J. Neurol. Neurosurg. Psychiat., 1966, 29, 196

An experimental study of the F wave in the baboon

J. G. McLEOD AND SHIRLEY H. WRAY

From the Institute of Neurology, Queen Square, London

Magladery and McDougal (1950) showed in man that when the ulnar nerve is stimulated at the wrist and the muscle action potential recorded from the hypothenar muscles, the direct response or M wave is followed by a small deflection, the F wave. These authors considered that the F wave was a reflex response due to stimulation of afferent fibres in the peripheral nerve, but Dawson and Merton (1956) produced evidence that it resulted from the discharge of motor neurones in the spinal cord following their antidromic activation by centripetal volleys. Additional evidence for this view has recently been provided by Thorne (1965). Gassel and Wiesendanger (1965) found a wave with certain characteristics of the F wave in the deafferented foot muscles of cats, and concluded that antidromic activation of motor neurones contributed to its production.

Since the measurement of the latency of the F wave may be of diagnostic value in the investigation of human neuropathy, it is important to understand the physiological mechanism by which it is produced. The present paper describes the results of experiments on baboons, which were selected as experimental animals because of the close anatomical resemblance of their forelimbs to those of man. In these animals, action potentials with the characteristics of F waves were recorded from the small muscles of the hand after complete deafferentation of the forelimb, and from these studies it is concluded that the main component of the F wave results from the antidromic activation of motor neurones in the spinal cord.

METHODS

Experiments were performed on four adult female baboons (*Papio anubis*) weighing 7 to 12 kg. Details of the operative procedures are given elsewhere (Wray, 1966).

A subperiosteal hemilaminectomy was performed on the left side from the level of C.4 to T.2. In all animals (baboons O, R, V, and W) the dorsal roots from segments C.5 to T.2 were cut extradurally at their zone of entry into the spinal cord with the aid of an operating microscope. Previous work (Wray, 1966) had established that division of these six roots of the brachial plexus was necessary to ensure complete deafferentation of the hand. In two of the animals (baboons O and R) the dorsal root ganglia themselves were excised from C.5 to T.2 inclusive; these animals were subsequently used for additional studies which will be reported elsewhere (McLeod and Wray, 1966).

Electrophysiological studies were carried out on the median and ulnar nerves of both forearms, at intervals which ranged from six to 28 days post-operatively. Details of the normal velocity of the fastest conducting fibres in the median and ulnar nerves of the baboon are reported elsewhere (McLeod and Wray, 1966). The animals were anaesthetised with phencyclidine hydrochloride (2 mg./kg.) and promazine hydrochloride (1 mg./kg.), and the deep intramuscular temperature of the forearm, measured with a thermistor, was maintained at 37-39°C. throughout the examination.

Action potentials were recorded from the thenar and hypothenar muscles with intramuscular needle electrodes on stimulation of the median and ulnar nerves at the wrist and elbow; a remote reference electrode was inserted into the distal part of the nearest digit. The stimulating electrodes were pairs of needle electrodes inserted subcutaneously close to the nerves, and an earth electrode was positioned between the stimulating and recording sites. The electrode arrangement in the case of the ulnar nerve is shown in Figure 1.

The stimulus was a condenser discharge with a time-constant of 100 μsec. derived from a thyratron stimulator and delivered through a 1:1 isolating transformer. The recording electrodes were connected to an R-C coupled amplifier, and the responses were displayed on the upper beam of a cathode-ray oscilloscope, the time-scale being displayed on the lower beam. Photographic records were taken on 35 mm. film, and several successive traces were taken on each frame by moving the sweep vertically

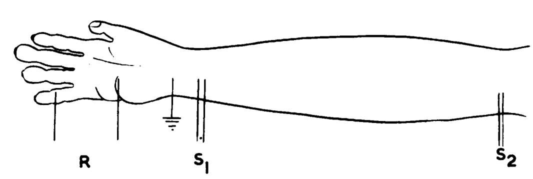

FIG. 1. *Position of stimulating (S) and recording (R) electrodes in case of ulnar nerve.*

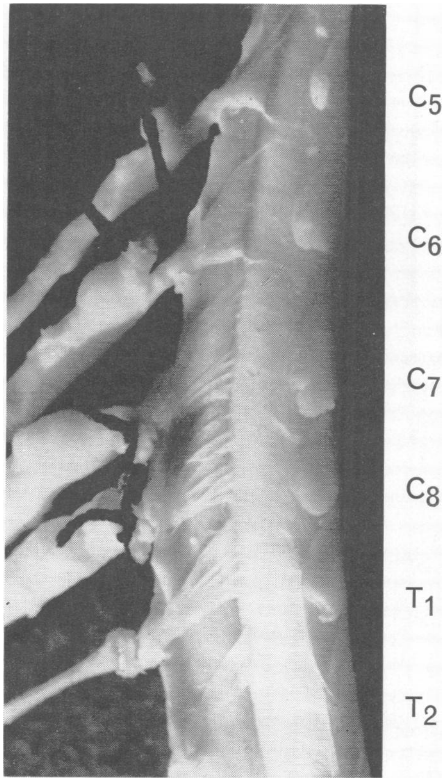

FIG. 2. *The left side of the cervical and thoracic spinal cord of baboon W. The dura has been opened to show the ventral roots. The distal parts of the dorsal roots with their ganglia are drawn forward. The proximal stumps of the divided dorsal roots can be seen on the right.*

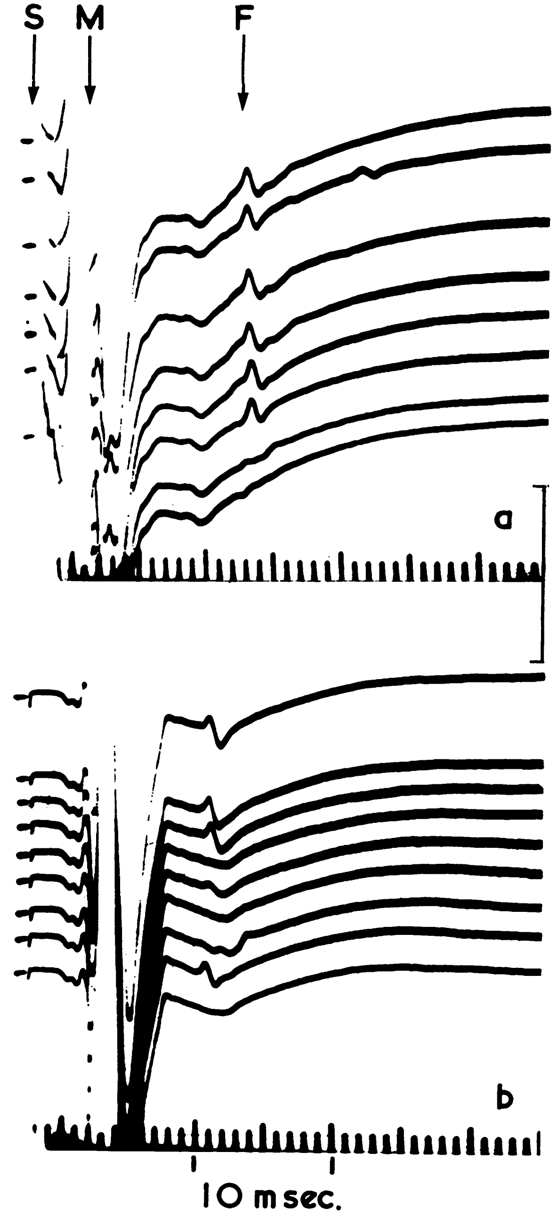

FIG. 3. *Baboon W. F waves recorded from hypothenar muscles of deafferented forelimb on stimulation of the ulnar nerve at level of* (a) *wrist and* (b) *elbow. Calibration 1 millivolt.*

between each stimulus. For analysis of records, the film was placed in an enlarger and measurements were made on the projected traces. Latencies were measured to the onset of the first negative deflection of the action potential.

After completion of the electrophysiological studies, the animals were killed at intervals ranging from six to 65 days after operation. In all animals the spinal cord and nerve roots were removed and it was confirmed that C.5, C.6, C.7, C.8, T.1, and T.2 dorsal roots had been completely divided. Figure 2 shows the left side of the cervical and thoracic spinal cord and nerve roots of baboon W.

RESULTS

In all animals studied, late waves following the direct response or M wave were recorded from the small muscles of the hand of the deafferented limbs on stimulating the median and ulnar nerves. These late waves, which were usually about 5% of the amplitude of the M response, had the characteristic features of F waves (Magladery and McDougal, 1950). They were present on supramaximal stimulation; they were variable in their occurrence and did not appear regularly after each stimulus; they were sometimes variable in latency and waveform; their latency shortened when the stimulus was applied at a more proximal site in the forearm, indicating that conduction was initially in a proximal direction.

Figure 3 shows responses recorded from the hypothenar muscles on stimulating the ulnar nerve of the deafferented limb of one animal (baboon W). When the ulnar nerve was stimulated at the wrist (Fig. 3a), the M response was followed by an F wave of latency 15·2 msec., the measurements being made to the first deflection of the response with the shortest latency. When the stimulating cathode was moved 16·5 cm. proximally to the elbow (Fig. 3b), the latency of the F wave shortened to 12·8 msec. The conduction velocity of the volley proceeding in a proximal direction in the forearm was 69 m./sec. This is slightly less than the conduction velocity of volleys in the fastest conducting fibres in the forearm giving rise to the direct response, which was found to be 75 m./sec. It is possible also to make an approximate calculation of the conduction velocity of volleys responsible for the production of the F wave over their complete pathway to the spinal cord and back to the periphery. In this animal the distance from wrist to the level of the C.7 vertebra was 48 cm.; after subtraction of the conduction time of 2·0 msec. from wrist to hypothenar muscles, the conduction time of the volley from wrist to spinal cord and back to wrist was 13·2 msec. From these figures the conduction velocity was calculated to be 73 m./sec. Table I summarizes the results from all the animals studied. In order to be sure that the F waves recorded from the deafferented limbs were not due to repetitive firing in peripheral nerves, it was demonstrated that they were abolished by cutting the nerve proximal to the stimulating electrodes. Figure 4 shows the results of an experiment in which F waves were recorded from the thenar muscles on stimulating the median nerve at the wrist (Fig. 4a) and elbow (Fig. 4b), but were abolished by transection of the median nerve in the upper arm (Fig. 4c).

TABLE I

Animal	*Nerve*	*Conduction Velocity of Volleys Causing F Wave (m./sec.)*		*Conduction Velocity of Volleys Causing M Wave (m./sec.)*
		Wrist-Elbow	*Wrist-Wrist*	
O	Median	61	70	76
	Ulnar	63	71	72
R	Median	70	83	76
	Ulnar	70	73	77
V	Ulnar	70	76	77
W	Median	67	75	67
	Ulnar	69	73	75
Mean[1]		67·1 ± 3·4	74·4 ± 4·0	74·3 ± 3·3

[1]Mean values are expressed with standard deviations.

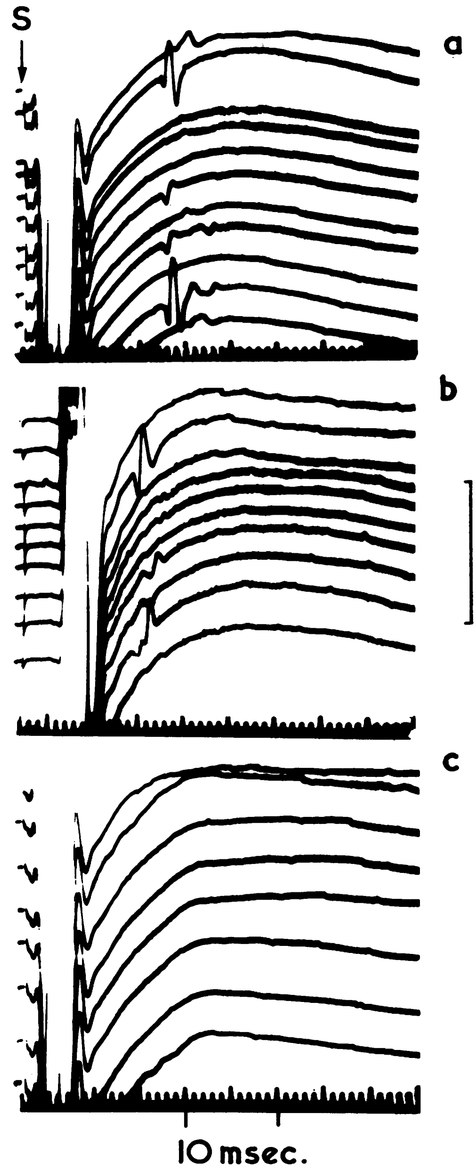

FIG. 4. *Baboon W. F waves recorded from thenar muscles of deafferented forelimb on stimulating the median nerve at level of* (a) *wrist and* (b) *elbow. After transection of the median nerve in the upper arm, F waves were abolished* (c). *Calibration* 1 *millivolt.*

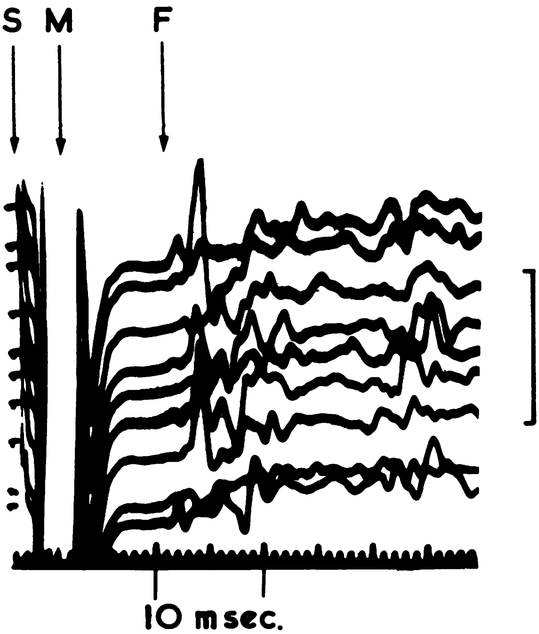

FIG. 5. *Baboon R. F waves recorded from hypothenar muscles of control limb on stimulating ulnar nerve at level of wrist. Calibration 2 millivolts.*

When responses recorded from the small hand muscles of the control side are compared with those recorded from the deafferented limb, it is apparent that although F waves are clearly distinguishable on the control side they are accompanied by irregular, low-voltage activity which is not seen after deafferentation (Fig. 5). This activity, which corresponds to the late component of Gassel and Wiesendanger (1965), was abolished by cutting the nerve proximal to the stimulating electrodes and may be presumed to result from the stimulation of polysynaptic spinal reflexes.

DISCUSSION

It has been shown in this investigation on baboons that F waves can be recorded from the small muscles of the hand after complete deafferentation of the forelimb. Renshaw (1941) demonstrated that centrifugal discharges could be initiated in motor axons by antidromic volleys, and it is most probable, as Dawson and Merton (1956) postulated, that the F wave is produced in this way. Although peripheral branching of motor fibres occurs (Eccles and Sherrington, 1930; Wray, 1966) the F wave is unlikely to be caused by the stimulation of axon reflexes, since Fullerton and Gilliatt (1965) found that they could only be elicited when pathological conditions affected the peripheral nerves and, moreover, that they were abolished by strong stimuli; this was not the case in the present experiments. Another possibility to be considered is that ephaptic connexions may have developed post-operatively between the cut dorsal and the ventral roots, but this could not have been the mechanism responsible for the production of the F waves as they were recorded in two animals 28 days after dorsal root ganglia had been removed and when degeneration of the afferent fibres had occurred.

The conduction velocity of the volleys proceeding in a proximal direction in the forearm was found to be slightly less than that of orthodromic volleys in the fastest conducting fibres which gave rise to the direct response. Magladery and McDougal (1950) found that this was also the case in man, and based their conclusion that the F wave was due to stimulation of polysynaptic reflexes partly on this evidence. The probable explanation of the discrepancy between the conduction velocity of the antidromic volleys giving rise to the F wave, and the conduction velocity of volleys in the fastest conducting fibres which cause the direct M response, is that since only some of the motor neurones are fired by antidromic impulses, the F wave is not necessarily produced by volleys in the fastest conducting motor fibres. It is interesting that in man F waves can sometimes be elicited by a weak shock which only activates a single motor unit; in these circumstances afferent and efferent conductions have been shown to be identical (Thorne, 1965). In our own animals conduction velocity for the F wave was slightly higher when determined over the whole pathway to the spinal cord and back to the periphery than when estimated for the forearm alone. This may be due to a slightly greater conduction velocity in the proximal than in the distal part of the long motor nerve fibres of the limbs (Trojaborg, 1964).

These studies lend support to the view first put forward by Dawson and Merton (1956) that the F wave in man is chiefly the result of antidromic stimulation of motor neurones in the spinal cord. The results of the experiments are in agreement with the findings in cats reported by Gassel and Wiesendanger (1965), and indicate that F waves are not dependent upon the activation of spinal cord reflexes, as suggested by Magladery and McDougal (1950) and Hagbarth (1962).

SUMMARY

On stimulation of the median and ulnar nerves of the baboon, recordings from the small hand muscles show a late response which is thought to be analogous

to the F wave originally described by Magladery and McDougal in man. In the baboon this late response persists after deafferentation of the forelimb. It is presumed to be due to antidromic activation of motor neurones in the spinal cord.

We wish to thank Professor Gilliatt for helpful criticism and advice. The work was carried out during the tenure by J. G. McLeod of a Nuffield Foundation Dominion travelling fellowship. A personal grant to S. H. Wray from the Medical Research Council is gratefully acknowledged. We also wish to thank the Polio Research Fund for their support of the work.

REFERENCES

Dawson, G. D., and Merton, P. A. (1956). 'Recurrent' discharges from motoneurones. 2e Congr. int. Physiol., Bruxelles, Abstr. comm., pp. 221-222.

Eccles, J. C., and Sherrington, C. S. (1930). Numbers and contraction-values of individual motor-units examined in some muscles of the limb. *Proc. Roy. Soc. B.*, **106**, 326-357.

Fullerton, P. M., and Gilliatt, R. W. (1965). Axon reflexes in human motor nerve fibres. *J. Neurol. Neurosurg. Psychiat.*, **28**, 1-11.

Gassel, M. M., and Wiesendanger, M. (1965). Recurrent and reflex discharges in plantar muscles of the cat. *Acta physiol. scand.*, **65**, 138-142.

Hagbarth, K-E. (1962). Post-tetanic potentiation of myotatic reflexes in man. *J. Neurol. Neurosurg. Psychiat.*, **25**, 1-10.

Magladery, J. W., and McDougal, D. B. (1950). Electrophysiological studies of nerve and reflex activity in normal man. I. Identification of certain reflexes in the electromyogram and the conduction velocity of peripheral nerve fibres. *Bull. Johns Hopk. Hosp.*, **86**, 265-290.

McLeod, J. G., and Wray, S. H. (1966). In preparation.

Renshaw, B. (1941). Influence of discharge of motoneurons upon excitation of neighboring motoneurons. *J. Neurophysiol.*, **4**, 167-183.

Thorne, J. (1965). Central responses to electrical activation of the peripheral nerves supplying the intrinsic hand muscles. *J. Neurol. Neurosurg. Psychiat.*, **28**, 482-495.

Trojaborg, W. (1964). Motor nerve conduction velocities in normal subjects with particular reference to the conduction in proximal and distal segments of median and ulnar nerve. *Electroenceph. clin. Neurophysiol.*, **17**, 314-321.

Wray, S. H. (1966). Anatomical studies on certain muscle nerves of primates. Thesis to be submitted for the degree of Ph.D. in the University of London.