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Review

Spinal interneuronal networks in the cat: Elementary components

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ABSTRACT

This review summarises features of networks of commissural interneurons co-ordinating muscle activity on both sides of the body as an example of feline elementary spinal interneuronal networks. The main feature of these elementary networks is that they are interconnected and incorporated into more complex networks as their building blocks. Links between networks of commissural interneurons and other networks are quite direct, with mono- and disynaptic input from the reticulospinal and vestibulospinal neurones, disynaptic from the contralateral and ipsilateral corticospinal neurones and fastigial neurones, di- or oligosynaptic from the mesencephalic locomotor region and mono-, di- or oligosynaptic from muscle afferents. The most direct links between commissural interneurons and motoneurons are likewise simple: monosynaptic and disynaptic via premotor interneurons with input from muscle afferents. By such connections, a particular elementary interneuronal network may subserve a wide range of movements, from simple reflex and postural adjustments to complex centrally initiated phasic and rhythmic movements, including voluntary movements and locomotion. Other common features of the commissural and other interneuronal networks investigated so far is that input from several sources is distributed to their constituent neurones in a semi-random fashion and that there are several possibilities of interactions between neurones both within and between various populations. Neurones of a particular elementary network are located at well-defined sites but intermixed with neurones of other networks and distributed over considerable lengths of the spinal cord, which precludes the topography to be used as their distinguishing feature.

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Abbreviations: 4-AP, 4-aminopyridine; 5-HT, 5-hydroxytryptamine (serotonin); c, commissural; co, contralateral; EPSP, excitatory postsynaptic potential; FN, fastigial nucleus; GABA, gamma aminobutyric acid; GS, gastrocnemius–soleus; i, ipsilateral; IPSP, inhibitory postsynaptic potential; L, lumbar; LVN, lateral vestibular nucleus; MLF, medial longitudinal fascicle; MLR, mesencephalic locomotor region; MN, motoneuron; NA, noradrenaline; Q, quadriceps nerve; PT, pyramidal tract; RS, reticulospinal; T, threshold; VS, vestibulospinal

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1. Introduction

Elementary spinal interneuronal networks are very simple. In the simplest cases, there are just one or two interneurons in series between input neurones and motoneurons. However, even in the simplest networks, there is a number of interneurons of each kind in parallel and these neurones integrate somewhat different combinations of information, from not only their main sources of input, e.g. muscle and skin afferents, but also from other neuronal networks. They forward it also to somewhat different combinations of their target neurones, including interneurons of other neuronal networks. Because of their links with other networks, all elementary networks may thus be considered to be components of more complex networks.

This arrangement may be illustrated with any of the previously investigated networks of spinal interneurons, from Renshaw cells and interneurons mediating Ia reciprocal inhibition, which were among the first interneurons to be analysed (for references, see Jankowska, 1992), through cervical propriospinal neurones (Lundberg, 1979) and interneurons mediating reflex actions of group II muscle spindle afferents (Jankowska et al., 2002a,b), to mention only those known in most detail. In this review it will be illustrated with the recently investigated networks of commissural interneurons. These networks have become of particular interest as being attributed a critical role in locomotor networks (for references, see Buchanan, 1999; Grillner, 2003; Kiehn, 2006; Soffe et al., 1984) because they are needed to adjust rhythmic activity of neurones on both sides of the spinal cord and because they are one of the major targets of reticulospinal neurones that are involved in initiation of locomotion. There is also a growing body of evidence that commissural interneurons may be of critical importance for other centrally or reflexly initiated phasic movements, including voluntary movements and postural adjustments, and that individual commissural interneurons may contribute to several of these movements.

2. Networks of commissural interneurons as examples of spinal elementary networks

2.1. Functional differentiation of the population of commissural interneurons

As other spinal interneuronal populations, the population of commissural interneurons is not homogenous. It includes

subpopulations of both excitatory (glutamatergic) and inhibitory (glycinergic) neurones (Bannatyne et al., 2003, 2006; Butt and Kiehn, 2003; Nissen et al., 2005; Roberts et al., 1988; Sugiuchi et al., 1995), at different locations (Bannatyne et al., 2003, 2006; Harrison et al., 1986; Huang et al., 2000; Kiehn and Butt, 2003; Lu et al., 2001; Ohta et al., 1991; Stokke et al., 2002), with different target cells (Bannatyne et al., 2003, 2006; Birinyi et al., 2003; Butt et al., 2002; Butt and Kiehn, 2003; Matsuyama et al., 2006, 2004a,b; Stokke et al., 2002) and with different types of input (Harrison et al., 1986; Jankowska et al., 2005a,b,c; Jankowska and Noga, 1990). For instance, commissural interneurons of the L3–L6 segments that target contralateral motoneurons in caudal lumbar segments fall into two main subpopulations, those with monosynaptic input from reticulospinal (RS) neurones, vestibulospinal (VS) neurones and group I afferents, and those with monosynaptic input from group II muscle afferents (Jankowska et al., 2005a,b,c).

In the adult cat, rat and mouse, the majority of commissural interneurons are located in lamina VIII on one side of the grey matter (Harrison et al., 1986; Hoover and Durkovic, 1992; Puskar and Antal, 1997; Stokke et al., 2002) and target neurones on the other side (Bannatyne et al., 2003; Matsuyama et al., 2006, 2004a, b; Nissen et al., 2005), as illustrated in Figs. 1A,B. This is true for both excitatory and inhibitory lamina VIII commissural interneurons but occasional bilateral projections have recently been reported (in one out of 34 lamina VIII neurones analysed by Matsuyama (2006). Bilateral projections have also been found in the case of two groups of interneurons with input from group II afferents: inhibitory (but not excitatory) dorsal horn interneurons (Bannatyne et al., 2006; Figs. 1C and D) and excitatory (but not inhibitory) lamina VII interneurons (B.A. Bannatyne, D.J. Maxwell K. Stecina, I. Hammar and E. Jankowska, unpublished). Contralateral projections have also been demonstrated for unidentified, primarily inhibitory dorsal horn neurones in the adult rat (Petko and Antal, 2000; Petko et al., 2004), but without specifying whether the same neurones projected ipsilaterally.

In contrast to projections in adult animals, projections of lamina VIII interneurons in neonatal animals appear to be more often bilateral, at least as judged by anatomical studies using the Golgi technique (Cajal, 1953; Scheibel and Scheibel, 1966), with examples in Figs. 1E and F. This may indicate that ipsilateral axon collaterals of these interneurons withdraw at some stage during the development. Bilateral projections may also be more frequent in genetically modified EphA4 knockout mice exhibiting synchronous (rabbit- or kangaroo-like) rather than alternating gait (Dottori et al., 1998; Kullander et al., 2003).

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