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RECIPROCAL INHIBITORY INTERNEURONES IN THE *XENOPUS* EMBRYO SPINAL CORD

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SUMMARY

1. The mechanism of reciprocal inhibition between antagonistic motor centres during swimming in the paralysed *Xenopus* embryo has been investigated further. Paired intracellular recordings have been made from interneurones and motoneurones in an attempt to identify neurones which make direct inhibitory synapses onto motoneurones on the opposite side of the spinal cord.

2. A physiological class of inhibitory interneurones is described which, when stimulated by intracellular current passage, evoke short-latency, probably monosynaptic, strychnine-sensitive inhibitory potentials in contralateral motoneurones.

3. These inhibitory interneurones fire once per swimming cycle in phase with the ipsilateral motor root discharge. They therefore have a pattern of activity which would cause them to inhibit motoneurones of the antagonistic motor centre at an appropriate part of the swimming cycle.

4. The intracellular injection of horseradish peroxidase (HRP) has allowed the morphology of these inhibitory interneurones to be characterized. They have unipolar cell bodies with a thick proximal process with short dendrites which crosses the spinal cord ventrally and then bifurcates with one axonal branch ascending into the hind brain and the other descending the spinal cord. These anatomical features are typical of the 'commissural interneurones' first described by Roberts & Clarke (1982).

5. There are also some inhibitory interneurones which can inhibit motoneurones on the same side of the spinal cord. At least some of these interneurones may be commissural interneurones with ipsilateral axons and they may play a role in the generation of the swimming rhythm.

INTRODUCTION

Inhibition is thought to play an important role in the co-ordination and generation of rhythmic motor patterns. Some hypothetical models of rhythm generators propose neurones arranged in reciprocally inhibitory pairs (Perkel & Mulloney, 1974). In the lobster stomatogastric ganglion and in the control of the leech heart beat reciprocal inhibition plays a crucial role in the generation of a rhythmic motor output

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(Selverston, Miller & Wadepuhl, 1983; Calabrese & Peterson, 1983). Recurrent cyclic inhibition has also been proposed as a mechanism for rhythm generation (Kling & Szekely, 1968; Friesen & Stent, 1977). Reciprocal inhibition may be involved in the co-ordination of bilateral and tetrapod locomotion. For example, the bilateral undulatory swimming movements of the lamprey and the *Xenopus* embryo seem to be co-ordinated by reciprocal inhibition originating from antagonistic motor centres (Buchanan, 1982; Cohen & Harris-Warrick, 1984; Soffe & Roberts 1982*b*). In the cat, motoneurones are inhibited by their antagonistic motor centres via the Ia inhibitory interneurones during locomotion (Jankowska & Roberts, 1972; Feldman & Orlovsky, 1975).

In the *Xenopus* embryo, motoneurones and rhythmically active interneurones receive mid-cycle inhibition during swimming (Roberts & Kahn, 1982; Soffe, Clarke & Roberts, 1984; Dale & Roberts, 1985). This inhibition, which originates from the opposite side of the spinal cord (Soffe & Roberts, 1982*b*), prevents motoneurones on one side firing at an inappropriate part of the swimming cycle when muscles on the opposite side are contracting. The reciprocal inhibition seems to be essential to phase-couple the two motor outputs which can arise independently from the two sides of the *Xenopus* embryo central nervous system (Kahn & Roberts, 1982). Given the widespread importance of reciprocal inhibition, further investigation of the underlying neuronal mechanisms in simple vertebrate systems like the *Xenopus* embryo is of great interest. Recently, Soffe *et al.* (1984) proposed that a class of neurone with crossed commissural axons, 'commissural interneurones' (Roberts & Clarke, 1982), could generate the reciprocal inhibition of antagonistic motor centres during swimming. They based their argument on two findings: commissural interneurones had an appropriate anatomy to contact neurones on the opposite side of the spinal cord and they had the correct firing pattern during swimming to generate the mid-cycle inhibitory post-synaptic potentials (i.p.s.p.s).

This paper provides evidence that commissural interneurones are indeed inhibitory. Paired intracellular recordings have been made from interneurones and contralateral motoneurones. This has revealed a class of interneurone which makes inhibitory synapses to contralateral motoneurones. These neurones have been filled with horseradish peroxidase (HRP) and have morphological features characteristic of the commissural cell class described previously (Roberts & Clarke, 1982; Soffe *et al.* (1984).

METHODS

Stage 37–38 *Xenopus* embryos (Nieuwkoop & Faber, 1956) were removed from their egg membranes, paralysed in 10^{-4} M-tubocurarine chloride (Sigma) in preparation for dissection and recording. The techniques of dissection, recording and HRP filling have been described previously (Dale & Roberts, 1985). All of the interneurones in this study were penetrated between the second and fifth post-otic myotomes (Roberts & Clarke, 1982) on or near the dorsoventral mid line and had resting potentials between −60 and −90 mV. Once a stable interneurone recording had been obtained a second electrode was used to search for motoneurones in the ventral part of the spinal cord (cf. Soffe & Roberts, 1982*a*) which were synaptically connected to the interneurone.

RESULTS

Crossed inhibitory interactions

Out of seventy-six interneurones tested, twelve were found to make inhibitory synapses to caudal motoneurones on the opposite side of the spinal cord. When the inhibitory interneurones were made to spike by intracellular current passage, an i.p.s.p. in the contralateral motoneurone followed each interneurone spike, one-for-one, at a constant latency (the interneurones were stimulated at 1 or 0·7 Hz). The latency of the i.p.s.p. was between 0·75 and 2 ms depending on the distance separating the micro-electrodes (100–350 μm). If a central conduction velocity of 0·1–0·2 m/s is assumed (a reasonable estimate in this preparation, cf. Clarke, Hayes, Hunt & Roberts, 1984; Dale & Roberts, 1985) then this latency is consistent with the post-synaptic potential (p.s.p.) being monosynaptic. In addition to this physiological evidence favouring a monosynaptic connexion, four out of the five successful dye fills revealed axonal projections long enough to allow direct synaptic contact between the interneurones and motoneurones (the other fill was too pale to allow the contralateral axon to be traced for a long enough distance). The i.p.s.p.s had amplitudes ranging from 0·8 to 6·0 mV (mean = 3·4, S.E. of mean = 0·49 mV) and rise times ranging from 1·5 to 5·0 ms (mean = 3·1, S.E. of mean = 0·32 ms) and half fall times between 7 and 14 ms (mean = 10·0, S.E. of mean = 0·64 ms, see Figs. 1 and 2). The time course of these i.p.s.p.s is very similar to those of the 'fast' excitatory post-synaptic potential (e.p.s.p.) recorded in *Xenopus* embryo motoneurones (Dale & Roberts, 1985) and could therefore be largely determined by the membrane time constant (cf. Curtis & Eccles, 1959). The i.p.s.p.s remained consistent in size and shape with repeated stimulation (at 0·7–1 Hz), and there were few failures in synaptic transmission. In contrast to this, the e.p.s.p.s seen in *Xenopus* embryo motoneurones were much more variable in size and shape (Dale & Roberts, 1985). The injection of depolarizing current in to the motoneurone through the recording electrode increased the size of the i.p.s.p.s and could reverse depolarizing i.p.s.p.s (Fig. 2) while hyperpolarizing current injection would decrease the amplitude of hyperpolarizing i.p.s.p.s and, if enough current was injected, bring them to their reversal potential. The bath application of 10^{-6} M-strychnine sulphate irreversibly blocked the intracellularly evoked crossed i.p.s.p.s ($n = 3$, Fig. 1). In parallel with these effects, 10^{-6} M-strychnine also changed the response to electrical stimulation of the trunk skin: it caused an irreversible loss of rhythmic activity and associated i.p.s.p.s, an effect very similar to that in spinal embryos (Roberts, Dale, Evoy & Soffe, 1985). The mid-cycle i.p.s.p.s during swimming can be markedly reduced by low levels of strychnine (5×10^{-7} M, S.R. Soffe, personal communication).

Ipsilateral inhibitory interactions

Another four interneurones were found which made inhibitory synapses to motoneurones on the same side of the spinal cord. Three of these interactions were descending (i.e. from rostral interneurones to caudal motoneurones) while the other was ascending. The i.p.s.p.s in the motoneurone followed the spike in the interneurone (evoked by intracellular current passage) one-for-one at a constant latency of 0·5–3·0 ms depending on the distance separating the recording electrodes

(150–300 μm). Since the latency was constant and short these i.p.s.p.s were probably monosynaptic. The ipsilateral i.p.s.p.s had amplitudes ranging from 0·8 to 3·0 mV (mean = 2·3, S.E. of mean = 0·52 mV), rise times in the range 3·0–8·0 ms (mean = 4·4, S.E. of mean = 1·21 ms) and half fall times ranging from 7·0 to 11·0 ms (mean = 9·8, S.E. of mean = 0·95 ms). These i.p.s.p.s were therefore indistinguishable in shape and size from those evoked in contralateral motoneurones. The ipsilateral i.p.s.p.s were also irreversibly blocked by 10^{-6} M-strychnine ($n = 2$).

The activity of inhibitory interneurones during swimming

All the inhibitory interneurones had a firing pattern during swimming which was similar to that of motoneurones (Soffe & Roberts, 1982*a*) and commissural interneurones (Soffe *et al.* 1984). They fired one spike per cycle superimposed on a depolarizing prepotential which was in phase with the ipsilateral motor root discharge (Figs. 1–3) and they received a mid-cycle i.p.s.p. One inhibitory interneurone could fire spikes just before the onset of the mid-cycle i.p.s.p. during swimming, evoking an on-cycle i.p.s.p. in a contralateral motoneurone (see Discussion section). This phasic activity was superimposed on a sustained depolarization of about 15–25 mV amplitude. One apparently consistent feature of inhibitory neurone activity during swimming was the negative slope of the plateau immediately following the spike (see Figs. 1–3). This was seen in all the good-quality recordings of inhibitory interneurones ($n = 14$). Motoneurones and excitatory interneurones do not appear to have this negatively sloping plateau: the plateau after the spike is either completely flat or has a slight positive slope (Roberts & Kahn, 1982; Soffe & Roberts, 1982*a*; Dale & Roberts, 1984; Dale & Roberts, 1985; compare the motoneurone and interneurone recordings of Figs. 1 and 3). The negative slope of the plateau seemed to be dependent on the interneurone resting potential: depolarizing current injection into the inhibitory neurones during swimming could flatten out the plateau following the spike. The negative-sloping plateau during swimming also seems to be a consistent feature of commissural cell activity (Soffe *et al.* 1984).

Fig. 1. The morphology and physiology of an inhibitory interneurone. *A*, low-magnification drawing showing the position of the cell body in the spinal cord and its spinal cord projections (*a*), hind brain (H), mid-brain (M) and forebrain (F). In this and all subsequent Figures rostral is to the right and dorsal is upwards. *b*, detail of the cell body and dendrites; *c*, detail of the contralateral axon; and *d*, a reconstructed transverse section of the neurone showing the dendrites projecting in to the lateral axon tracts on the outside of the spinal cord and the proximal process crossing the spinal cord ventrally under the neurocoel, to branch in to an ascending and descending axon (small dots). *B*, the activity of an inhibitory interneurone (i.i.) and contralateral motoneurone (m.n.) and ventral root (v.r.) during swimming. *a*, a long time base record showing the sustained excitation received during an episode of swimming evoked by a shock to the skin (*). In this and all subsequent Figures the dotted lines indicate the resting potential. *b*, spikes in the interneurone occur exactly mid-cycle to those in the contralateral motoneurone and contralateral ventral root. *C*, a spike in the interneurone (top trace) evokes a short-latency i.p.s.p. in the contralateral motoneurone (bottom trace) which was about 150 μm caudal to the interneurone. *a*, one subthreshold current pulse passed in to the interneurone fails to evoke an i.p.s.p. and a suprathreshold current pulse which does. *b*, five consecutive evoked i.p.s.p.s superimposed. *c*, 2 min of 10^{-6} M-strychnine application abolishes the i.p.s.p. in the motoneurone (five consecutive superimposed traces).

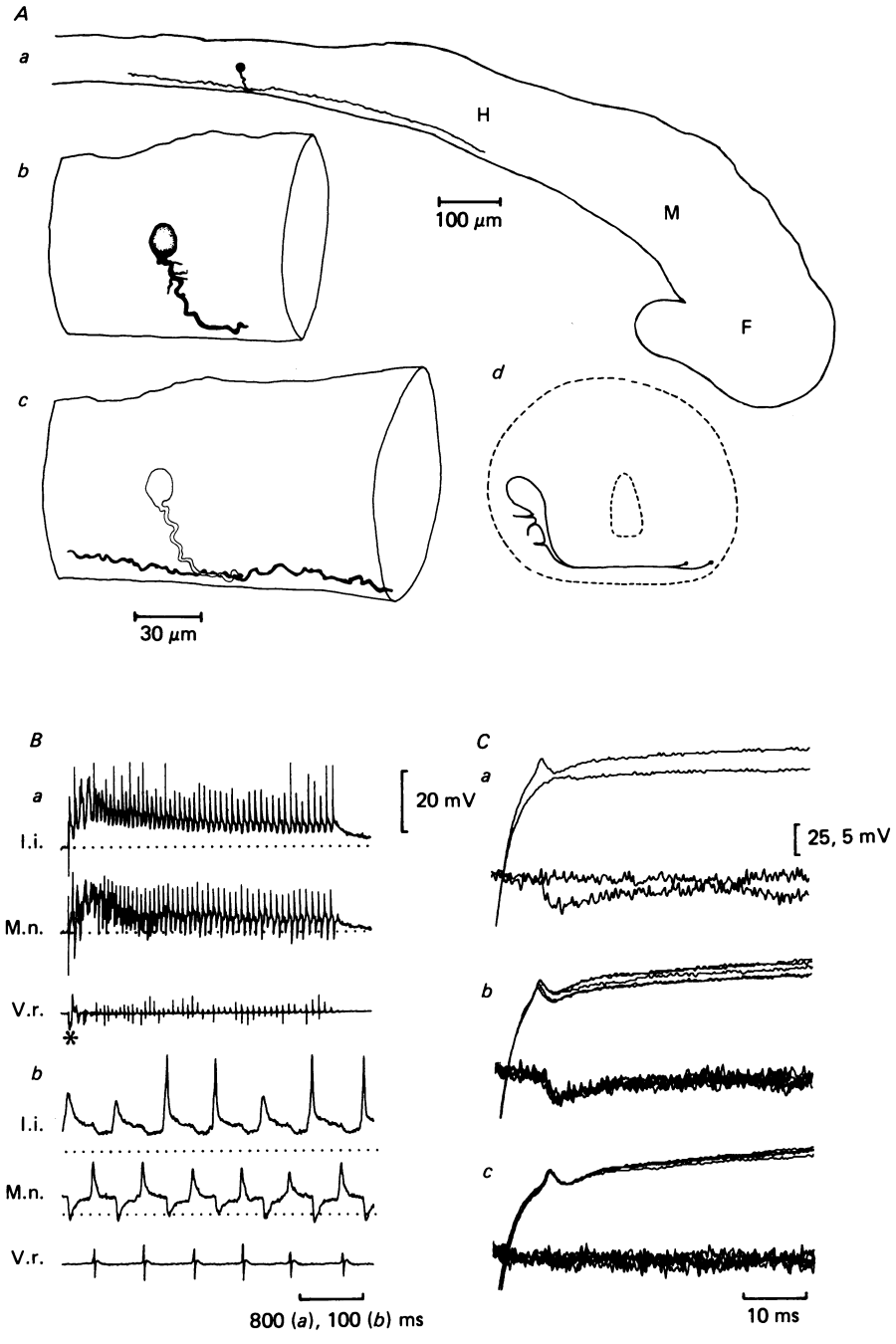

Fig. 1. For legend see opposite.

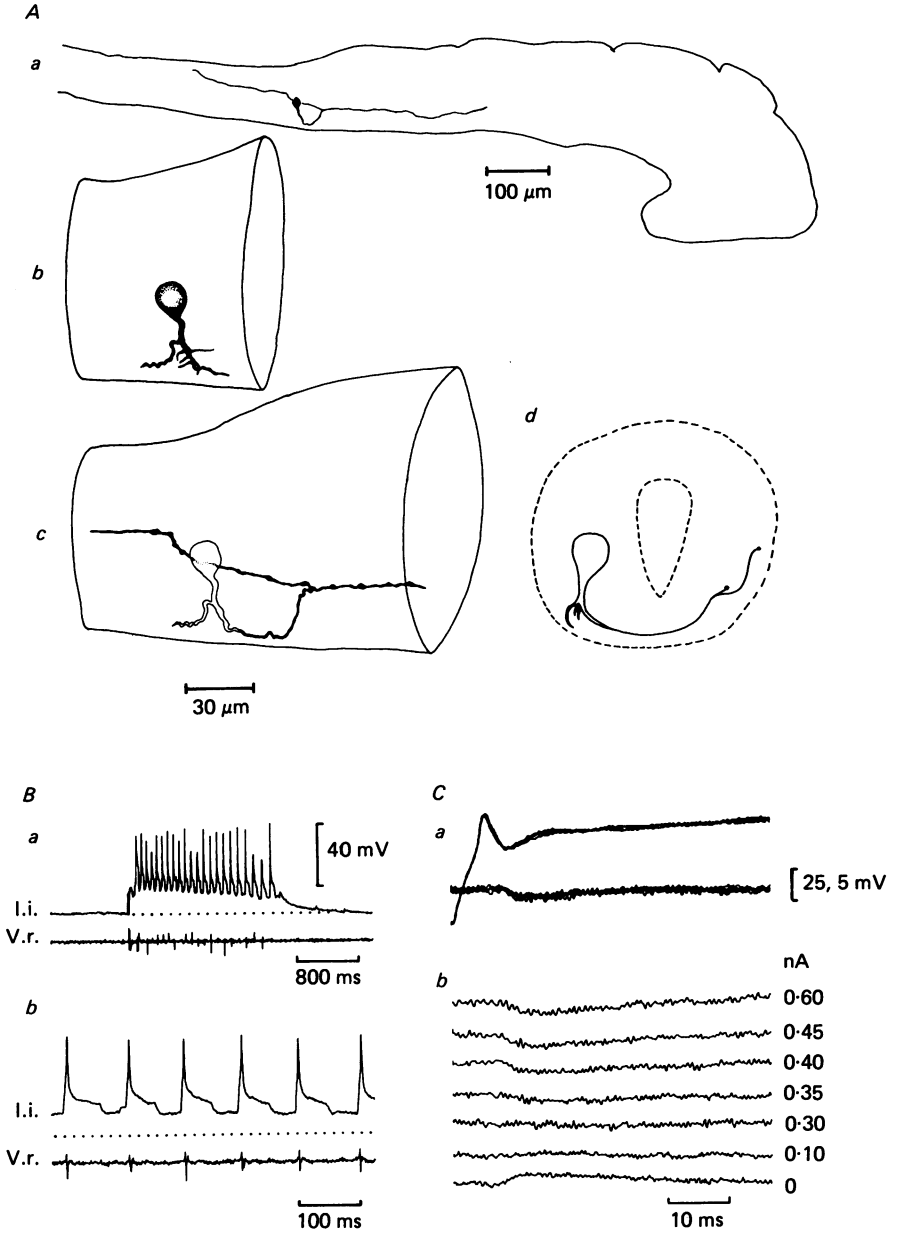

Fig. 2. *A*, the anatomy of an inhibitory interneurone, *a–d* as in Fig. 1. *B*, a swimming episode evoked by a transient dimming of the lights (*a*). This interneurone (i.i.) fired one spike per swimming cycle in phase with the ipsilateral ventral root (v.r.) and received mid-cycle i.p.s.p.s and sustained excitation (*b*). *C*, a spike in the interneurone evoked a short-latency i.p.s.p. (five superimposed consecutive traces) in a contralateral motoneurone some 150 μm caudal to it (*a*). This i.p.s.p. became depolarizing later on in the experiment (*b*) and could be reversed by the injection of depolarizing current. The amount of current injected is shown rather than the resting potential due to uncertainty about the electrode balance.

The morphology of inhibitory interneurones

Five inhibitory interneurones were successfully filled with HRP. Four of these made crossed inhibitory connexions and had a unipolar cell body with a thick proximal process from which dendrites could arise. The process crossed the spinal cord ventrally and T-branched giving rise to long ascending and descending axons (Figs. 1 and 2). This morphology is characteristic of the commissural interneurones which have previously been put forward as candidate reciprocal inhibitory inter-

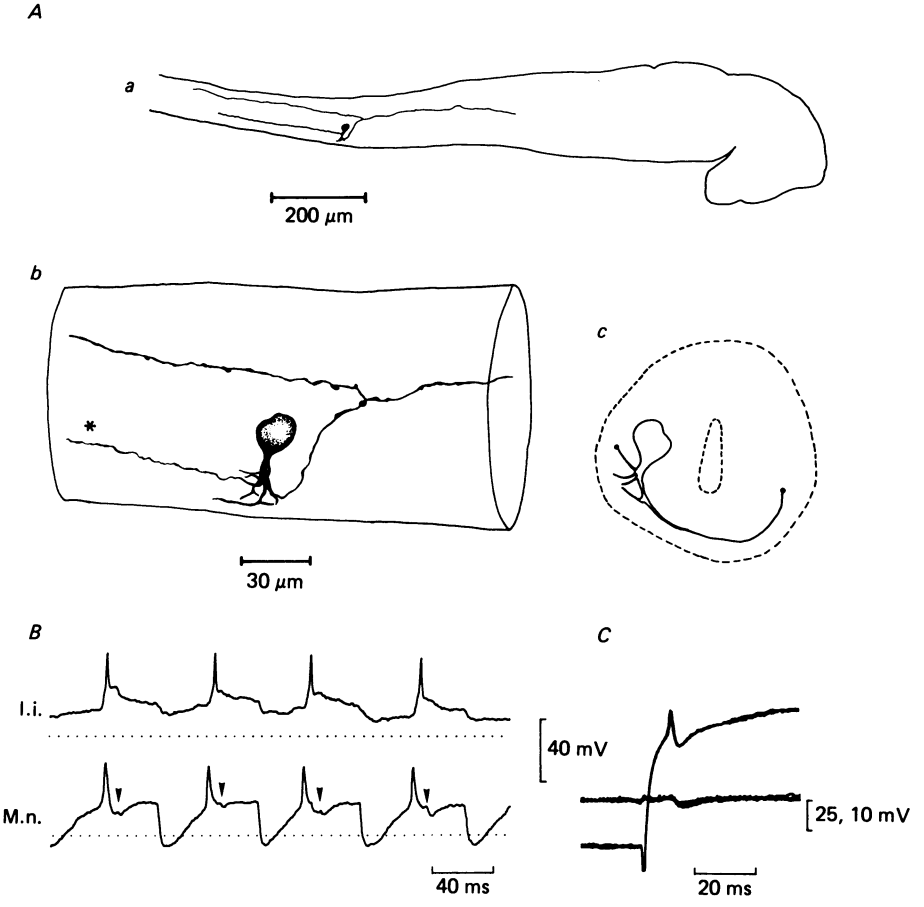

Fig. 3. The anatomy and physiology of an inhibitory interneurone producing ipsilateral i.p.s.p.s. *A a*, a low-magnification drawing showing its position and axonal projections in the spinal cord. *b*, detail of the cell body and dendrites: it has an ipsilateral descending axon (*) and a process which crosses the spinal cord and divides to give rise to an ascending and descending axon. *c*, a reconstructed transverse section of the neurone showing the dendritic and axonal projections. *B*, the activity of the interneurone (i.i.) and a simultaneously recorded ipsilateral motoneurone (m.n.) during swimming. The motoneurone was about 100 μm caudal to the interneurone, and both neurones fired in phase with each other and the ipsilateral ventral root discharge (not shown); the arrowheads indicate 'on-cycle' i.p.s.p.s in the motoneurone which originate at least in part from the interneurone. *C*, a spike in the interneurone evoked a short-latency i.p.s.p. in the ipsilateral motoneurone (three superimposed traces).

neurones (Soffe *et al.* 1984). One neurone which made an ipsilateral descending synapse was also filled. This turned out to be a commissural interneurone with an ipsilateral descending axon about 200 μm long (Fig. 3). These results clearly establish that commissural interneurones can make strychnine-sensitive inhibitory synapses to contralateral motoneurones. Since they fire once per swimming cycle in phase with the ipsilateral motor root discharge their post-synaptic actions would summate to produce the mid-cycle i.p.s.p.s. seen in all rhythmically active motoneurones and interneurones during swimming.

DISCUSSION

Inhibition in other vertebrate systems

The inhibitory interneurones described here are directly comparable to the CC interneurones of the lamprey (Buchanan, 1982). The CC interneurones have contralateral axons, are rhythmically active during swimming and inhibit myotomal motoneurones. They are thought to help co-ordinate the motor pattern to allow the left and right alternation of muscle contractions on the two sides of the lamprey. The i.p.s.p.s evoked in motoneurones by CC interneurones are of similar size and time course to those evoked by *Xenopus* embryo inhibitory interneurones. One difference is that the CC interneurones do not form a homogeneous functional class: some are excitatory. The possibility that some commissural cells could perform a role other than mediating mid-cycle inhibition (e.g. crossed excitation) cannot be excluded, but seems unlikely (Soffe *et al.* 1984).

In the cat, motoneurones receive monosynaptic inhibition from Ia inhibitory interneurones activated by the group Ia afferents from the antagonistic muscles (Jankowska & Roberts, 1972). During walking, the Ia interneurones fire rhythmically in phase with the motoneurones of their corresponding motor centre. This might be expected since they receive input from Ia afferents; however, they also fire rhythmically during walking in cats with restrained deafferented limbs (Feldman & Orlovsky, 1975). The Ia interneurones thus receive synaptic drive from the central pattern generator for walking. These interneurones therefore mediate reciprocal inhibition between antagonistic motor centres during walking and are to that extent comparable to the commissural interneurones described here and the CC interneurones of the lamprey.

Reciprocal inhibition in the Xenopus embryo spinal cord

Both halves of the *Xenopus* embryo central nervous system are capable of independent rhythm generation (Kahn & Roberts, 1982). The motor output from the two sides of the spinal cord is normally phase-coupled in intact embryos. When the spinal cord and hind brain are longitudinally divided along their entire length this phase coupling is lost (Kahn & Roberts, 1982). Soffe & Roberts (1982*b*) demonstrated that the mid-cycle i.p.s.p.s seen during swimming originated from the opposite side of the spinal cord and proposed that they were responsible for phase-coupling the motor outputs of the spinal cord. This paper provides evidence that the mid-cycle i.p.s.p.s come directly from the antagonistic motor centre and are generated by neurones with commissural axons.

The activity of inhibitory interneurones during swimming

Inhibitory interneurones have a very similar pattern of activity during swimming to that of motoneurones (Soffe & Roberts, 1982*a*). This seems to result from a similar pattern of synaptic input: the spikes have fast pre-potentials (see also Soffe *et al.* 1984), and they receive mid-cycle inhibition and a sustained excitation. Like motoneurones, inhibitory interneurones are activated by the bath application of the excitatory amino acid agonists *N*-methyl-D-aspartate, kainate and quisqualate (Dale & Roberts, 1984) and appear to receive amino-acid-dependent excitation during swimming (Dale & Roberts, 1985). As pointed out earlier, the activity of inhibitory interneurones differs slightly from that of motoneurones in that the plateau following the spike during swimming has a negative slope instead of being flat or having a positive slope. This is unexpected, since inhibitory interneurones appear to receive the same synaptic drive during swimming as other rhythmically active neurones. Motoneurones have multipolar cell bodies while those of the inhibitory interneurones (commissural interneurones) are unipolar. This difference in morphology between the two cell classes could account for the slightly different pattern of activity recorded in the soma, even though the two cell classes receive the same synaptic drive.

The sources and role of on-cycle inhibition

Four interneurones made connexions to ipsilateral motoneurones and would therefore be able to evoke on-cycle inhibition in motoneurones and presumably other spinal cord neurones during swimming. At least one of these interneurones was a commissural interneurone with an ipsilateral axon (Fig. 3). Such neurones may be rather rare since they were not found in the study by Soffe *et al.* (1984) or reported in a previous anatomical study by Roberts & Clarke (1982). One other interneurone could also evoke on-cycle i.p.s.p.s in a *contralateral* motoneurone (see Results section). These observations suggest that the on-cycle inhibition which is seen during swimming in a small proportion of motoneurones (Roberts & Kahn, 1982; Roberts, Dale, Evoy & Soffe, 1985; N. Dale & S. R. Soffe, unpublished observations; see Fig. 3), some excitatory interneurones (see Figs. 12 and 13 of Dale & Roberts, 1985) and some dorsolateral second-order sensory interneurones (Clarke & Roberts, 1984) could be generated, at least in part, by the actions of commissural interneurones. There could also be some other class of cell with ipsilateral axons which could generate on-cycle or recurrent i.p.s.p.s. Ascending interneurones (Roberts & Clarke, 1982) are a possible candidate for this role.

Rhythm generation can occur in the absence of mid-cycle inhibition: in preparations where the two sides of the hind brain and spinal cord have been longitudinally divided (i.e. all crossed axons have been cut) both sides of the nervous system are capable of independent rhythm generation (Kahn & Roberts, 1982). Under these circumstances, recurrent or on-cycle inhibition to motoneurones and premotor interneurones could contribute to the generation and stabilization of a rhythmic motor output (cf. Szekely, 1965; Kling & Szekely, 1968; Friesen & Stent, 1977; Roberts, Dale & Soffe, 1984).

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