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# CEREBRO-CEREBELLAR PROJECTIONS FROM THE LATERAL SUPRASYLVIAN VISUAL AREA IN THE CAT

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SUMMARY

1. A projection from the medial bank of the lateral suprasylvian visual area, one of the targets of the cerebello-cerebral projection, back to the cerebellar cortex was demonstrated electrophysiologically in the cat. The anatomical pathways underlying this projection were investigated using orthograde and retrograde transport of wheatgerm-agglutinin-conjugated horseradish peroxidase (WGA–HRP).

2. Responses were recorded in the cerebellar cortex on stimulation of the medial bank of the lateral suprasylvian area, and were compared with those evoked by stimulation of the motor cortex and the crown part of the parietal association cortex.

3. Responses induced by stimulation of the lateral suprasylvian area were shown to consist of early mossy and late climbing fibre responses. The mossy fibre response was evoked, at a latency of 2–3 ms, predominantly in the lateral part of the contralateral cerebellar cortex (mainly, crus I, crus II, dorsal paraflocculus and paramedian lobule) and the posterior part of the vermis (mainly, lobules VII and VIII). Climbing fibre responses were elicited with the preceding mossy fibre responses and were elicited at a much longer latency than the motor cortex-induced climbing fibre response.

4. The orthograde and retrograde HRP studies suggested that the mossy fibre response is mediated by the pontine grey whereas the climbing fibre response is conveyed indirectly to the inferior olive which sends the climbing fibres to the cerebellar cortex. After WGA–HRP injections into both the medial bank of the lateral suprasylvian area and the cerebellar responsive area, orthogradely labelled terminals of cortico-pontine projection fibres and retrogradely labelled ponto-cerebellar neurones were found in the pontine grey, where distributions of the two kinds of labelling overlapped. On the other hand, retrograde neuronal labelling alone was found in the inferior olive, implying that the climbing fibre responses evoked from the lateral suprasylvian area were relayed via indirect cortico-olivary pathways.

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## INTRODUCTION

The cerebellum and the cerebral cortex are reciprocally linked in both monkeys and cats. This linkage is considered indispensable for performing skilful and co-ordinated movements (Sasaki, 1979). In cats, the motor cortex and the crown part of the parietal association cortex, which are known to receive projections from the cerebellar interpositus and lateral nuclei, project back onto the cerebellar cortex (Sasaki, 1979, for a review; Sasaki, Oka, Matsuda, Shimono & Mizuno, 1975). Recently, we have discovered projections from the same cerebellar nuclei onto the rostral half of the medial bank of the lateral suprasylvian (LS) visual area (Kawaguchi, Miyata & Kato, 1983; Kato, Kawaguchi & Miyata, 1987). We therefore set out to investigate whether this visual area also projects back onto the cerebellum, thus forming another cerebro-cerebellar loop.

Anatomically, the cerebro-cerebellar projection from the LS area has not been well investigated. Although the presence of a cerebro-pontine projection from the LS area has been documented previously (Baker, Gibson, Glickstein & Stein, 1976; Albus, Donate-Oliver, Sanides & Fries, 1981; Bjaalie, 1986), it has not yet been examined whether this projection is relayed further to the cerebellar cortex. As for climbing fibre inputs originating from the LS area, an absence of direct projections from the LS area onto the inferior olive has been claimed (Bishop, McCrea & Kitai, 1976; Saint-Cyr, 1983).

Thus, the present experiments were aimed firstly at examining whether stimulation of the LS area, in particular the rostral half of the medial bank of the LS area, elicits mossy and climbing fibre responses in the cerebellar cortex. Since these responses were actually induced, morphological substrates for them were further studied by using orthograde and retrograde transport of WGA–HRP. A part of the present study has appeared in an abstract (Kato, Kawaguchi & Miyata, 1986*a*).

## METHODS

### *Electrophysiological study*

Thirty-nine adult cats (weighing 2·0–4·5 kg) were used. Twenty-three of these were normal. In the other sixteen cats, the crown part of the parietal association cortex was ablated 2–8 weeks before recording experiments with the following procedure. Under pentobarbitone anaesthesia (35 mg/kg, I.V.), the animals were placed in a stereotaxic apparatus. Whenever necessary, the anaesthesia was supplemented by giving a small dose of pentobarbitone via the cephalic vein which was cannulated. Respiration was always natural. The cranium was cut so that a piece of bone could come off over the crown part of the parietal cortex. The dura under the piece of bone was incised and folded up on the cranium. The grey matter was aspirated from the anterior half of the crown and medial bank of the middle suprasylvian gyrus (the stippled area in a frontal section shown in Fig. 1*D*). The unveiled white matter was covered with the folded dura and the piece of bone that had been removed was replaced. The skin was sutured. The animals were brought back to their cages, to await recovery from the anaesthesia.

Both the normal and previously operated cats were placed in a stereotaxic apparatus after anaesthesia with pentobarbitone (35 mg/kg, I.V.). The state of anaesthesia was monitored by electrocorticogram. Whenever necessary, anaesthesia was supplemented by giving a small dose of pentobarbitone via the cephalic vein which was cannulated. The skull and dura over the middle suprasylvian gyrus and the cerebellum were opened. As shown in Fig. 1*A*, two sets of bipolar electrodes were inserted into each of the anterior sigmoid gyrus (F) and the anterior part of the medial bank of the LS area (LS; for the ablated cats, Fig. 1*E* depicts the frontal plane through

which one of these electrodes penetrates the cortex) and, in the intact cats alone, also into the anterior part of the middle suprasylvian area (P; Fig. 1*A* and *B*). Brief pulse currents (0·3 ms in duration) were delivered through these electrodes. A train of two or three pulses (duration, 0·3 ms; intensity, 0·5–1·0 mA) was usually provided to ensure the stability of responses. A concentric electrode (Loc in Fig. 1*A*) was also attached on the cerebellar cortex to stimulate parallel fibres for

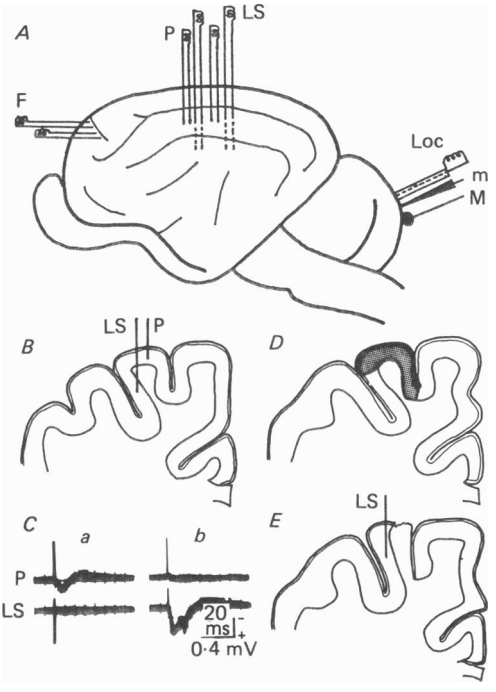


Fig. 1. *A*, an illustration showing the experimental arrangement. Biopolar stimulating electrodes are inserted into the medial bank of the LS area (LS), crown part of the parietal cortex (P), and the motor cortex (F). For recording, a gross silver-ball electrode (M) and a microelectrode (m) were placed on or in the cerebellar cortex. Parallel fibres were stimulated with a concentric electrode (Loc) situated near the microelectrode. *B*, a diagram showing a frontal section of the parietal cortex, where electrodes for stimulation of the crown (P) or medial bank of the LS area (LS) are illustrated schematically. *C*, field potentials recorded with the gross electrode in response to stimulation of the crown (P) or medial bank (LS), obtained from different cerebellar areas in two cats. The stimulation current was at such a low level that the electrode for LS stimulation failed to activate the crown itself or axons therefrom in one cat (*a*), and vice versa in another cat (*b*). *D*, an illustration showing a frontal section of the parietal cortex, where the stippled area indicates the region that was aspirated prior to the recording. *E*, a diagram showing a frontal section of the aspirated parietal cortex at the time of the recording. An electrode is seen placed in the remaining medial bank. The sulci and gyri are moderately distorted.

the purpose of identifying mossy and climbing fibre responses elicited by cerebral cortical stimulation (Eccles, Llinás & Sasaki, 1966*b*). For recordings from the cerebellar cortex, we placed a silver-ball electrode (M in Fig. 1*A*) and a microelectrode (m) filled with 2% Pontamine Sky Blue dissolved in 0·5 M-potassium citrate (DC resistance 2–10 MΩ) on the cerebellar surface. Some of the recording sites were marked with the dye by passing a DC current (5 $\mu$A × 5 min). After the recordings, the cats were perfused with a 10% formaline solution through the ascending aorta under deep pentobarbitone anaesthesia (65 mg/kg). Brains were removed, frozen and cut at 70 $\mu$m. The sections were examined under a microscope, so as to locate the dye spots and to identify the recording sites.

*Morphological study*

Four cats were used. The methods of anaesthesia and operation were the same as described for the electrophysiological study. A 5% solution of wheatgerm-agglutinin-conjugated horseradish peroxidase (L-9008, Sigma; WGA–HRP) in 0·1 M-Tris-HCl buffer was injected both into the anterior part of the medial bank of the LS area (presumed anteromedial lateral suprasylvian area, AMLS) and into parts of the cerebellar cortical areas responsive to the LS stimulation. The injections were made by using a Hamilton syringe (0·05 $\mu$l × 1 for the LS injections; 0·05 $\mu$l × 3 for the cerebellar injections) under visual guidance. For the injections into the LS area, the syringe was inserted in parallel with the medial bank of the LS area from the suprasylvian fringe area. The animals recovered from anaesthesia and were left alive in their cages for another 24–36 h, until they were perfused through the ascending aorta with a fixative (7% formaline solution in 0·1 M-phosphate buffer) under deep pentobarbitone anaesthesia (65 mg/kg, I.P.). Brains were removed, soaked in a 30% phosphate-buffered sucrose solution for a few weeks, frozen and cut in the frontal plane at 70 $\mu$m. The sections were treated with benzidine dihydrochloride (DeOlmos & Heimer, 1977).

## RESULTS

*Control experiments*

As expected from Fig. 1*B*, there is a possibility that the electrodes used for the LS stimulation (LS) might excite cortico-pontine fibres arising from the crown part of the parietal cortex, which pass just below the grey matter of the LS area. Conversely, the electrodes used for crown stimulation (P) might stimulate efferent fibres from the LS area. For such undesired stimulation to be avoided, the intensity of stimulation was kept low. As a result, we were able to record cerebellar responses elicited by the crown electrode alone, or induced by the LS electrode alone (Fig. 1*Ca* and *b*). Thus, it is unlikely that current spread stimulated the adjoining structures. Therefore, if a part of the cerebellar cortex responds to both the LS and crown stimulation, this means that inputs from both of the cerebral cortical areas reach that part of the cerebellar cortex.

In a further attempt to achieve an unambiguously selective stimulation of the LS area, we used cats in which the crown part and adjacent lateral bank of the lateral sulcus had been ablated 2–3 weeks before the recording. Figure 1*D* shows the ablated area (stippled). At the time of recording, the LS area was penetrated by the stimulating electrode (Fig. 1*E*). Responses from the cerebellar cortex in the intact and ablated animals were qualitatively much the same.

We present below various responses recorded from the intact or ablated cats, and distribution of cerebellar responses obtained from the intact cats.

*Mossy and climbing fibre responses elicited by LS stimulation*

Stimulation of the medial bank of the LS area elicited marked responses in the cerebellar cortex. When recorded from the cortical surface with a silver-ball electrode, the responses consisted of two successive surface-positive potentials (Fig. 2*Aa*). As the recording electrode was introduced to a depth of a few hundred micrometres, the two potentials reversed to become negative (Fig. 2*Ab*). These two potentials were presumed to be the mossy and climbing fibre responses, considering previous findings that stimulation of the sensorimotor cortex evoked two surface-positive, depth-negative waves which proved to be mossy and climbing fibre responses, respectively (Sasaki *et al.* 1975; Sasaki, 1979). This presumption was

confirmed by examining the effect of parallel fibre stimulation upon the amplitudes of the two responses recorded from the molecular layer (Fig. 2*Ab* and *c*). When stimulation of the cerebellar cortex in the vicinity of the microelectrode was given 20 ms prior to the cerebral cortical stimulation, the earlier potential was suppressed

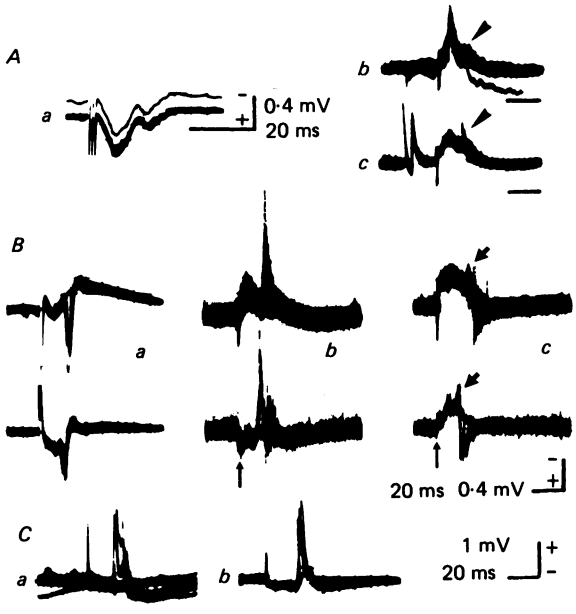


Fig 2. Responses recorded from the cerebellar cortex in response to stimulation of the medial bank of the LS area (*A*, upper row in *B* and *C*) or the motor cortex (lower row in *B*). *A*, specimen records of the mossy and climbing fibre responses. Early and late responses were recorded through a gross electrode put on the cortical surface (*a*) or a microelectrode placed deep in the cortex (*b* and *c*). When parallel fibre stimulation was delivered 20 ms prior to LS stimulation, the early response was suppressed whereas the late one (arrow-head) was enhanced (*c*) as compared with the non-conditioned ones (*b*). *B*, comparison between the LS-induced responses (upper row) and motor cortex-induced ones (lower row): field potentials recorded through the gross electrode (*a*) and microelectrode (*b*), extracellular units of complex spikes (arrows, *c*). Where invisible, stimuli are marked by arrows. *C*, examples of putative intracellular recording of Purkinje cells in response to LS stimulation.

whereas the later one (arrow-heads) was enhanced. The cerebellar cortical stimulation certainly activated parallel fibres that innervate Purkinje cells around the microelectrode (on-beam), because the stimulation induced a large negative wave which is assumed to be due to parallel fibre action potentials, and EPSP currents generated in the superficial parts of Purkinje cell dendrites situated in the molecular layer (Eccles, Sasaki & Strata, 1966*c*). Therefore, the earlier and later components of the response were assigned to the mossy and climbing fibres, respectively. Parallel fibre stimulation is considered to suppress the mossy fibre response through Golgi cell inhibition and to enhance the climbing fibre response by hyperpolarizing Purkinje cells through inhibitory interneurones (Eccles *et al.* 1966*b*).

Cerebellar responses elicited by stimulation of the LS area and frontal motor cortex were compared in Fig. 2*B* which shows: surface recording with a silver-ball

electrode (*a*), field potentials recorded from the molecular layer by a microelectrode (*b*), extracellular recordings of complex spikes (*c*). Mossy fibre responses elicited by the LS (upper row) and motor cortex (lower row) stimulation have virtually the same latency (2–3 ms) while climbing fibre responses due to LS stimulation were induced at a much longer latency (17–19 ms) than those due to motor cortical stimulation (12–13 ms), as shown in surface recordings. This finding was further confirmed by field potentials recorded from the molecular layer, and extracellular recordings of complex spikes. Figure 2*C a* and *b* shows examples of putative intracellular recording from Purkinje cells in response to LS stimulation, which show the typical configuration of the complex spike (Eccles, Llinás & Sasaki, 1966*a*).

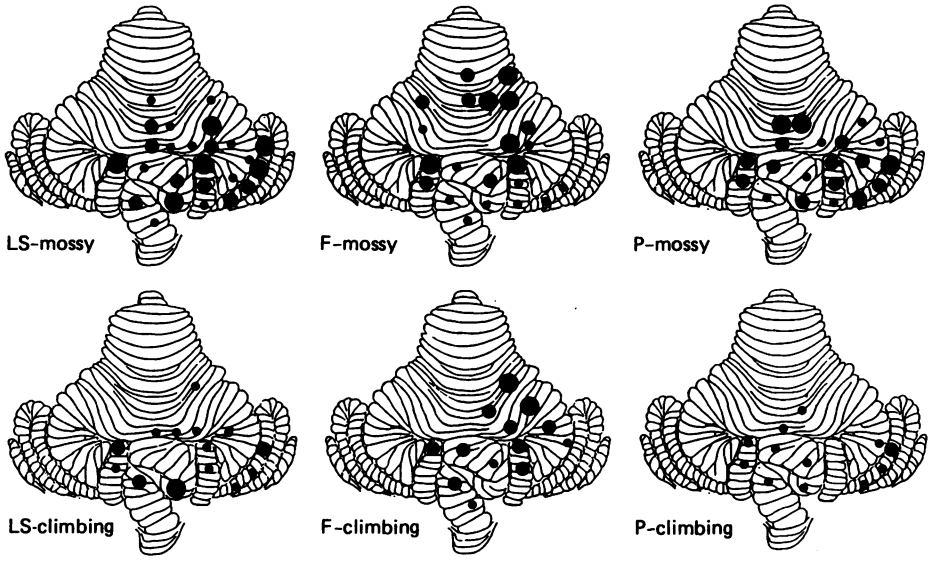


Fig 3. Distribution of mossy and climbing fibre responses on stimulation of the medial bank of the LS area (LS), crown of the parietal cortex (P), and the motor cortex (F). Amplitudes of the responses are averaged from fifteen animals, classified into three groups depending on the averaged values, and illustrated in this Figure with circles of three different diameters. Larger diameters indicate larger amplitudes.

*Distributions of mossy and climbing fibre responses*

Responses elicited by LS stimulation were recorded from various areas of the cerebellar cortex, and were compared with those induced by stimulation of the motor cortex or the crown part of the parietal cortex. Figure 3 summarizes the results obtained from fifteen normal cats. Amplitudes of the mossy and climbing fibre responses recorded from various areas were averaged among the fifteen animals, graded into three classes, and are illustrated in Fig. 3 with filled circles of three different diameters: large diameters indicate relatively larger amplitudes. For this reason, the diagrams in Fig. 3 do not necessarily provide an absolute measure of response amplitude. Nevertheless, this Figure appears to show the overall difference in distribution among the responses elicited on stimulation to the LS area (LS), motor cortex (F) and the crown part of the parietal area (P). The mossy fibre responses (mossy) elicited by LS stimulation were found mainly in the contralateral

dorsal paraflocculus, crus I, crus II, paramedian lobule and the lobules VI–VIII, but hardly, if ever, in the anterior lobules. A similar distribution of responses was obtained with crown stimulation (P). In contrast, the responses elicited by the motor cortical stimulation (F) have a different distribution. Their amplitude is larger over lobules IV–VI and paramedian lobule than over the more posterolateral part, i.e. crus I, crus II and the dorsal paraflocculus.

Climbing fibre responses (climbing) elicited by LS stimulation were recorded from much the same area as the mossy fibre responses. The distribution of the LS-evoked climbing fibre response was by and large similar to that induced by stimulation of the motor cortex or crown of the parietal cortex.

*Morphological correlates for the LS-induced mossy and climbing fibre responses*

In an attempt to examine the pathways that transmit the LS-induced mossy and climbing fibre responses, WGA–HRP was injected into both the medial bank of the LS area and the cerebellar cortex in four cats. The cerebellar areas injected were the dorsal paraflocculus ($n = 2$), crus II ($n = 1$), and lobule VIII ($n = 1$), where mossy and climbing fibre responses were always conspicuous. The injection into the LS area was placed in the rostral third of the medial bank of the LS area, where electrical stimulation effectively elicited mossy and climbing fibre responses. After injections into the two structures, orthograde terminal and retrograde neuronal labellings were seen in the thalamus and brain stem of all four cats. In this report, we describe the labelling in the brain stem, which is regarded as the unique structure relevant for the cerebro-cerebellar relay.

In the brain stem, the distributions of the orthograde terminal and retrograde neuronal labellings were always found to overlap with each other within the pontine grey. Retrograde labelling was observed in the inferior olive but was only sparsely scattered in the reticular formation. Orthograde labelling was further seen in the pretectum and superior colliculus, but not in the inferior olive and little if any in the reticular formation. These orthograde and retrograde labellings were ascribed to the LS and cerebellar injections, respectively, because the brain stem is known not to project directly onto the cerebral cortex and the cerebellar cortex is regarded as sending corticofugal fibres exclusively to the cerebellar and vestibular nuclei. Therefore, the pontine grey is likely to mediate the cerebro-cerebellar projections from the LS area via mossy fibres. On the other hand, the inferior olive, known as the exclusive source of climbing fibres, was found not to be reached by cerebral cortical afferents from the LS area. This appears to indicate that indirect cortico-olivary pathways exist and are responsible for the climbing fibre responses.

Figures 4 and 5 show two examples of the HRP experiments. Cerebellar injection sites were situated in lobule VIII (Fig. 4) or the dorsal paraflocculus (Fig. 5). In both Figures, orthograde and retrograde labelling was seen in the pontine grey, where the two kinds of labelling overlapped. The orthograde labelling was always found on the side ipsilateral to the injected LS area. The retrograde labelling was bilateral after the injection into lobule VIII while it was largely contralateral after the injection into the dorsal paraflocculus. In the case of the dorsal paraflocculus injection, labelled terminals were found on the contralateral side to the labelled neurones; however, if the laterality were disregarded, the two kinds of labelling would overlap.

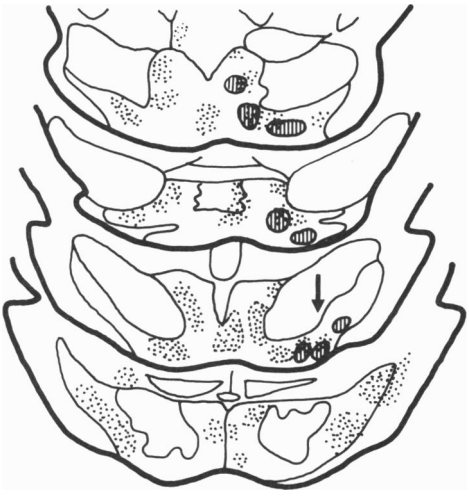

Fig. 4. Illustration showing distributions of cortico-pontine projection terminals (hatched areas) and ponto-cerebellar projection neurones (stippled areas) labelled in the pontine grey by WGA–HRP injected into the medial bank of the LS area and cerebellar cortex (lobule VIII). Note that the distributions of the terminals and neurones overlap. The arrow indicates the part of the grey from which the photomicrograph of Plate 1 was taken.

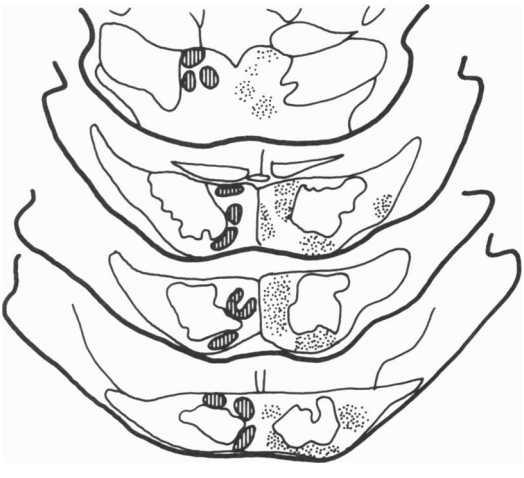

Fig. 5. Illustration showing distributions of cortico-pontine projection terminals (hatched areas) and ponto-cerebellar projection neurones (stippled areas) labelled in the pontine grey by WGA–HRP injected into the medial bank of the LS area and cerebellar cortex (ipsilateral dorsal paraflocculus). The distribution of the terminals and neurones would overlap if the laterality were disregarded.

This indicates that the LS area contralateral to the injected side projects onto pontine neuronal pools that send fibres to the injected dorsal paraflocculus. A photograph taken from a part of the pontine grey (arrow in Fig. 4) is shown in Plate 1. In the middle of Plate 1, the labelled terminals and neurones share their distribution zone. Terminals alone were labelled in the lower right corner. Labelled neurones were scattered in the upper part without any labelled terminals in the immediate vicinity.

## DISCUSSION

The present study revealed that stimulation of the medial bank of the LS area elicited both mossy and climbing fibre responses mainly in the posterolateral part of the cerebellar cortex. Direct cortico-pontine and indirect cortico-olivary projections are suggested to convey these two responses, respectively.

### *Pathways transmitting the responses*

The present morphological study suggested that the main pathway responsible for mossy fibre responses appears to be cerebro-ponto-cerebellar projections. WGA–HRP injections into the LS area and cerebellar cortex produced terminal and neuronal labelling, respectively, in the pontine grey which overlapped. In the thalamus, dense-labelled terminals and neurones were certainly seen; however, these must be cortico-thalamic terminals and thalamo-cortical neurones labelled by the WGA–HRP injection into the LS area alone and have nothing to do with the injection into the cerebellar cortex, because no direct thalamo-cerebellar projections have been found in the cat.

Robinson, Cohen, May, Sestokas & Glickstein (1984) reported visually related cerebro-ponto-cerebellar projections by using combined retrograde and orthograde tracer methods. However, since their cerebral injections of tritiated amino acid were made into both the LS area and the lateral gyrus, their study failed to specify the origin of the visual cerebro-ponto-cerebellar projections. In the present experiments, these projections were shown to originate at least partly from the anterior third of the medial bank of the LS area (presumed anteromedial lateral suprasylvian area, AMLS).

Mower, Gibson & Glickstein (1979) reported that the dorsolateral pontine grey projects onto the vermis and ipsilateral hemisphere while the rostromedial pontine grey projects onto the contralateral hemisphere. Our injections into the vermis and those into the hemisphere, as reported by Mower *et al.* (1979), produced retrogradely labelled neurones most densely in the dorsolateral and the medial pontine grey respectively. However, unlike their findings, the present study revealed a considerable number of labelled neurones in the medial pons after injections into the vermis. On this point, our present results are consistent with the results of Robinson *et al.* (1984), obtained by autoradiography, which demonstrated that the medial pontine nucleus sends dense mossy fibres to the vermis.

Brain stem structures other than the pontine grey, such as the reticular nuclei (Allen, Azzena & Ohno, 1972) or the nucleus reticularis tegmenti pontis (Maekawa, Takeda & Kimura, 1981), have been reported to mediate mossy fibre responses. However, such structures are unlikely to be the principal relay station for the projections from the LS area, because our present HRP study was unable to detect corticofugal fibres terminating therein. This does not necessarily mean that such fibres do not exist because of the limited sensitivity of the method, but at the very least it rules out a noticeable contribution from them to transmission of the mossy fibre response. In addition to the direct pathways, the indirect path through the superior colliculus (Kawamura & Brodal, 1973; Mower *et al.* 1979) should be considered. In other words, there is a possibility that a cortico-colliculo-pontine

projection might exist and be primarily responsible for generating the mossy fibre responses elicited by LS stimulation. However, even if such a projection should exist, this is unlikely to play a major part in exciting pontine neurones that give rise to mossy fibres, in view of the present finding that the LS-induced mossy fibre response was elicited at much the same latency as that elicited by motor cortical stimulation, which has been considered to be conveyed mainly by direct cortico-pontine projection fibres (Sasaki *et al.* 1975). Thus, the mossy fibre response to LS stimulation appears to be transmitted by direct cortico-pontine fibres and successively conveyed by ponto-cerebellar projections.

The inferior olive is known to be the exclusive source of the climbing fibres, indicating that the olivocerebellar projections are the final common path for the climbing fibre response. Indeed, the present HRP study showed that a WGA–HRP injection into the cerebellar cortical areas, from which climbing as well as mossy fibre responses are recorded on stimulation of the LS area, resulted in neuronal labelling in the inferior olive. As for cerebro-olivary paths, both direct and indirect projections are possible. Indirect projections appear more likely to transmit the LS-induced climbing fibre response for the following reasons. First and foremost, a number of anatomical studies showed that the frontal, but not parietal cortical areas, project directly onto the inferior olive (Mizuno, Mochizuki, Akimoto, Matsushima & Sasaki, 1973; Bishop *et al.* 1976; Saint-Cyr, 1983). The present HRP study confirmed the absence of cortico-olivary projections from the LS area, a visual association area situated in the parietal cortex. Second, the LS-induced response, like the crown-induced one (Sasaki *et al.* 1975), is more unstable and has longer latency than the motor cortex-induced response. So far, some indirect cortico-olivary pathways originating from cortical areas other than the LS area have been reported. Anatomical studies have revealed a motor cortex–Darkschewitsch nucleus–olivary projection (Nakamura, Kitao & Okayama, 1983), and a motor cortex–pretectum–olivary projection (Kitao, Nakamura & Okayama, 1983). The parieto-rubro-olivary pathway was reported to be most likely responsible for transmission of the crown-induced climbing fibre response (Oka, Jinnai & Yamamoto, 1979). Whether or not these pathways also convey the LS-induced response is unanswered.

*Functional significance*

There are various cerebellar cortical areas to which visual information has access. Different sorts of visual information appear to reach different parts of these areas. Lateral parts of the cerebellar cortex are provided with information processed in the visual cortex, while flocculo-nodular parts receive that processed in lower-order visual centres such as the pretectum (Takeda & Maekawa, 1976; Maekawa *et al.* 1981) or superior colliculus (Kawamura & Brodal, 1973). In posterior vermal parts, cortically and non-cortically processed information both arrive (Brodal, 1981). Recently the paraflocculus has been reported to be a primary receiving lobule of the cerebellum for inputs from the visual cortices in rats (Burne & Woodward, 1983). In so far as their report claims that the paraflocculus is not the unique, but merely one of the major recipient areas, their finding in rats and ours in cats agree with each other.

LS-induced mossy fibre responses are distributed mainly in the posterior and lateral, rather than the anterior, parts of the cerebellar cortex. This is generally

similar to the distribution of mossy fibre responses elicited by stimulation of the crown part (Sasaki *et al.* 1975), except that LS stimulation alone evoked large responses in the posterior vermal part, i.e. lobules VI–VIII. These lobules have been reported to respond to visual stimulation or electrical stimulation of the optic nerve (Buchtel, Iosif, Marchesi, Provini & Strata, 1972; Donaldson & Hawthorne, 1979). Since the LS area is a visual association area, it is conceivable that the cerebellar cortical areas that are related to inputs from the optic nerve and association cortex, respectively, are both responsive to LS stimulation.

It is possible that a message for motion, initiated or simply relayed in the visual cortex, may be transmitted to the motor cortex by way of cerebro-cerebellar loops, i.e. visual cortices → lateral part of the cerebellar cortex → lateral or interpositus cerebellar nucleus or both → ventroanterior–ventrolateral nuclear complex of the thalamus → motor cortex. Unlike the loop originating from the primary visual cortices to the motor cortex (Baker *et al.* 1976), the loop starting from the LS area to the motor cortex has a branch that comes back to the origin, i.e. the LS area, as shown in our previous finding that cerebellar lateral and interpositus nuclei project onto the medial bank of the LS area (Kawaguchi *et al.* 1983). This branch closes the loop, which might enable the LS area to perform a highly associative visual function that the primary visual cortex cannot carry out, such as lens accommodation (Bando, Yamamoto & Tsukahara, 1984) or perception of approaching objects (Toyama & Kozasa, 1982).

The distribution of inputs from the cerebellum and outputs thereto coincides well within the LS area. Our previous finding (Kawaguchi *et al.* 1983) showed that cerebellar nuclei project onto the rostral, but not caudal, half of the medial bank of the LS area. Correspondingly, the thalamic ventroanterior–ventrolateral complex, which receives dense cerebellofugal fibres (Sugimoto, Mizuno & Itoh, 1981), projects onto the rostral part of the medial bank of the LS area, but not to the caudal part or the lateral bank (Kato, Kawaguchi & Miyata, 1986*b*). These findings agree with the result of the HRP study (Albus *et al.* 1981) that the rostral part of the medial bank contains many more cortico-pontine neurones than the lateral bank or the caudal part of the medial bank of the LS area.

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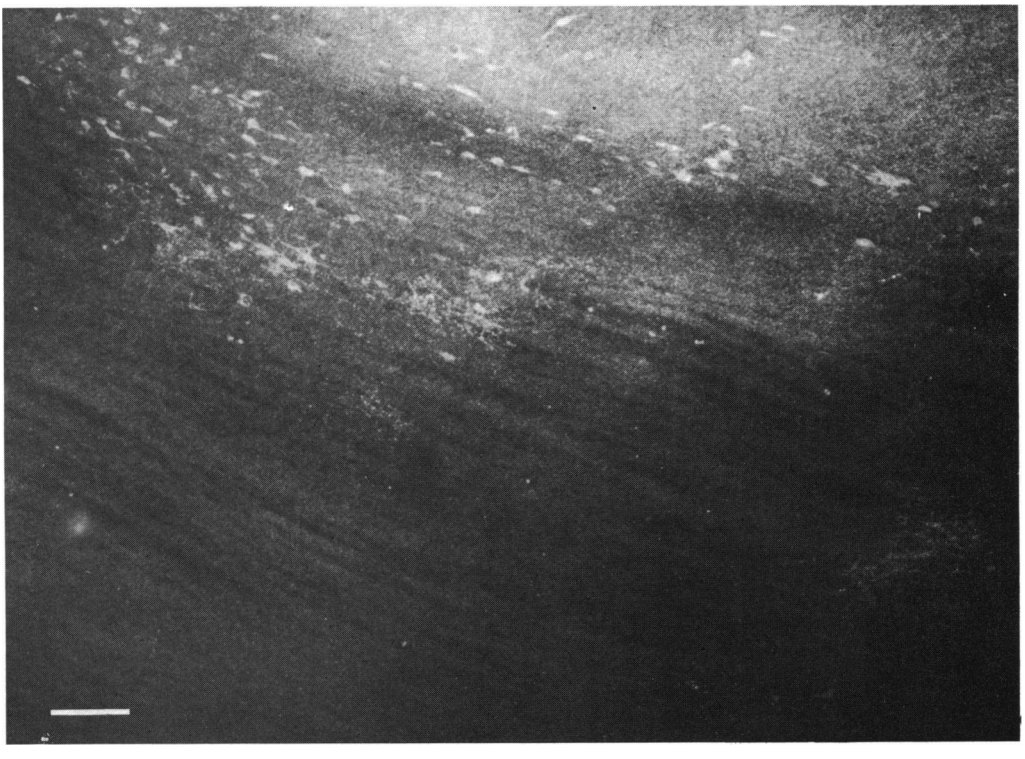

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EXPLANATION OF PLATE

A photomicrograph illustrating labelled cortico-pontine terminals and ponto-cerebellar neurones, which are, in part, overlapping. In the upper part of the Plate, a part of the pyramidal tract is seen as an artifact, probably due to insufficient dehydration during the HRP histochemical procedure. Scale bar, 0·2 mm.