broad listening preference is tuned specifically to human vocalizations”[31].

7-month-olds but not 4-month-olds showed increased responses in left and right superior temporal cortex to the human voice when compared to nonvocal sounds, suggesting that voice-sensitive brain systems emerge between 4 and 7 months of age [32]. Emotion specifically enhances voice processing in the right hemisphere in infants. Moreover, a region in right inferior frontal cortex taken to serve evaluative functions in the adult brain showed particular sensitivity to happy prosody[32].

There is ample evidence suggesting that children already know to distinguish between the genders at an early age and use that ability to develop various related behavior patterns [33]: “Infants as young as three to four months of age distinguish between categories of female and male faces, as demonstrated in habituation and preferential looking paradigms” [34]. By about six months, infants can discriminate faces and voices by sex, habituate to faces of both sexes, and make intermodal associations between faces and voices (e.g., [35,36,37]).

By 10 months, infants are able to form stereotypic associations between faces of women and men and gender-typed objects (e.g., a scarf, a hammer), suggesting that they have the capacity to form primitive stereotypes [38].

Implications

Prenatally and during infancy, children distinguish between human and non-human sounds and between voices of men and women. That suggests that voices of men and women serve as innate cues for that recognition ability. Later during infancy, children form rudimentary categories of “humans”, “men”, and “women” that include vocal and visual human features and visual cues of other objects that are associated with men and women. That suggests that the learning process that started by relying on the auditory features is expanded to include visual cues. Moreover, other auditory cues, such as prosody, that have emotional significance, are also learned at that early stage. Those could serve as the cores of the evolving emotion categories that are used in mate-recognition.

Observations

Twenty-four- and thirty-month-old children knew the gender groups to which they and others belonged [39]. Similarly, most 24- and 28-month-old children select the correct picture in response to gender labels provided by an experimenter [38,40]. Taken together, these studies suggest that most children develop the ability to label gender groups and to use gender labels in their speech between 18 and 24 months.

CONCLUSION: SEX-RECOGNITION

Apparently, neonates already have rudimentary perceptions of 'human', 'men' and 'women' at birth. At that stage, 'humans' are those objects that produce sounds at a certain frequency range and with a certain timbre, prosody and some other typical temporal features. Men are those humans that produce low pitch voice, and women are those humans that produce high pitch voice. With time, those concepts are expanded to include cues from other modalities including visual, tactile, and olfactory. Some of those cues are sex-specific and some are common to both sexes. Some hint about the sex, others hint about emotion inducing characteristics of the other person. Those observations suggest that voices of men and women serve as innate cues as the skill of sex-recognition is evolving, and as visual cues are learned.

Learning mate-recognition by humans

Sex-recognition is a critical component of mate-recognition. While sex-recognition is expressed in early childhood, mate-recognition is fully expressed only at puberty. There are some observations that provide insights about the development of mate-recognition during childhood.

Observations

Responses of the amygdala of boys and girls that were observing pictures of adults expressing emotions were recorded by fMRI [41]. It was found that in general, the responses were stronger when children were observing pictures of the opposite sex compared to the same sex. There was a peak in the difference at puberty.

Implications

During childhood, gender-dependent and sex-dependent behaviors are developed at the same time. It is not simple to separate brain areas that process gender-related information from those processing pure sex-related information. The increased activity of the amygdala that was observed at the onset of puberty may be related to the final stages of the development of mate-recognition.

Observations

Without any person present around, children can feel pleasure by touching their genitals, a sensation that could be accompanied by the physical response of tumescence. Similar sensations and physical reactions are experienced after puberty in sexual interactions, real or imaginary.

Implications

That is an example of a sub-system that becomes fully operational when its neural circuitries are integrated with the entire system. The reward and reflexive circuitries of the pre-mature sub-system are integrated with the mate-recognition system. They are then deployed by it in various mature sexual activities and contribute to the system as a whole.

Observations

At puberty, as the sex organs have matured, secondary sex characteristics, which distinguish between the sexes, mature too. Those characteristics include the deepening of the voice of boys, hair distribution patterns, shoulders to waist ratios, thighs to waist ratios, fat distribution, muscularity, body size, and more [42].

Implications

At puberty, coinciding with the onset of mature sexual activities, male voice becomes the most salient cue that distinguishes between the sexes. All the other secondary sex cues could be relied upon, and they are, but voice is the only cue that always satisfies all the three saliency requirements listed above. Therefore, relying on voice becomes the dominant learning process. The other cues are apparently learned subconsciously due to their direct and indirect associations with men's and women's voices. Deaf children, who cannot rely on voice, have all those other innate secondary characteristics to rely upon. Their learning process must be different from that of hearing children.

Observations in birds and anurans

Auditory signals play a major role in the sexual and reproductive activities of birds and anurans. The following is a sample of those activities, that illustrate the biological feasibility of the model's assumptions about the roles that voice plays in human sex-recognition and mate-recognition.

Observations

Like humans, birds too do not have a VNO. In female songbirds, male song induced Egr-1 expression in the mediobasal hypothalamus (MBH) that was correlated with the expression in midbrain and forebrain auditory centers, homologous to the inferior colliculus and to auditory cortex, respectively [43]. Cooing of female ring doves and not of male ring doves promoted responses in the POA–AMH areas and promoted greater follicular growth [44].

Implications

Those observations illustrate that the birds analogs of the pheromones and VNOP are auditory signals that are merged with other information and eventually trigger analog sexual responses of the hypothalamus.

Observations

Young birds learn their songs by being immersed in their flocks [45]. Young birds that had never before heard songs of conspecifics increase their heart rate and their beg when they hear playback of songs of conspecifics [46].

Implications

Before hatching, chicks are already wired to recognize some innate auditory cues and to use them for learning other cues of sexual and reproductive behaviors.

Observations

Male frogs use courtship calls to attract females. Anatomical investigations have demonstrated the existence of pathways from thalamic and midbrain auditory structures to areas involved in responding, including the preoptic area (POA) and ventral hypothalamus VHY [47,48]. The responses of POA and VHY neurons varied in accordance with the type of stimulus (conspecific, heterospecific, white noise) and the season. [49].

Implications

Like in birds, auditory cues reach the hypothalamus and regulate sexual and reproductive activities.

Translating from rodents to humans

The model assumes that the brain relies on the same sex-recognition cues in sex-recognition and in mate-recognition tasks. The model assumes that in mate-recognition, the human MGN is the analog of the rodents AOB and MOB, and that the human MGN, amygdala, bnST, and hypothalamus (MASH) pathway is the analog of the VNOP. The following are literature-search findings in rodents that are related to those assumptions.

Observation

Individual pheromonal compounds have been shown to modulate, rather than trigger specific social response. MeA neurons respond differently in males and females to conspecifics cues [3,50,51,1]. Pre-exposure of mice to the male pheromone ESP1 prior to their encounter with a male intruder enhances aggressive behavior in males and sexual receptivity in females [52,53,54]. Subpopulations of MeApv neurons activated by ESP1 project to different hypothalamic nuclei, modulating those different types of responses [54]. Darcin and other female sex pheromones have similar effects [1].

Translation

The human auditory analogs of rodents sex pheromones would be processes differently by dimorphic subpopulations of the human amygdala, and would be projected to different hypothalamic centers, resulting in different responses of men and women. That could explain the different behavioral responses of men and women to men's and women's voices and to their associated cues.

(***Figure 1***)

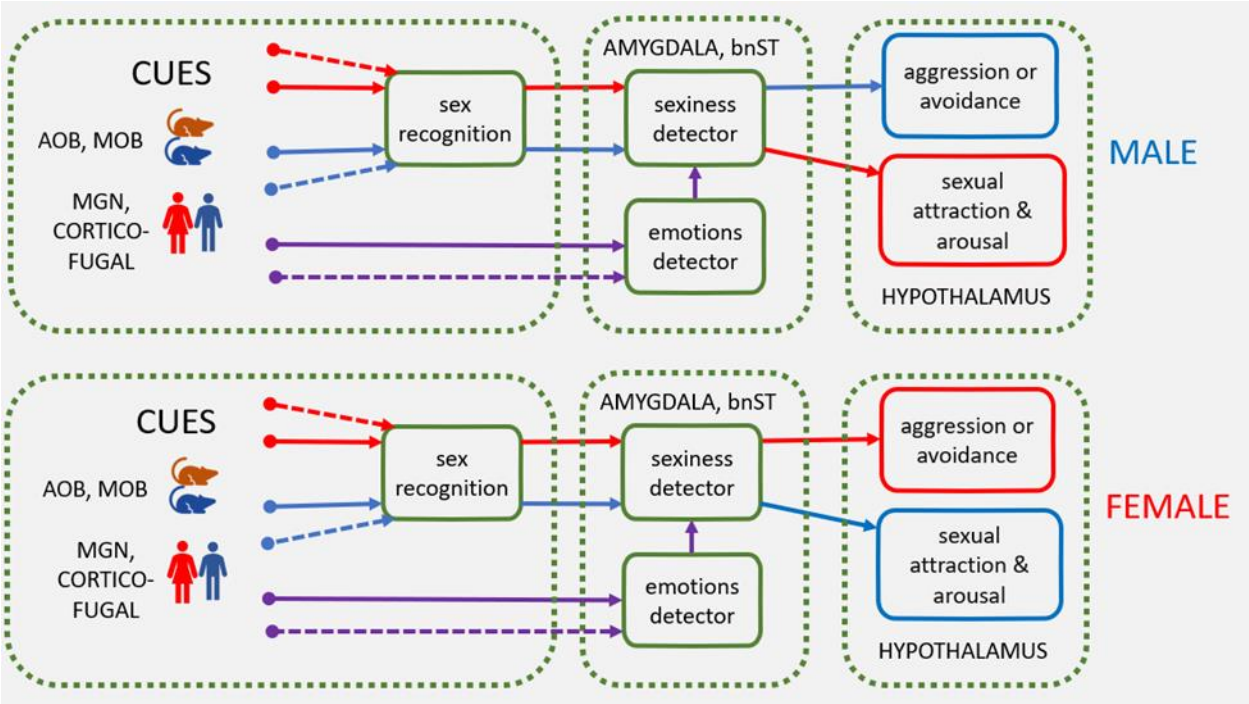


Figure 1. Routes of sex-recognition and mate recognition cues in humans and in rodents. Humans rely mostly on learned visual cues in their sex-recognition and mate-recognition, while rodents rely mostly on innate pheromonal cues. The model suggests that in humans, the voices of men and women are the innate cues for sex- and mate-recognition, and the visual cues are acquired by associative learning mechanisms. The model assumes that in sex- and mate-recognition, the amygdala, bnST, and hypothalamus play in humans similar roles to those they play in rodents. In rodents, pheromones enter those centers via the accessory-olfactory-bulb (AOB) and the main-olfactory-bulb (MOB), whereas in humans, the innate auditory cues enter those centers through the medial-geniculate-nucleus (MGN), and the learned cues enter via corticofugal pathways. The model assumes that both pheromonal cues [1,2,3] and their human analogs propagate in similar routes (the same arrows for humans and rodents). Male cues (blue arrows) and female cues (red arrows) reach hypothalamic centers in separate routes. Those cues mediate the activity of hypothalamic centers that regulate the responses to male cues (blue frames) and to female cues (red frames). Only some of the learned inputs to the centers are illustrated. Dashed arrows: learned cues. Purple arrows: emotional cues.

Observation

Sex-specific responses in the MeA are not detectable in juveniles but emerge at puberty, at a time when animals develop secondary sex traits as well as social behaviors characteristic of adults. During rodent postnatal development, sex hormones, in particular estrogen converted

from testosterone by the enzyme aromatase, play an essential role in generating sex-specific patterns of sensory responses observed in the adult MeA [50]. However, the identity of the neurons targeted by sex hormones and their mode of regulation in males and females remain unclear.

Implications

Those observations are consistent with the assumption of the model that during childhood, mate-recognition cues are learned without the actual expression of sexual responses. Those are expressed only at puberty, after the circuitries have been completed by hormonal activity.

Observation

Auditory information is relayed tonotopically and diffusely from the inferior colliculus to the MGN, and from there it splits to the cortex and the amygdala [54,55,56,57,58]. About 10% of MGN projection bifurcate and go to both cortex and amygdala, and other projections go separately to their targets [54].

Implications

The model assumes that conditioned stimuli (CS), such as mates' visual features, which are associated with the unconditioned stimuli (e.g., men's voice) develop functional connectivity to unconditioned responses (in the amygdala, and from there to the hypothalamus). Those bifurcating MGN cells may be tagging both the cortical visual representations of the CS and the subcortical UR's to facilitate the formation of their functional CS-UR's connections.

Observation

In addition to olfactory communication, mice communicate also by voice (reviewed in [4]). The voice frequencies include frequencies in the human audible range, and ultrasonic voice frequencies (USV), which are outside the human range. Mice rely on both frequencies in sexual and reproductive behaviors. It was observed that females are attracted to the voice of males [59]. Like in birds, the song quality of male mice is affected by the level of testosterone in their system, which affects their social status [60]. Dominant males emit more USV toward a female than male of lower rank [61], which results in more mating opportunities. Sensitizing females by male-soiled bedding or ESP1 enhances their relying on USV in their mate preference [4].

Implications

Mice have mate-selection circuitries that rely on innate multi-sensory cues, including voice. This is in line with the model's assumptions. Only sparse information is available on the interactions of those circuitries.

Observation

"A functional magnetic resonance imaging (fMRI) study revealed that MOB activation in female mice occurred slightly earlier than activation in the AOB in response to male urinary volatiles

[62]. These results suggest that the VNO responses to volatile pheromones are typically preceded by MOE detection, which then leads the animal to make nasal contact with a non-volatile pheromone, thus activating the VNO. Once animals are in close nasal contact with the scent source, the VNO pump is activated to gain additional information through the VNS. Therefore, detecting airborne scents through the MOS may be necessary to activate scent delivery to the VNO [4,63,11].

Implications

A possible translation to humans of those observations could be that the long-range stage of sex-recognition cues (volatile pheromone in mice and voice in humans) sets the system to the second stage of mate-recognition (non-volatile pheromones in mice and emotional cues in humans).

Narrowing the visual-pheromonal gap

It is widely accepted that in rodents, humans, and in many other vertebrates, sex-specific cues that affect mate-recognition reach the hypothalamus. The amygdala, the bnST, or their homologs, and other pathways are also involved in those processes. In rodents, the MeA and the bnST are the main hubs that integrate inputs of sex pheromones with various emotional information and relay their outputs to the hypothalamus. However, auditory inputs both in humans and rodents are first handled by the BLA and the CeA, which relays the information to the hypothalamus [23]. This dichotomy between the CeA and the MeA is one part of the visual-pheromonal gap. How does the human auditory information reach the sex nuclei of the hypothalamus? The human pathways and their nuclei are known in a much smaller resolution than those of rodents. However, there are indications of various unexplored projections from the MGN to the amygdala, hypothalamus, and other targets [64]. It has also been reported that thalamic nuclei mediate between sensory cortical areas, and that corticofugal pathways project to subcortical areas, including the amygdala and the inferior colliculus [65]. Further studies would be needed for mapping the detailed connectivity of MASH nuclei that handle the auditory cues and their associated cues. Therefore, based on the available information, the model could only propose that certain human pathways exist, outline their general features, and draw general conclusions.

The mate-recognition mechanisms and circuitries that the model proposes could explain the development during childhood of sexual orientation. The model implies that innate direct and indirect connections between auditory hubs, such as the MGN, emotional hubs such as the amygdala, and sex-control hubs, such as the hypothalamus, vary across three groups of children. Those innate connections guide the conditioning processes of mate-recognition during childhood. In one group of children, only men's voice (the US) contributes to the activation of the child's hypothalamus (the UR). In a second group, only women's voice contributes to the hypothalamic activation, and in a third group both men's and women's voices contribute to that activation. Those connections determine the sex of the role models from whom the child

learns the mate-recognition cues. Thus, those connections determine the child's sexual orientation that emerges at puberty. The children of the first group, that automatically learn their cues from men, will be attracted at puberty to men, (A boy will be gay, and a girl will be straight). Similarly, the children of the second group will be attracted to women, and the children of the third group will be attracted to men and women [17,18]. The model also proposes that the human MASH pathway is the analog of the rodents' VNOP in handling sex-recognition cues on their way to hypothalamus. The MASH centers are also hubs in larger activity patterns such as the sexual wanting pattern and the sexual liking pattern [10,11,12,13]. Those patterns handle all the aspects of the behaviors, including the appetitive and consummatory aspects.

SUMMARY

There is ample empirical evidence of the involvement of the amygdala, bnST and hypothalamus in sex- and mate-recognition in humans, rodents, and many other species. There is also ample evidence that auditory stimuli reach the hypothalamus in birds and anurans and invoke sexual and reproductive reactions. In addition to suggesting that the voices of men and women are the innate cues based on which visual sex-recognition is learned, the model presented here hypothesizes that in humans, the same auditory signals that serve as innate cues in sex-recognition also serve as innate cues in mate-recognition, and that those cues are integrated with other relevant information in the amygdala, bnST and the hypothalamus. If found, human auditory cues that bypass the MGN on their way to the hypothalamus [57] could be added to a later version of the model. The model's hypotheses could be tested by multi-disciplinary approaches such as:

So far, most fMRI experiments that studied sexual behaviors employed visual stimuli. fMRI studies of auditory stimuli (such as [66,67,68,69,70,71,72]) in the contexts of sexual behavior, could uncover important underlying processes of sexual behaviors, including processes that bridge the pheromonal-visual gap. Also, longitudinal studies that combine imaging and psychological assays (e.g., like [41]) could shed light on the development of sexual behaviors during childhood.

Genetic approaches might find correlations between progenitors of auditory-sexual processes in birds and in humans.

Much like weather, sex-recognition and mate-recognition are complex phenomena expressed by complex systems. Several models would be needed for describing their intricacies. Like in weather prediction and other complex systems, understanding is gained by expanding basic models with modules that handle more intricate details. Expansions of the model presented here, as well as other models, could be compared, contrasted, and merged, thus adding to our understanding of those behaviors that are crucial for the wellbeing of individuals and society as a whole.

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