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TOPIC PAPER

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Central nervous system control of ejaculation

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Abstract An overview is given of the regions in the spinal cord that are active during ejaculation. Motoneurons involved are the preganglionic sympathetic motoneurons in the upper lumbar spinal cord and the motoneurons in the nucleus of Onuf, located in the upper sacral cord. The first group is involved in the so-called emission phase of ejaculation, the last group in the expulsion phase. Both groups receive afferents from premotor interneurons in the so-called intermediomedial cell groups located at about the same level as the motoneurons themselves. A concept is put forward in which these premotor cell groups represent the central spinal pattern generators for ejaculation, one for the emission phase and one for the expulsion phase. Clinical observations in patients suffering from transection of the spinal cord indicate that the ejaculation motoneurons as well as their spinal central pattern generators are under strong influence of descending pathways originating in supraspinal parts of the brain. The various pathways possibly involved in ejaculation control are reviewed. Finally, the results of the brain activation of a PET-scan study in human males, ejaculating after penile stimulation by their female partner are discussed. Especially the ventral tegmental area and the cerebellum seem to be activated during ejaculation, while the amygdala region is deactivated. Apparently, a general lack of fear is necessary for ejaculation to occur.

Keywords Central pattern generator for ejaculation · Emission phase of ejaculation · Expulsion phase of ejaculation · Cerebellum · Amygdala

Central nervous system control of ejaculation is difficult to study, not only in humans but also in animals. For example, some studies on ejaculation in rodents have used C-fos, an immediate early gene which is expressed in highly activated neurons. The problem with these C-fos experiments is low temporal resolution. After ejaculation, rats are killed, and the C-fos positive cells are traced. These activated cells, however, not only represent the cells that have been active during ejaculation, but also the cells that were active before or after ejaculation. On the other hand, the spatial resolution is very good, because the C-fos positive cells can be exactly localized.

In neuroimaging experiments on ejaculation, the spatial resolution is much lower, and the resulting brain scans only show activated brain regions or cell groups. Conversely, neuroimaging experiments have two important advantages: (1) the time resolution is much better, and (2) they allow the study of humans.

A problem with these experiments in animals and humans is that ejaculation is accompanied by feelings of sexual orgasm, the reward for performing sexual activity. Neither in neuroimaging studies, nor in C-fos studies in animals, can the brain activity producing ejaculation be separated from the brain activation involved in feelings of orgasm.

Despite these drawbacks, a better understanding of which regions in the brain and spinal cord are involved in ejaculation and orgasm has been achieved during recent years. Here, we will deal with the motoneurons involved in ejaculation, the possible spinal or supraspinal regions that control these motoneurons, and other brain regions that are known to be involved in ejaculation in one way or the other, but of which we do not yet know how they contact the motoneuronal cell groups that finally produce ejaculation.

Ejaculation motoneurons

Ejaculation consists of two phases, the emission and the expulsion phase. During the emission phase the secretions from the periurethral glands, seminal vesicles and prostate, along with sperm from the vas deferens, are deposited into the posterior urethra and drain into the

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anterior urethra, while the bladder neck is closed. Emission as well as closure of the bladder neck [1] are primarily alpha-adrenergically mediated thoracolumbar sympathetic reflex events, but with a strong supraspinal modulation. The emission phase is preceded by the erection phase, also the result of sympathetic innervation of the penis. Perhaps the erection and emission phases cannot be separated, which explains why during the erection phase there is usually delivery of fluid from the periurethral glands, seminal vesicles and prostate, without expulsion of this combined fluid with sperm cells.

During the expulsion phase, striated muscles play a role, of which the bulbocavernosus muscle is the most important. This muscle forms an integral part of the external anal sphincter [41]. Other muscles that play a role in the expulsion phase are the ischiocavernosus and the transverse perineal muscles. All of these muscles are innervated by the pudendal nerve, the motoneurons of which are located in the so-called nucleus of Onuf, (ON) after Onufrowicz, who called himself Onuf. He described this nucleus as early as 1899 [35]. For a long time, ON was called group Y [37], and only 25 years ago was ON identified as containing perineal motoneurons [38]. In non-experimental sections, ON can be recognized by its wealth of longitudinally oriented dendrites [15], indicating that ON motoneurons have many intranuclear connections. ON motoneurons belong to a distinct class of motoneurons between somatic and autonomic (sympathetic and parasympathetic) motoneurons. Arguments in favor of ON motoneurons being somatic motoneurons are that they innervate striated perineal muscles, including the urethral and anal sphincters [38, 39], and that they are under voluntary control. Animals and humans can voluntarily contract the two sphincters, although not separately. Arguments against ON motoneurons being somatic are: (1) in contrast to most other motoneuronal cell groups, they do not receive direct cortical afferents [25], (2) ON, unlike somatic motoneuronal cell groups, contains nervous tissue-specific growth-associated protein, B-50 (GAP-43) [33], (3) they play a role in ''autonomic-like'' motor activities such as micturition, ejaculation, defecation and parturition, (4) they receive direct hypothalamic afferents [18], (5) they have a similar appearance to autonomic preganglionic motoneurons, (6) unlike all other somatic motoneurons, they are not affected in amyotrophic lateral sclerosis [29], and (7) they degenerate in Shy-Dräger syndrome [11, 30], which is characterized by degeneration of autonomic (sympathetic and parasympathetic) but not of somatic motoneurons. In conclusion, ON motoneurons have properties of both somatic and autonomic motoneurons, and occupy a position between these two kinds of motoneurons.

Two spinal central ejaculation pattern generators

Since ejaculation is the result of activity of the sympathetic preganglionic and ON motoneurons, it is important to find out which neurons control these two groups of motoneurons. Interestingly, the premotor spinal interneurons for the sympathetic preganglionics [45] as well as for ON motoneurons [34, 43] are located in the dorsal gray commissure in the central part of the spinal cord, (lamina X). These premotor interneurons are located at about the same level in the spinal cord as the motoneurons they innervate. For example, in rats the bulbospongiosus muscle motoneurons and their premotor interneurons were located in the L5 and L6 segments. Premotor interneurons were not found, or found to only a very limited extent, at the levels L1/L4 or S1. Also the premotor interneurons of the sympathetic preganglionic motoneurons were found at the same level as the preganglionic motoneurons they innervate, T13/L1, and not, or only to a very limited extent, at the L3/L5 level [45]. These results indicate that the premotor interneurons for the sympathetic preganglionic motoneurons are not the same as for the ON motoneurons.

The concept that there exists a spinal pattern generator for ejaculation [10], as there is for other functions such as locomotion [27], might well be true. In all likelihood, the neurons that constitute this central pattern generator for ejaculation are the premotor interneurons for the ejaculation motoneurons, and, thus, must be located in the central part of the spinal cord at approximately the same levels as the ejaculation motoneurons themselves. Perhaps the cells that express neurokinin-1 receptor and galanin, demonstrated by Coolen and co-workers [14] in the rat, might take part in the ejaculation pattern generator. These cells are located around the central canal in the L3/L4 lumbar cord, and specific ablation of these cells results in the disruption of ejaculatory behavior, while other components of sexual behavior remain intact. Interestingly, these same neurons are thought to play a role in the relay of ejaculation related signals from reproductive organs to the medial part of the parvocellular subparafascicular nucleus in the caudal thalamus, a region that is thought to be involved in ejaculation. It remains to be elucidated whether these neurokinin-1 receptor and galanin neurons really are the premotor interneurons for the sympathetic preganglionic motoneurons in the L3/L4 lumbar cord, cells that are involved in the erection and emission phase of ejaculation. It is not likely, however, that these L3/L4 neurokinin-1 receptor and galanin cells serve as premotor interneurons for the bulbospongiosus motoneurons, because at L3/L4 almost no premotor interneurons were found [43].

The conclusion that the premotor interneurons for the sympathetic preganglionic motoneurons are not the same as those for ON motoneurons leads to the concept of two central pattern generators for ejaculation located centrally in the spinal cord, one for the erection/emission phase, centrally in the upper lumbar cord (L2/L4), and one for the expulsion phase (L5/L6 in the rat, probably S1/S2 in cats and humans). It is unlikely that these central ejaculation generators act independently, and one might predict that the two generators are strongly interconnected [44].

Descending pathways to ejaculation motoneurons and ejaculatory pattern generator(s)

Obviously, the thoracolumbar preganglionic and ON motoneurons as well as their pattern generators are not separate from the rest of the central nervous system, but are heavily influenced by descending systems that give the go/no go signal. For example, in situations in which the individual is in danger, erection or ejaculation is almost impossible, despite strong afferent penile stimulation. On the other hand, immediately after the occurrence of a transection of the spinal cord, there often is erection of the penis [12], probably because of the disappearance of the inhibitory descending influence of supraspinal centers.

With regard to the lumbar preganglionic motoneurons, no specific projection is known that also terminates on neurons in other parts of the intermediolateral cell column.

Diffuse descending systems from the brainstem

SPN and ON not only play a role in ejaculation, but also in several other mechanisms. For example, level-setting mechanisms, reviewed by Holstege [19], send fibers to almost all parts of the spinal cord including SPN and ON motoneurons. These serotonergic and other projections originate from the caudal raphe nuclei and the adjoining ventral tegmentum of the medulla. They not only project to SPN and ON, but also to the cells belonging to the central pattern generators (CPGs). Perhaps, these diffuse descending pathways, by determining the general level of neuronal activity of the cells in the CPGs, decide whether the CPGs, after receiving the proper afferent information from the penis, initiates erection, emission and expulsion. In this respect the ventromedial medullary tegmentum receives a great many afferents from various parts of the limbic system, such as the periaqueductal gray, various parts of hypothalamus, amygdala, bed nucleus of the stria terminalis, and the infralimbic and prefrontal cortex.

In addition, the nor-adrenergic projections from the dorsolateral pontine tegmentum (locus coeruleus and nucleus subcoeruleus) and the dopamine projections from the A11 cell group in the rostral mesencephalon take part in these very diffuse descending systems, and may also play, together with the medullary diffuse descending pathways, a role in the initiation of the CPGs for ejaculation.

Paraventricular hypothalamic nucleus

The only projection that seems to terminate more strongly to the lumbar preganglionic motoneurons than to the other parts of IML is the projection from the paraventricular hypothalamic nucleus (PVN) [18]. Interestingly, this same projection system also terminates on ON and on sacral parasympathetic motoneurons as well as on neurons in the area of lamina X, where the ejaculation generators are thought to be located. It is quite possible, therefore, that this PVN descending projection system might have a strong effect on ejaculation, also because, according to Chen et al. [13], electrical stimulation of PVN elicits penile erection and ejaculation in the rat.

Other supraspinal afferents to ON motoneurons

There are several descending pathways originating at supraspinal levels that specifically project to ON motoneurons.

Nucleus retroambiguus

The perineum, together with the pelvic floor, forms the bottom of the abdominal cavity. Increased abdominal pressure is needed for strong expiration, vocalization, vomiting, and parturition. The perineum plays an important role in these motor activities. The nucleus retroambiguus, located in the ventrolateral part of the most caudal medulla oblongata, controls abdominal pressure by innervating abdominal wall muscle motoneurons located in the T5/L3 thoracolumbar cord and ON motoneurons in the sacral cord [21]. The question is whether ejaculation is accompanied by changes in abdominal pressure, but if not, the descending fibers from the nucleus retroambiguus do not seem to play a role in ejaculation.

L-region

Laterally, in the pontine tegmental field, is another area, the so-called L-region (L = lateral) which maintains direct projections to ON motoneurons [20, 22]. Stimulation in this region results in strong excitation of the perineal musculature and an increase in the urethral pressure [23]. Bilateral lesions in the L-region give rise to an inability to store urine; bladder capacity is reduced and urine is expelled prematurely by excessive detrusor activity, accompanied by urethral relaxation. Outside the episodes of detrusor activity, the urethral pressure is not depressed below normal values [28]. These observations suggest that during the bladder filling phase the L-region has a continuous excitatory effect on ON. In the PET-study of Holstege and co-workers [5, 6], about half of the volunteers were willing to micturate, but, for emotional reasons, could not perform and tightly contracted their perineum. The PET-scan results in these volunteers revealed increased rCBF in an area in the ventrolateral pontine tegmentum, which might represent the L-region. Perhaps the L-region should be considered as a "continence" center, especially since the PET-scan

studies suggest the existence of such a center in humans. Whether the L-region also plays a role in ejaculation remains to be determined.

Mes-, di- and telencephalic cell groups, possibly involved in ejaculation and orgasm in animals

Studies in rats [3, 14] and gerbils [16] have shown that there are four regions that express C-Fos immunoreactivity after ejaculation; the medial preoptic area (MPOA), the medial nucleus of the amygdala (MeA), the bed nucleus of the stria terminalis (BNST), and the midbrain lateral central tegmental field (LCTF)/subparafascicular nucleus (SPF). Baum and Everitt [3] suggested that genital and olfactory vomeronasal input activates the LCTF/SPF and MeA, respectively, and that these regions interact to activate the MPOA and BNST.

Lesions in the posterodorsal preoptic nucleus and the posterodorsal part of the MeA of gerbils resulted in delay of ejaculation, but lesions in the subparafascicular nucleus did not [17]. Brackett and Edwards [8] concluded that the connection between MPOA and LCTF is essential for copulation, because bilateral lesions in the area of LCTF eliminated mating behavior in male rats and reproductive behavior was also eliminated after an MPOA lesion on one side combined with a lesion in the LCTF on the other.

Stimulation of the MPOA has been shown to evoke rhythmic motor patterns of the bulbospongiosus muscle, but the descending fibers of the MPOA cells relaying this effect probably terminate in the periaqueductal gray (PAG), because discrete lesions in the PAG blocked the bulbospongiosus activity [31]. The PAG is known to have extremely strong projections to the ventromedial medulla, where the diffuse pathways, as described above, originate. Thus, MPOA stimulation might evoke bulbospongiosus activation via the PAG and the ventromedial tegmentum to ''excite'' the spinal central pattern generator for ejaculation that controls expulsion [32].

Central control of ejaculation in human males

The introduction of positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) has made it possible to register and map neuronal activity in all parts of the human brain including the brainstem. Several investigators have studied brain activation during human sexual arousal [2,7,26, 36, 42], but not during ejaculation, the most critical component of male sexual behavior.

Holstege et al. [21] performed a PET study, in which heterosexual male volunteers were asked to have an ejaculation, brought about by manual stimulation by their female partner. The PET technique, using radioactive water ($H_2{}^{15}O$), shows increases or decreases in blood flow in distinct parts of the brain, representing increases or decreases of activation of neurons in these areas. Although the resolution of PET is relatively limited, the results of the ejaculation/orgasm studies were remarkable. During ejaculation, compared to manual stimulation of the penis, the strongest activation was in the so-called meso-diencephalic region, with structures such as the ventral tegmental area (VTA), known as the 'reward' area, the subparafascicular nucleus, ventromedial posterior thalamic nucleus, intralaminar nuclei, and the lateral central tegmental field. A similar region in the meso-diencephalic transition zone was activated during cocaine use [9], and especially heroin rush [40], suggesting that these experiences are similar to sexual orgasm. It might also explain why substances such as cocaine and heroin are so addictive.

Other findings in ejaculation/orgasm studies are the increased activation of the lateral putamen, certain parts of the prefrontal, temporal, parietal and insular cortex and a very strong activation of the cerebellum. Strong activation was also found in the medial pontine tegmentum. Surprisingly, no activation was found in the hypothalamus or preoptic area. One might speculate that these regions play a role in creating the conditions in which mating can take place, e.g. estrous versus non-estrous, but that they are not involved in the motor act itself.

An important decrease of activation was also found. The medial parts of the amygdalar regions were deactivated, not only during ejaculation or orgasm, but also during sexual stimulation and erection. A similar decrease of amygdalar activity was found during romantic love [4]. An active amygdala is crucial for individual survival by constantly monitoring environmental stimuli. In the case of possibly hazardous events, the amygdala elicits a fear response to protect the organism from harm. However, in the context of sexual behavior, such vigilance could easily block the sexual act, leading to unsuccessful reproduction. One might hypothesize that, in order to prevent such a disruption, brain structures involved in sexual behavior decrease vigilance by inhibiting amygdalar activity. Although deactivation of the amygdala may make the organism less concerned about potential danger, it enhances the odds of the individual reproducing successfully.

The PET-studies revealed important differences when compared with studies on rodents. This is important, because almost all research on sexual behavior in general is carried out on rodents, and not cats or primates, including humans. Of all areas that were shown to be involved in ejaculation in rodents, only the midbrain lateral central tegmental field (LCTF) and the parvocellular part of the subparafascicular nucleus (SPFp) were found to be activated in humans.

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