Initiation of a Goal-directed Movement in the Monkey

Role of the Cerebellar Dentate Nucleus

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Summary. The participation of the dentate nucleus (DN) in the initiation of a voluntary movement was investigated in five baboons (Papio papio). In these experiments, we have analyzed the effects of excluding the DN on the latency (reaction time, RT) of a learned goal-directed movement.

Two techniques were used for excluding the DN. In three animals, the structure was cooled with a probe, stereotaxically implanted on the side ipsilateral to the active hand. In two others, a partial electrolytic destruction of the DN ipsilateral to the operant hand was undertaken. In one further animal, both DNs were destroyed electrolytically.

A comparison was made of the effect of DN inactivation on the latency of stereotyped goal-directed movements of constant amplitude and direction, and of goal-directed movements whose amplitude and/or direction were varied in random fashion.

The exclusion of DN brought about a prolongation of RTs in all animals. This prolongation was not accentuated by variation of different characteristics (amplitude and/or direction) of the impending goal-directed movement.

A recovery of the RTs to their prelesion values was observed after irreversible unilateral DN lesion, but not so easily after bilateral destruction.

These results show that in the monkey DN is concerned with the initiation of a goal-directed movement, but is not critically implicated in the encoding of direction and amplitude parameters. These findings are discussed in view of the role that is usually attributed to the neocerebellum in programming voluntary movements.

Key words: Dentate nucleus – Reaction time – Goal-directed movement initiation – Cooling – Lesion – Monkey

The delay in initiation of muscular contraction is one of the fundamental symptoms of neocerebellar lesions (Holmes 1917, 1939; Fulton and Dow 1937), since it appears to be an underlying cause of many other subsequent disturbances (Sasaki 1979). These clinical results, along with anatomical and physiological findings on the existence of cerebello-cortical interrelations (Allen and Tsukahara 1974), have led some workers to attribute a critical role to the cerebellum in the initiation of voluntary movements (Evarts and Thach 1969; Brooks 1979b), and particularly ballistic movements (Kornhuber 1971).

The cerebellar dentate nucleus exhibits a prominent development in phylogeny (Verdie 1976; Chan-Palay 1977; Sasaki 1979). In humans it accounts for 90% of the intracerebellar neurones (Heidary and Tomasch 1969) and constitutes the principal output of the cerebellar hemispheres. Its development parallels that of the primate motor cortical hand area and coincides with the appearance of manipulatory ability (Sasaki 1979). Electrophysiological (Grimm and Rushmer 1974; Robertson and Grimm 1975; Allen et al. 1978; Thach 1978) and anatomical (Chan-Palay 1977; Thach and Jones 1979) studies have demonstrated the complexity of its organization. Experimental data suggests that this nucleus participates in movement generation, with units altering their firing rate slightly before those in the motor cortex, prior to the onset of movement (Thach 1975). In addition, Meyer-Lohmann et al. (1977) have shown that cooling the interpositus and dentate nuclei of the cerebellum causes a prolongation of the latency of flexion-
extension movements of the elbow. While these observations suggest that the dentate nucleus is concerned in the initiation of voluntary movement, it is more difficult to pinpoint the precise manner in which this may occur. The existence of a repertory of motor programs within the central nervous system is at present not questioned (Keele 1968; Paillard and Beaubaton 1978; Brooks 1979a); such central program may intervene in goal-directed limb movements, as shown by the persistence of these movements in deafferented monkeys (Taub et al. 1975; Polit and Bizzi 1979). Within this context, important questions are whether the dentate nucleus merely releases motor programs elaborated in other structures, or whether it intervenes more directly in motor preparation, that is to say, in the elaboration of such programs (Massion and Sasaki 1979).

The observations of Thach (1978) and Strick (1979) suggest that the dentate nucleus is concerned with specifying the directional parameters of movements and therefore plays a critical role in programming these parameters; such programming appears necessary for the execution of goal-directed movements (Paillard 1980). In the experiments reported here, the role of the dentate nucleus in the initiation of goal-directed movements in the monkey was analyzed by using a task that involved pointing a finger at a luminous target. More precisely, the effect of suppressing dentate control on the latency of movements (with variable amplitude and/or direction) was studied.

Recovery phenomena have frequently been reported after various lesions of the dentate nucleus (Carrea and Mettler 1947; Growdon et al. 1967; Zervas et al. 1967; Goldberger and Growdon 1973; Poirier et al. 1974), but they mainly concerned disorders of movement execution, such as dyskinesias and intention tremor. No quantitative studies of the recovery of movement initiation following destruction of the dentate nucleus have been carried out. Yet one purpose of the present study was to determine the occurrence and rate of any functional recovery from impairment of initiation observed after unilateral or bilateral dentate lesion.

Preliminary accounts of these results have been published (Beaubaton et al. 1978; Trouche et al. 1979).

Methods

Material

The experiments were carried out on five adult baboons (Papio papio) weighing between 8 and 10 kg. Three of the animals (LIL, PEN, BER) had cryoprobes chronically implanted in DN. The other two (NEF, BAS) underwent unilaterally on electrolytic lesions, followed in one case (BAS) by a lesion in the contralateral DN.

Techniques for Exclusion of the Dentate Nucleus

Implantation of thermodes and electrocoagulation were carried out under nembutal (35 mg/kg I.V.) and under aseptic surgical conditions. DN was located stereotaxically using the atlas of Riche et al. (1971) and electrophysiologically by recording its spontaneous activity. The latter is characterized by fast, high-amplitude activity, contrasting with the scarce, low-amplitude activity of the white matter.

The cryoprobe was implanted ipsilateral to the operant hand. The probes and the cooling device were of the type developed and described by Dondey et al. (1962) and Benita (1972). The external diameter of the probe did not exceed 1.1 mm. The tip was insulated by a deposit of gold to avoid too fast a destruction of the nervous tissue (Schmied et al. 1979). A copper-constantan thermocouple fixed to the tip of the probe allowed continuous temperature control. The probe was introduced in the lateral part of the nucleus, thus avoiding a possible spread of cooling to nucleus interpositus. The probe was held by a special support (Massarino et al. 1979a) fixed to the skull by a series of screws cemented into the bone.

The cooling temperature was chosen using previous observations by Benita (1972) on the effects of local cooling upon nervous transmission. In our experiments, two cooling temperatures were used: one tip temperature at 0°C, and another at 25°C; this latter has no effect on nervous transmission any longer but still elicits the mechanical disturbances due to the cooling device itself, to freon circulation and to vibration of the system.

Electrolytic DN lesions were performed by passing a DC current (1.5 mA for 15 s), using against a broad reference electrode. Twenty partially overlapping coagulation points were made.

The recording sessions began 5 days after probe implantation or electrolytic lesion.

Experimental Apparatus

In each session, the baboon was placed in a work cage (Fig. 1) situated in a dimly lighted and soundproof room. A cage of the type designed and described by Trevarthen (1972) was adapted to the requirements of the present experiment. An apparatus for partial head restraint consisted of a series of grooved horizontal and vertical plates. The incompletely immobilized head was fixed in a mask placed in the front part of the cage, facing the pointing board. This ensemble made it possible to standardize the animal posture, and easy to connect the thermode with the tubes of the cooling apparatus.

For successful trials, reinforcement consisted of apple juice (2 ml), delivered directly to the mask in which the animal's muzzle was placed.

Facing the cage, a vertical, 60 cm × 45 cm panel was placed about 20 cm away from the animal. On its lower part there was a lever, 4 cm × 1.5 cm, that opened a microswitch when pressed with a minimal force of 30 g. On the upper part of the board was a square screen on which visual stimuli were presented. These stimuli consisted of LEDs (5 mm in diameter) with a luminosity of 500 μcd and were used as pointing targets. The screen consisted of a printed circuit in a 5 mm grid, which registered the spatial coordinates of the first contact of the finger with the board.

The programmed sequences and reinforcement were controlled on-line by a microprocessor system (MOTOROLA) which