The basic neural circuitry for sexual behavior
van der Horst, Veronica Gerarda Johanna Maria

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Chapter 4
Nucleus retroambiguus projections to lumbosacral motoneuronal cell groups in the male cat, possibly representing the final common pathway for mounting behavior

ABSTRACT
Recently, in the female cat nucleus retroambiguus (NRA) projections have been described to distinct motoneuronal cell groups in the lumbar enlargement, possibly involved in lordosis behavior. The present paper deals with the NRA-lumbosacral pathway in the male cat. Lumbosacral injections of wheat germ agglutinin-horseradish peroxidase (WGA-HRP) were made to localize and quantify retrogradely labeled neurons in the caudal medulla. These injections were preceded by spinal hemisections in order to distinguish between neurons with ipsi- and neurons with contralaterally descending axons. The NRA-lumbosacral fibers descended almost exclusively contralaterally, but neurons in areas surrounding the NRA projected mainly ipsilaterally. Injections of WGA-HRP were made in the region of the NRA to determine its targets in the lumbosacral cord. To distinguish between the contralateral NRA pathways and the ipsilateral projections from neurons in the adjoining lateral tegmentum, the injections were preceded by ipsilateral hemisections in C2. A new scaling method was used to compare the results of the different cases, despite variations in size and segmental organization. The results show that the distribution pattern of anterogradely labeled fibers in the lumbosacral cord matched precisely the location of certain motoneuronal cell groups. The NRA projected densely to abdominal wall and pelvic floor motoneurons in Onuf’s nucleus, moderately to adductor longus, semimembranosus, and biceps femoris anterior motoneuronal cell groups, and only sparsely to iliopsoas and semitendinosus motoneuronal cell groups. Compared with the findings in the female, the NRA in the male cat projects more heavily to the biceps anterior and adductor longus, and only sparsely to the iliopsoas and semitendinosus motoneuronal cell groups. These male-female differences are discussed.

INTRODUCTION
The nucleus retroambiguus (NRA) is a group of neurons in the ventrolateral part of the caudal medulla oblongata which has been described in humans (Olszewski and Baxter, 1954), cats (Merrill, 1970; Holstege, 1989), rats (Ellenberger and Feldman, 1990), and songbirds (Wild, 1993). In the cat, these interneurons form a column extending between 1 and 8 mm caudal to the obex (VanderHorst and Holstege, 1995).
NRA neurons have been shown to be respiration related (Merrill, 1970,1974). The caudal part of the NRA contains expiration related neurons, whereas rostrally expiration and inspiration related neurons are intermingled (Merrill, 1970; 1974). By workers in the field of respiration, the NRA is referred to as the caudal part of the ventral respiratory group (see Feldman, 1986 for review). More recent studies have demonstrated that NRA neurons are not only involved in expiration, but also in vomiting (Miller et al., 1987, 1995), defection (Fukuda and Fukai, 1986, 1988), vocalization (Jürgens and Pratt, 1979; Larson and Kistler, 1984; Holstege, 1989; Larson, 1991; Zhang et al., 1992) and possibly lordosis (VanderHorst and Holstege, 1995). NRA interneurons mediate these activities by way of very distinct, direct projections to a selection of brainstem (Holstege, 1989; Zhang et al., 1992) and spinal cord motor nuclei (Merrill, 1971; Holstege and Kuypers, 1982; Feldman et al., 1985; Holstege and Tan, 1987; Miller et al., 1989; VanderHorst et al., 1994; VanderHorst and Holstege, 1995). Regarding its involvement in respiration, vocalization, and lordosis, the NRA receives major afferent input from respiratory related neuronal cell groups in the lateral tegmental field of the medulla and pons (for review see Feldman, 1986; Smith et al., 1989; Gerrits and Holstege, in press), from two cell groups in the ventral medullary medial tegmental field (Gerrits and Holstege, in press), as well as from the midbrain periaqueductal gray (PAG; Holstege, 1989; Davis and Zhang, 1991; VanderHorst and Holstege, 1996a). The PAG is the final integrator for vocalization (Zhang et al., 1994) and lordosis (Sakuma and Pfaff, 1979; Ogawa et al., 1991), but also for various other components of emotional (aggressive and defensive) behavior, such as blood pressure control, nociception control, and possibly micturition (Besson and Chaouch, 1987; Bandler et al., 1991; Lovick, 1993; Blok and Holstege, 1994).
In a preceding study in the female cat, it has been demonstrated that the NRA projects to certain moto-
neuronal cell groups in the lumbosacral cord, innervating muscles of the hindlimb (i.e. iliopsoas, small adductors, and hamstrings), pelvic floor and lower back (VanderHorst and Holstege, 1995). Based on the specificity of this projection pattern, it was hypothesized that the NRA is involved in lordosis behavior, the receptive posture of the mating female. These findings raise the question whether such projections also exist in males.

In order to precisely determine the lumbosacral motoneuronal cell groups receiving NRA afferents, a detailed overview of the location of all lumbosacral motoneuronal cell groups was necessary. Thus far, it was difficult to integrate retro- and anterograde tracing findings in the lumbosacral cord of different animals because of sometimes large differences in length and segmental subdivision (Sherrington, 1892; Romanes, 1951). A new method was developed which made such an integration possible (see accompanying paper VanderHorst and Holstege, 1996b). The results demonstrate that also in the male cat a specific NRA-motoneuronal projection system exists, which precisely matches the location of a distinct set of motoneuronal cell groups innervating hindlimb and pelvic floor muscles.

**MATERIAL AND METHODS**

Six adult male cats were used. See Chapter 1 for the general surgical and histological procedures.

**Retrograde study**

In order to precisely localize the neuronal cell groups in the caudal medulla oblongata projecting to the lumbosacral cord in the male cat, in 2 cases injections of 3 µ 2.5% WGA-HRP were made in the L5 (case 2309) and S1-S3 (2329) segments, respectively, after laminectomy. Both injections were made bilaterally and were preceded by a hemisection a few segments rostrally. This was done to separate the neurons that send their axons to the lumbosacral cord via the ipsi- and contralateral funiculus, respectively. The lumbosacral cord, the caudal medulla and the C1 segment were cut and a 1 out of 4 series of consecutive sections was processed and microscopically studied.

**Anterograde study**

The purpose of these experiments was to study all NRA projections to the lumbosacral cord. This meant that, in each of 4 male cats, 3-5 injections of 30-50 µl 2.5% WGA-HRP had to be made to involve all rostrocaudal levels of the NRA in the injection site. In all cases the caudal medulla and the first two cervical segments were exposed dorsally. The injections not only involved the NRA, but extended into the adjacent lateral tegmentum, which implies that the labeled fibers in the spinal cord would be derived from NRA neurons and from neurons in the adjacent tegmentum.

The retrograde tracing experiments demonstrated that the non-NRA spinal cord projecting neurons send their axons through the ipsilateral white matter (see also VanderHorst and Holstege, 1995), whereas the NRA sends its fibers through the contralateral cord. In order to ascertain that the anterogradely labeled fibers are derived from neurons in the NRA, an ipsilateral C2 hemisection was made prior to the injection in the NRA. Segments L3 to S3 were cut and a 1 out of 4 series of consecutive sections was processed and microscopically studied.

**Comparison of motoneuronal cell groups and NRA fibers in different cases**

In order to match the rostrocaudal distribution of labeled lumbosacral motoneuronal cell groups and the distribution pattern of anterogradely labeled NRA fibers in the 4 cases, two problems had to be solved (see also accompanying paper VanderHorst and Holstege, 1996b). The first problem concerned the differences in the organization of dorsal and ventral rootlets forming the lumbosacral plexus (Romanes, 1951; Sherrington, 1892) between individual cases. These differences resulted in a considerable variation in length and level of the lumbosacral segments. The second problem was that the absolute total length of the lumbar enlargement also varied greatly between the cases due to differences in size of the animals. To overcome these problems, the same method had to be applied in the NRA injected cases as had been used for the motoneuronal cell groups in the accompanying paper (VanderHorst and Holstege, 1996b). Two landmarks were chosen in the enlargement, one rostrally (level 0) and one caudally (level 100). Caudal to level 0, ventrolateral part of the ventral horn extends latterly due to the presence of psoas major motoneurons which form the most rostral motoneuronal cell group of the hindlimb. At level 100, the ventrolateral ventral horn suddenly decreases due to the disappearance of motoneuronal cell groups innervating gluteal muscles and muscles of the distal hindlimb. These landmarks always can be identified independent of the presence of labeled motoneurons. In this way, it was possible to precisely match the distribution of motoneuronal cell groups with the distribution pattern of labeled NRA fibers. In one representative case (2287) color photomicrographs were taken from every sixth (1:4) collected section, representing a length of 6 x 4 x 40µm = 0.96 mm, and every photomicrograph was matched with the corresponding overview drawing of the lumbosacral motoneuronal cell groups of the accompanying paper (VanderHorst and Holstege, 1996b).
Figure 1  Plottings of labeled neurons in the caudal medulla oblongata after injections into the L5 and S1-S3 segments (cases 2309 and 2329, respectively).
Chapter 4

RESULTS

Retrograde study

After bilateral injections the L5 and S1-S3 segments (see Fig. 1 for location of the injections and hemisections), ipsilateral to the hemisection numerous retrogradely labeled neurons were found in the NRA and only few in the area adjacent to the NRA (Figs. 1 and 2; Table 1). Labeled NRA neurons were present between 1 and 8 mm caudal to the obex and their axons crossed the midline ventral to the central canal, at the level of the NRA itself. Contralateral to the hemisection, the NRA contained hardly any labeled neurons, whereas many were present just ventromedial to the NRA (Table 1). This ventromedial group extended further rostrally than the NRA, where it increased in size. These results demonstrate that the NRA project to the lumbosacral cord via the contralateral funiculus, whereas the neurons in the tegmentum medially adjoining the NRA project mainly ipsilaterally to the lumbosacral cord.

Anterograde study

Location of injections and hemisections

In all 4 cases (2287, 2294, 2326, and 2360), the injections involved the entire rostrocaudal extent of the NRA but extended into the adjoining lateral tegmental field and the lateral funiculus (Fig. 3). The ipsilateral C2 hemisections were complete and ventrally did not extend across the midline.

Distribution pattern of NRA-fibers in the lumbosacral cord

All 4 males showed a similar distribution pattern of NRA fibers in the L3-S3 lumbosacral segments. Descending labeled fibers were found in the dorsolateral, ventrolateral, and ventral funiculi of the cervical, thoracic and lumbosacral segments. From L1 to S3 their number gradually decreased. From rostral L4 to caudal L5, the labeled fibers in the ventrolateral funiculus gradually shifted into a more peripheral position. Only a very limited number of retrogradely labeled neurons was found in the lumbosacral cord, which indicates that the bulk of the labeled fibers in the white matter represent descending fibers.

Projections to laminae V-VII and X

A few labeled fibers were distributed to laminae V to VII and many to lamina X (Figs. 4 and 5). All these projections were bilateral, but with a strong contralateral preponderance, and were denser at sacral than at lumbar levels. The ipsilateral projections were derived from fibers descending through the contralateral funiculi and that had recrossed in the ventral gray commissure at the level of termination.

Projections to motoneuronal cell groups

In addition to the projections to laminae V-VII and X, specific projections were found to certain motoneuronal cell groups in lamina IX. These projections were much denser than the projections to the intermediate zone and equally dense as the projections to lamina X. After applying the same relative 0-100 method for the NRA cases as had been used for the drawings of motoneuronal cell groups (VanderHorst and Holstege, 1996b), the distribution pattern of labeled NRA fibers was matched with the location of the lumbosacral motoneuronal cell groups (Fig. 5).

Table 1

<table>
<thead>
<tr>
<th>Case</th>
<th>Number of labeled neurons</th>
<th>N/A</th>
<th>medial to NRA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>left (%)</td>
<td>right (%)</td>
<td>left (%)</td>
</tr>
<tr>
<td>2309</td>
<td>168 (97)</td>
<td>5 (3)</td>
<td>26 (10)</td>
</tr>
<tr>
<td>2329</td>
<td>203 (96)</td>
<td>9 (4)</td>
<td>24 (8)</td>
</tr>
</tbody>
</table>

Total number of retrogradely labeled neurons in the caudal medulla counted in 1:4 sections after bilateral injections in the L5 (case 2309) and S1-S3 (case 2339), preceded by left sided hemisections.

Level minus 220 to minus 30

In the L3 segment (± level minus 200), which does not contain hindlimb moto-neuronal cell groups, a very dense, bilateral projection was present in the motoneuronal cell group.
innervating the internal and external oblique abdominal wall muscles (Holstege et al., 1987; Miller, 1987; Fig. 4). This projection continued caudal until halfway the L3 segment (approximately level minus 120).

Level minus 30 to 50 Just rostral to the enlargement (level minus 30 to 0, corresponding to the caudal L4), a sparse projection was found to the psoas minor motoneuronal cell group. Slightly more caudally (levels 0 to 10), in the most rostral part of the enlargement, a limited number of labeled NRA fibers was present in the group containing mm. psoas minor and major motoneurons (level 3 of Fig. 5). The NRA projection did not continue further caudally, in contrast to the psoas major motoneuronal cell group (see Fig. 4 of VanderHorst and Holstege, 1996b). This finding suggests that only psoas minor motoneurons received NRA-afferents. A few fibers were found more medially, possibly representing terminations onto dendrites of psoas minor moto-neurons.

More caudally, (levels 10 to 20), a dense projection to the adductor longus motoneuronal cell group was present (see levels 27 and 30 of Fig. 5). The termination pattern precisely matched the entire (levels 15 to 45) cell group. The densest projection to this group was found at level 30, where adductor longus motoneurons are most numerous. The sartorius motoneuronal cell group (see levels 27 and 30 of Fig. 5; VanderHorst and Holstege, 1996b) was devoid of NRA afferents. Apart from the projection to the adductor longus, between levels 35 and 40 a distinct projection was observed to a restricted area in the dorsomedial ventral horn, which contains multifidi motoneurons (Vander-Horst and Holstege, 1996b). These motoneurons are located at the rostral end of each lumbarosacral segment. In case 2287, levels 35-45 correspond with the rostral part of L6.

In the motoneuronal cell groups of the remaining adductors of the thigh and of the quadriceps muscles only occasional labeled fibers were observed (see levels 27, 30, and 47 of Fig. 5). In all likelihood, these fibers did not terminate in these cell groups, but were fibers of passage on their way to their target motoneuronal cell groups.

Level 50 to120 At levels 50 to 70, a relatively dense projection was present in the center of the ventral horn which precisely overlaps the semimembranosus motoneuronal cell group (see level 60 of Fig. 5). The semitendinosus motoneuronal cell group at levels 65 to 90 did receive only very few, if any, labeled fibers (see level 73 of Fig. 5). At the other hand, at levels 75 to 90 a dense projection to the biceps anterior motoneuronal cell group was present (see level 83 of Fig. 5). The posterior biceps motoneuronal cell group, located medial to the anterior biceps group (levels 85 to 95), also received a dense NRA projection (see level 90 of Fig. 5). Only a few labeled fibers were found in other motoneuronal cell groups, innervating the gluteal muscles, the peroneus longus and the flexor digitorum longus (see levels 60, 75, 85, and 90 of Fig. 5). Around level 100, many labeled NRA fibers projected to pelvic floor motoneurons in Onuf’s nucleus (see levels 100 and 107 of Fig. 5). Dendrites of these motoneurons, extending dorsally into the intermediate zone (Beattie et al., 1990; Sasaki, 1994), also received heavy NRA input. Although the projection to Onuf’s nucleus involved the entire motoneuronal cell group, it was more predominant in its dorsomedial part, containing motoneurons innervating the anal sphincter. Between levels 110 and 120, a few thick labeled fibers were found in the ventromedial corner of the ventral horn (see level 113 of Fig. 5). This very dense but restricted projection involved the levator ani/ abductor caudae internus motoneuronal cell group (see accompanying paper VanderHorst and Holstege, 1996b). Around level 110, a few labeled fibers were present dorsolaterally in the ventral horn, where the motoneurons of the intrinsic foot muscles as well as ischiocavernosus and sacral parasympathetic neurons are located. Although it was not possible to determine which of these motoneuronal cell groups was the target of the NRA afferents, it is expected that the projection concerns the ischiocavernosus motoneurons. This idea is based upon the observation that, unlike the ischiocavernosus cell group, at adjoining rostral and caudal levels the motoneurons of the intrinsic foot muscles and the parasympathetic motoneurons did not receive a significant NRA projection.

For a summary of the involvement of lumbarosacral motoneuronal cel groups in the NRA projection, see Table 2.
Figure 4  Low power photomicrograph showing anterogradely labeled NRA fibers in the L3 segment. Note that NRA fibers descend throughout the contralateral funiculi and at this level terminate heavily and bilaterally in the ventrolateral part of the ventral horn. Bar represents 1 mm.

Figure 5  Comparison of the distribution of labeled NRA fibers (left; case 2287) and the location of lumbosacral motoneuronal cell groups (right) at different levels in the lumbosacral cord. In each of the drawings of motoneuronal cell groups, the location of motoneuronal cell groups as described by VanderHorst and Holstege (accompanying paper) was adapted to the shape of the ventral horn of case 2287 at corresponding levels. It must be emphasized that the photographs represent only one section, whereas the drawings of motoneuronal cell groups contain the information of 12 alternate sections. Bar represents 0.5 mm.
NRA projections to lumbosacral motoneurons: males

- Level 47: gracilis, iliacus, adductor magnus, adductor brevis, tensor fasciae latae
- Level 60: flexor digitorum longus, semimembranosus, obturatorius internus, tensor fasciae latae and gluteus medius
- Level 73: flexor digitorum longus, plantaris, semitendinosus, obturatorius internus
- Level 83: gastrocnemius lateralis, gastrocnemius medialis and soleus, semitendinosus, medial longissimus, gluteus maximus, caudo-femoralis, biceps femoris anterior
Chapter 4

- gastrocnemius
- medialis
- multifidi
- medial longissimus
- caudofemoralis
- gluteus medius
- biceps femoris posterior
- levator ani and abductor caudae internus
- external anal sphincter
- bladder
- intrinsic foot
- external urethral sphincter and ischiocavernosus

levels:
- level 90
- level 100
- level 107
- level 113
DISCUSSION

Comparison of the lumbosacral NRA projection in males and females

The retrograde results demonstrated that in the male cat, similar to the female, the NRA neurons projecting to the lumbosacral cord are located between 1 and 8 mm caudal to the obex, similar to the female. The anterograde results of the present study showed that the NRA in the male projects to distinct hindlimb and pelvic floor motoneuronal cell groups. These projections most heavily involved the adductor longus, semimembranosus, anterior and posterior biceps femoris motoneuronal cell groups, and Onuf’s nucleus. Previously, the NRA projections to the lumbosacral motoneurons in female non-estrous (VanderHorst and Holstege, 1995) and in estrous cats (VanderHorst et al., 1995; VanderHorst and Holstege, in preparation) have been described. Comparing the results in the female with those of the present study in the male suggests some differences in the NRA motoneuronal projection between males and females (Table 3). In the following comparison between male/female NRA-motoneuronal projection patterns, the findings in the estrous female will be used. In males, the iliacus, psoas major, semitendinosus and levator ani/abductor caudae internus motoneuronal cell groups received much sparser projections than in the estrous female, whereas the adductor longus and anterior biceps motoneurons were more densely innervated. The projection to Onuf’s nucleus including its dendrites is more prominent in males than in females. In both males and females, the

NRA projection is stronger in the dorsomedial part of Onuf’s nucleus, innervating the anal sphincter and bulbocavernosus muscles, than in Onuf’s ventrolateral part, innervating the urethral sphincter and the ischiocavernosus (Sato et al., 1978; Yamamoto et al., 1978; Pullen, 1988; Thor et al., 1989; Beattie et al., 1990). The NRA projection to levator ani/abductor caudae internus motoneurons, was denser in females than in males. Furthermore, this projection was mainly ipsilateral in the estrous female and mainly contralateral in the male. No clear male/female differences were found in the NRA projections to the psoas minor, multifidi, and posterior biceps motoneuronal cell groups. The motoneuronal cell groups of the sartorius, large adductors, quadriceps and distal muscles of the hindlimb did not receive significant projections from the NRA in either males or females.

Functional implications

Abdominal pressure control

Interneurons in the NRA have been shown to be involved in multiple behavioral patterns, such as respiration (Merrill, 1970, 1974; Feldman, 1986), vocalization (Holstege, 1989; Zhang et al., 1992, 1994), defecation (Fukuda and Fukai, 1986), and vomiting (Miller et al., 1987; Miller et al., 1995). These functions have in common that they are accompanied by elevation of intra-abdominal pressure, which is caused by activation of abdominal wall and pelvic floor. The dense NRA projections to motoneurons of the abdominal wall and pelvic floor muscles probably form the anatomical framework of these behaviors.

Table 2. Lumbosacral motoneuronal cell groups receiving NRA projections in the male cat

<table>
<thead>
<tr>
<th>Distinct projection to entire motoneuronal cell group</th>
<th>No distinct projection*</th>
<th>No projection</th>
</tr>
</thead>
<tbody>
<tr>
<td>Psoas minor</td>
<td>Psoas major</td>
<td>Sartorius</td>
</tr>
<tr>
<td>Adductor longus</td>
<td>Iliacus</td>
<td>Vastus medialis</td>
</tr>
<tr>
<td>Semimembranosus</td>
<td>Pectineus</td>
<td>Vastus lateralis</td>
</tr>
<tr>
<td>Biceps femoris anterior</td>
<td>Gracilis</td>
<td>Vastus intermedius</td>
</tr>
<tr>
<td>Biceps femoris posterior</td>
<td>Semitendinosus</td>
<td>Rectus femoris</td>
</tr>
<tr>
<td>External anal sphincter</td>
<td>Tensor fasciae latae</td>
<td>Adductor femoris brevis</td>
</tr>
<tr>
<td>Bulbocavernosus</td>
<td>Gluteus medius</td>
<td>Adductor femoris magnus</td>
</tr>
<tr>
<td>External urethral sphincter</td>
<td>Gluteus maximus</td>
<td>Abductor cruris caudalis</td>
</tr>
<tr>
<td>Ischiocavernosus</td>
<td>Caudofemoralis</td>
<td>Obturatorius internus</td>
</tr>
<tr>
<td>Levator ani</td>
<td>Peroneus longus</td>
<td>Gastrocnemius lateralis</td>
</tr>
<tr>
<td>Abductor caudae internus</td>
<td>Flexor digitorum longus</td>
<td>Gastrocnemius medialis</td>
</tr>
<tr>
<td>Multifidi (L6)</td>
<td>Intrinsic foot</td>
<td>Soleus</td>
</tr>
<tr>
<td></td>
<td>Medial longissimus (S1)</td>
<td>Plantaris</td>
</tr>
</tbody>
</table>

* The middle column represents the cell groups in which only a limited number of labeled NRA fibers was found in only part of the respective groups. In all likelihood, these fibers represent fibers of passage on their way to their target motoneuronal cell groups (left column).
Chapter 4

NRA projections to cutanei trunci (Holstege and Blok, 1989), and pectoralis major (Holstege and Kuypers, 1982) motoneurons in the cervical cord and to iliopsoas, adductor longus, and hamstring motoneurons in the lumbosacral cord are more delicate and suggest that the NRA is involved in other functions than abdominal pressure control.

Lordosis behavior
In a previous paper (VanderHorst and Holstege, 1995) it has been proposed that in the female cat, the NRA-lumbosacral pathway plays a role in receptive behavior or lordosis behavior (Fig. 6). This behavior consists of crouching, elevation of the lower back (lordosis), treading (movements of the hindlimbs), and lateral deviation of the tail (Michael, 1960). It is only displayed by estrous females and is so strong that it overrules almost all other behavioral patterns. The findings in the present study in the male cat raise the question whether the NRA lumbosacral pathway in the male is involved in mating behavior as well.

Mounting behavior
Most studies on male mating behavior have focussed on the regulation of ejaculatory and erectile (autonomic) responses. However, the neural circuitry underlying the male mating posture has never been studied before. Males show a different type of mating behavior than females. It consists of the neck grip, grasping with the forelimbs (forelimb rubbing), hindlimb stepping, arching of the back, stamping on the mounted females cat’s rump (palpation of the flanks), and pelvic thrusting (Fig. 6; Whalen, 1963). In contrast to females, adult male cats are able to mate any time if an estrous female is available. In order to verify the hypothesis that NRA-lumbosacral pathways form the final common pathway for mating behavior, it is necessary to study the electromyographic (EMG) activity of hindlimb muscles during mating. If the concept is true, during mating both males and females should demonstrated strong involvement of the psoas minor, semimembranosus, biceps femoris posterior, and no involvement of muscles as the quadriceps, adductor magnus, sartorius and triceps surae. The activity of the psoas major, semitendinosus and biceps femoris anterior would differ between males and females.

Brain structures known to be involved in male sexual behavior
Lesion and electrical stimulation studies in rodents, cats, dogs, and monkeys have revealed several important areas in the forebrain which play a role in male reproductive behavior, such as the neocortex (for

Table 3. Differences in the NRA-lumbosacral motoneuronal projection between males and females

<table>
<thead>
<tr>
<th>Motoneuronal cell group</th>
<th>Male</th>
<th>Female</th>
<th>Function</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oculi externus and internus</td>
<td>+++</td>
<td>+++</td>
<td>Expiration</td>
</tr>
<tr>
<td>Psoas minor</td>
<td>+</td>
<td>+</td>
<td>Flexion of lumbosacral vertebral column to pelvis</td>
</tr>
<tr>
<td>Psoas major</td>
<td>++</td>
<td>+</td>
<td>Flexion hip; fixation spine</td>
</tr>
<tr>
<td>Iliacus</td>
<td>+</td>
<td>+</td>
<td>Flexion of pelvis to lumbosacral vertebral column; flexion hip</td>
</tr>
<tr>
<td>Adductor longus</td>
<td>++</td>
<td>+</td>
<td>Adduction thigh</td>
</tr>
<tr>
<td>Semimembranosus</td>
<td>+</td>
<td>+</td>
<td>Extension hip; flexion knee; some inward rotation thigh</td>
</tr>
<tr>
<td>Semitendinosus</td>
<td>+</td>
<td>+</td>
<td>Flexion knee; extension hip</td>
</tr>
<tr>
<td>Biceps femoris anterior</td>
<td>++</td>
<td>+</td>
<td>Extension hip; some extension knee; some outward rotation thigh</td>
</tr>
<tr>
<td>Biceps femoris posterior</td>
<td>+</td>
<td>+</td>
<td>Flexion knee</td>
</tr>
<tr>
<td>External anal sphincter/ Bulbocavernosus</td>
<td>+++</td>
<td>++</td>
<td>Close anus; erection</td>
</tr>
<tr>
<td>External urethral sphincter/ Ischiocavernosus</td>
<td>++</td>
<td>+</td>
<td>Close urethra; erection and anteroflexion penis</td>
</tr>
<tr>
<td>Levator ani/ Abductor caudae internus</td>
<td>+</td>
<td>++</td>
<td>Compression rectum; abduction and flexion tail</td>
</tr>
<tr>
<td>Multifidi (L6)</td>
<td>+</td>
<td>+</td>
<td>Extension lower back</td>
</tr>
<tr>
<td>Medial longissimus (S1)</td>
<td>+</td>
<td>+</td>
<td>Extension lower back</td>
</tr>
</tbody>
</table>

• indicates that there is only a very sparse or no projection (see Table 2).
review see Meisel and Sachs, 1994), the main and accessory olfactory systems in rats but not in other species (Giantonia et al., 1970; Aronson and Cooper, 1974; Hart and Haugen, 1972; Goldfoot et al., 1978), the corticomedial nucleus of the amygdala (Giantonia et al., 1970; for review see Meisel and Sachs, 1994), the caudal medial preoptic area/anterior hypothalamus (e.g. Larsson and Heimer, 1964; Heimer and Larsson, 1966; Roberts et al., 1967; Malsbury, 1971; van Dis and Larsson, 1971; Hart et al., 1973; van de Poll and van Dis, 1979; Hansen et al., 1982; Hart and Leedy, 1983; for review see Meisel and Sachs, 1994).

It is not known which structures in the mesencephalon, pons, and medulla oblongata are involved in this behavior. The present study points to the NRA-lumbosacral pathway to play an important role in this respect. Although the central nucleus of the amygdala and the medial preoptic area/anterior hypothalamus do not directly project to the NRA (Hopkins and Holstege, 1978; Holstege, 1987), they may do so indirectly via the PAG (Holstege, 1989; VanderHorst and Holstege, 1996a) or the ventral medullary medial tegmental field (Gerrits and Holstege, in press). The PAG has been shown to be involved in the integration of survival behavior including female mating behavior (Sakuma and Pfaff, 1979; Ogawa et al., 1991), but its role has never been studied in relation to male sexual behavior. Stimulation in the PAG is known to elicit hindlimb movements and arching of the back which have been interpreted as being part of aversive and defensive responses (Bandler et al., 1991). Possibly, part of these movements also play a role in mounting behavior.

In summary, a concept is proposed in which the PAG-NRA-lumbosacral projection is involved in both female and male mating behavior. This hypothesis is in line with reports that mounting and lordosis are not exclusively displayed by males and females, respectively (Beach, 1948; Michael, 1960; Emerey and Sachs, 1975; Krieger and Barfield, 1976; Davidson and Block, 1969; Larsson et al., 1976; Sodersten and Larsson, 1975; van de Poll and van Dis, 1977). Possibly, part of the differences in male and female mating behavior are based on the differences observed in the NRA-motoneuronal projections.