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THALAMIC UNIT ACTIVITY AND DELAYED ALTERNATION PERFORMANCE IN THE MONKEY

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Abstract. Single unit activity was recorded from the thalamus of rhesus monkeys while they performed a delayed-alternation bar-pressing task. Nine units in the dorsomedial nucleus of the thalamus were activated prior to the lever presses of the contralateral hand, as indicated by an EMG of the triceps brachii muscle. In this same region, no units were found that became active during the delay period. In contrast, three units in the ventralis lateralis nucleus of the thalamus were activated simultaneously with lever presses. The results indicate that the dorsomedial nucleus may be involved with the initiation of lever pressing responses in the delayed alternation task. The thalamic units studied here were compared with those observed previously in the prefrontal cortex and the caudate nucleus.

The present study is a continuation of a neurophysiological approach toward understanding the functions of the prefrontal cortex in the rhesus monkey. Accordingly, we began by recording single unit activity from the prefrontal cortex of the unanesthetized monkey while the monkey performed a task for which this cortex is important. The task chosen was a slight modification of the classical spatial delayed-alternation test. For the purposes of this study, the monkey was trained to alternately press levers while seated in a restraining chair rather than to push plaques or uncover foodwells in a Wisconsin General Test Apparatus. Our observations that the activity of units recorded from the cortex in the middle third of the principal sulcus was correlated with performance in different phases of the alternation task support the recent findings of Butters and Pandya (1969) that this mid-principalis region is the cortical focus for performance on spatial delayed-response tasks.

Following the publication of our first paper on this topic (Kubota and Niki 1971), we pursued this line of investigation by recording from structures, such as the head of the caudate nucleus and the dorsomedial nucleus of the thalamus, that are intimately related to the prefrontal cortex. The results of our investigations on the caudate nucleus, and on the medial orbito-frontal cortex as well, will soon be published (Niki et al., in press). In this presentation, therefore, I should rather like to concentrate on the studies of the thalamic neurons and to discuss problems arising from this and the previous studies.

It is well known that lesions of the dorsolateral prefrontal cortex in the monkey result in severe retrograde degeneration homolaterally in the lateral parvocellular portion of the thalamic nucleus, n. medialis dorsalis (Walker 1940, Blum 1952, Pribram et al. 1953, Akert 1964, Nauta 1964). It might be supposed, then, that the loss of these cells in the thalamus might contribute at least partialy to the deficits on delayed-response tasks seen after dorsolateral prefrontal ablations. However, behavioral studies on monkeys with bilateral lesions of the dorsomedial nucleus have failed to reveal consistent prefrontal dificits. Chow (1954), for example, reported that delayed-response performance was spared in monkeys with electrolytic lesions in this nucleus. Likewise, Peters, Rosvold and Mirsky (1956) destroyed as much as 80% of the dorsomedial nucleus bilaterally and found no significant correlation between alternation performance and the degree of damage to this thalamic nucleus. They concluded that the loss of cells in n. medials dorsalis was not responsible for the inability of prefrontal animals to perform delayed response. Schulman (1964), on the other hand, suggested that the negative results obtained by Chow (1954) and Peters et al. (1956) could be due to an incomplete destruction of the nucleus and, to confirm this suggestion, he made extensive bilateral lesions of the dorsomedial nuclei by introducing a radioactive substance into them. He observed severe and enduring impairments in delayed-response performance. The findings led him to propose that a small remnant of the dorsomedial nucleus may suffice for normal delayed-response performance because surviving neurons could behave in a compensatory fashion. His results have not yet been confirmed and are subject to the criticism that the lesions were too large to attribute the behavioral effects solely to the dorsomedial nucleus. This report, however, provides evidence that the dorsomedial nucleus may indeed be involved in the performance of spatial delayed alternation (Kubota et al. 1971*ab*).

The experimental arrangements for this study were the same as those reported previously (Kubota and Niki 1971). As illustrated in Fig. 1, the monkey was seated in a primate chair and his head was tightly fixed to

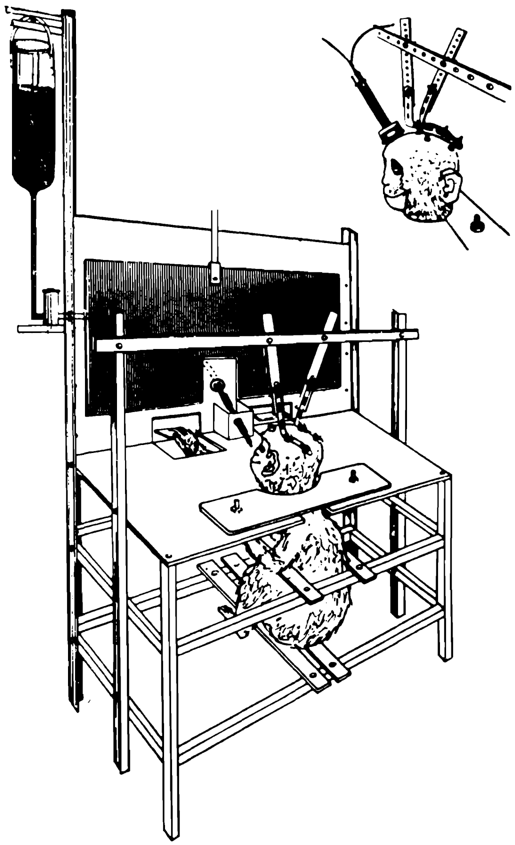

Fig. 1. A monkey in the primate chair. His head is tightly fixed to the chair. The monkey reached the levers by stretching his arm through rectangular holes in the horizontal plexiglas plate. Juice reward was delivered through a solenoid valve from the resevoir to the left. Access to the levers was prevented during delay periods by lowering the opaque screen shown as a vertically lined panel. Details of the head restraint and micromanipulator attachment are shown at the upper right. (From Kubota and Niki 1971.)

the frames of the chair. He could obtain a small quantity of juice as a reward for correct responses from a tube situated directly in front of him. An opaque screen placed in front of the monkey could be raised and lowered manually. Between the screen and monkey were there two square holes through which the monkey could stretch his arm to reach one or the other of the two levers situated on the other side of the screen. During the delay phase of the test, the screen remained lowered and the monkey could not see the levers.

A 4-channel FM magnetic tape recorder (R-400, TEAC) was used to record the single unit activity of the thalamus, the EMG of the triceps brachii muscle, the raising and lowering of the screen, and the occurrence of left and right lever presses, rewarded and unrewarded. The diagram in Fig. 2 illustrates how these events were fed into the logic modules and amplifier (MZ-3B, Nihon Kohden) and how they were transmitted to the tape recorder. Operational amplifiers (Analog Devices; Philbrick-Nexus) and modules (Molektron, Mitsubishi; K-series, DEC) were used.

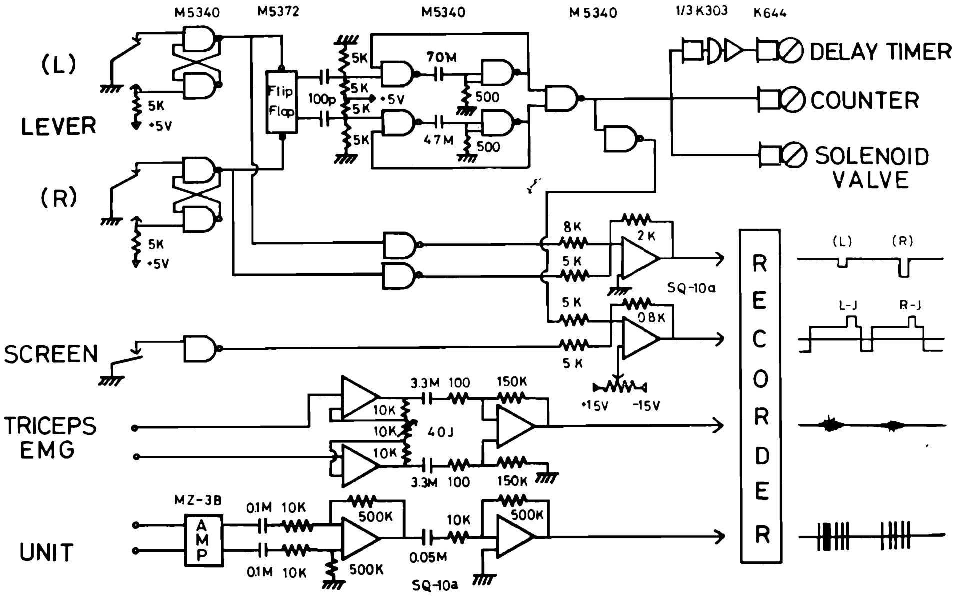

Fig. 2. Circuits to illustrate how lever presses, screen raising and lowering, triceps brachii EMG and unit activity are sampled, amplified, and logically sequenced. All of these activities were recorded by a 4-channel FM magnetic tape recorder. The duration of the lever press was recorded on channel 1. Signals were summated into an operational amplifier (SQ-10a, Nexus). The side of the press was detected by a difference in the size of the pulse. Juice delivery was recorded on channel 2. The raising of the screen was also recorded on channel 2. Channel 3 records EMGs after an appropriate amplification. Finally, the unit activity was recorded on channel 4. Signals of lever-press responses were fed to a Flip-Flop circuit and further connected to drivers of counters and a solenoid valve through monostable multivibrators. Thus alternate opening of the solenoid valve by left and right lever presses were accomplished.

Seven monkeys were trained on delayed alternation (DA), i.e., to alternate between pressing the right and left levers. The opaque screen was lowered after each response and then raised again after 5 sec. Thus, the animal had to remember after some delay which side he had responded to on the preceding trial. Once the monkeys had learned this, they could be tested, as the need arose, for their ability to alternate presses without interposing a screen or a delay. We call this version of the test simple alternation (SA). Some monkeys, then, were tested on both delayed alternation and simple alternation. In order to be sure that the results thus obtained on simple alternation were not influenced by the training on delayed alternation, two additional monkeys were trained from the beginning only on simple alternation.

After the experiments were completed, the monkeys were sacrificed and perfused with Ringer's solution followed by formalin. The brains were cut exactly parallel to the vertical plane in a stereotactic apparatus. Serial sections of the brain were made at 50 μ thickness and stained with cresyl violet.

The thalamic area was searched for units whose activity could be correlated with delayed alternation performance. The units were recorded from the side of the brain contralateral to the hand used. A tungsten microelectrode (2–10 MΩ) was moved upwards or downwards, recording the single unit activity in the thalamus as the monkey performed the task. The microelectrode penetrations covered the thalamic area rostrocaudally from A = +1.0 to +8.0, laterally from L = 0.0 to 7.0, and

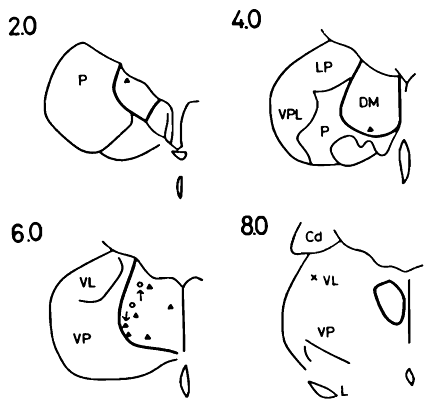

Fig. 3. Anatomical locations of the thalamic units whose activity was correlated with delayed alternation performance. The locations of the histologically identified units were projected onto the brain maps of Snider and Lee at four horizontal levels, as indicated to the left of each map in millimeters from AP = 0. Filled triangles represent E units in the dorsomedial region. Open circles represent the units from a monkey trained only on the simple alternation task. These units were activated prior to the alternate lever presses. The three units in the ventralis lateralis area are indicated by a cross. Nomenclature: DM, n. dorsomedialis; LP, n. lateralis posterior; VL, n. ventralis lateralis; VPL, n. ventralis postero-lateralis; P, n. posterior. The activity of the unit indicated by a downwardly directed arrow above it is shown in Fig. 4. The activity of the unit with an upwardly directed arrow below it is shown in Fig. 8.

horizontally from H = 0.0 to 8.0. Each penetration was separated from every other penetration by 1 mm transversely or rostrocaudally at the dural surface. A special attempt was made to find units in the dorsomedial region. Out of 495 penetrations in 9 monkeys, only 12 units in 4 monkeys showed activity correlated with performance on delayed alternation. The locations of these units are indicated in Fig. 3. Nine of these units were located in the dorsomedial region of the thalamus (*A*) and the remaining three units were in the ventrolateral region (×). All of them exhibited an acceleration in the rate of firing when the monkey pressed the lever. Following the designation used in the previous study (Kubota and Niki 1971), these units would be categorized as dorsomedial thalamic E units. In contrast to the prefrontal units studied previously, none of the present units were activated during the delay phase of the alternation test. Thus, no D units (designation used in Kubota and Niki 1971) were found in the thalamus in the present study.

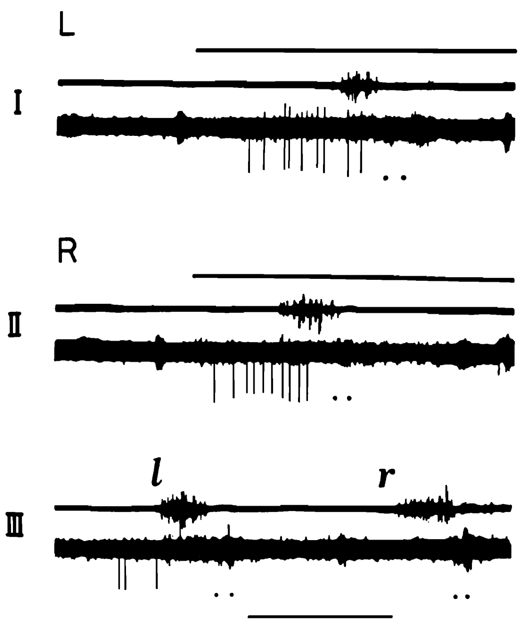

Fig. 4. E unit activity of the dorsomedial nucleus during delayed and simple alternation performance. *L* and *l* represent left-lever presses, and *R* and *r* right-lever presses. *I* and *II* represent the delayed task performance, and *III* the simple task performance. Bars above traces indicate the period during which the screen was raised. The EMG in the upper traces was from the triceps brachii muscle of the contralateral side. The unit in the lower traces was recorded at A = +6.0 at the laterocaudal portion of the dorsomedial nucleus. This is the same unit depicted in Fig. 3 by a downwardly directed arrow. The time bar indicates 0.5 sec. The two dots below the unit traces indicate depression of the lever.

An example of E unit activity recorded from the thalamus is presented in Fig. 4. The unit in question is the one shown in Fig. 3 by a triangle with a downward pointing arrow above it. The activity associated with a left-sided lever press (Fig. 4*I*) and that accompanying a right-sided press (Fig. 4*II*) are shown. For both, the unit activity (lower traces) appeared in no less than 100-150 msec after the opaque screen was raised and continued for several hundred milliseconds until the triceps EMG (upper traces) attained a maximal value, immediately preceding the lever press. The initiation of the lever press is indicated by the two dots below the pairs of traces. The E unit did not respond to a simple displacement of the screen and was activated only preceding the EMG activity, i.e., before the monkey pressed the levers. The activity of this unit was also studied in relation to performance on the simple alternation task in which the monkey alternately pressed the levers without the screen and without the delays. As may be seen in Fig. 4*III*, when a left-sided lever press occurred, 3 spikes appeared preceding the EMG while, when a right-sided press was made, no activity was observed. Compared with the activity obtained during delayed-response performance, during simple alternation performance, the number of spikes was less and the time interval from the first spike to EMG onset was shorter.

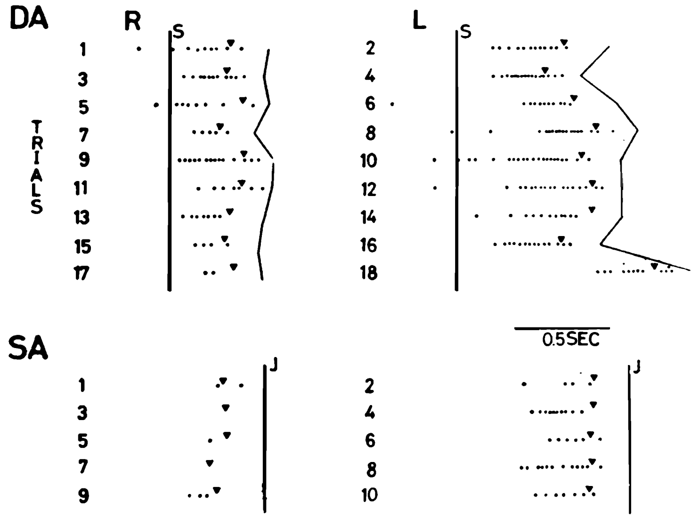

Fig. 5. Dot displays of thalamic E unit activity during delayed (DA) and simple alternation (SA) performance. Above: DA, lever presses were performed in the order indicated by numerals to the left of each display (odd numbers, right lever presses: even numbers, left presses). S indicates the raising of the screen. The inverted triangles indicate onset of the EMG activity. Thin vertical lines indicate onset of the juice reward. Below: SA, displays of a unit during a sequence similar to that described above. J indicates the onset of a lever press.

The variability of this same unit's activity over trials is shown in Fig. 5. The upper two diagrams contain the record of activity during performance on delayed alternation. The lever was pressed alternately in the order indicated by the numerals to the left of each line. The heavy line with a superscript S indicates the point in time when the screen was raised, the inverted triangles indicate the onset of the right triceps EMG, and the thin vertical lines signify the onset of a lever press. As the Figure shows, the latency from screen raising to the lever press was longer for responses on the left than for responses on the right. Similarly, the time from the first spike activity to EMG onset was longer (200 msec) on the left than on the right (100 msec). Finally, the latency from the raising of the screen to the spike activity could be as long as 120 msec on the left side or as short as 50 msec on the right side. The two lower diagrams in Fig. 5 indicate how the unit responded during performance on the simple alternation task. Spike activity again preceded the EMG. Compared with the spike activity during the delayed

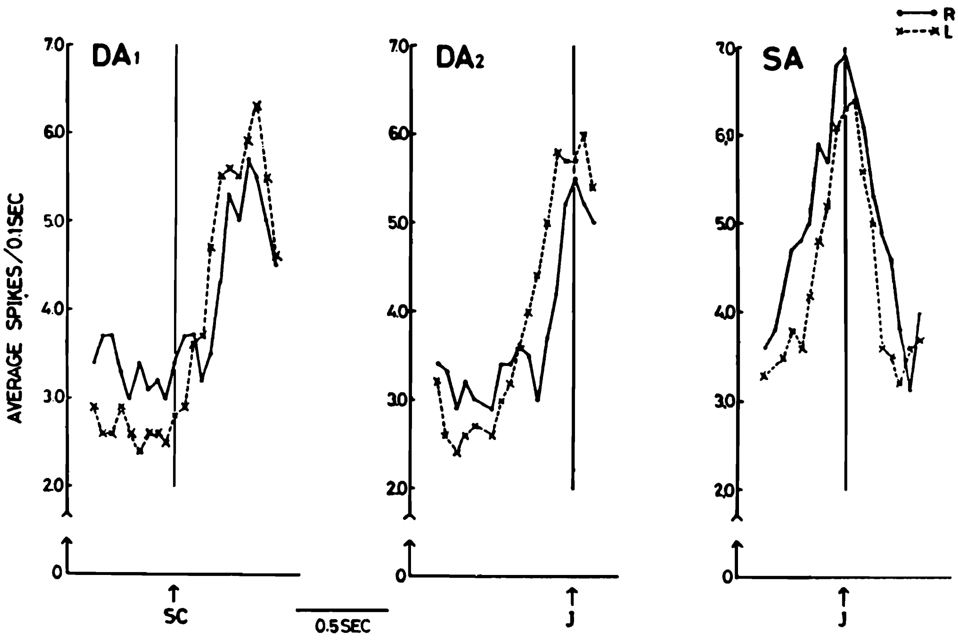

Fig. 6. Averaged time course of the discharge of a thalamic E unit which showed spontaneous activity preceeding the delay phase. Spikes were counted for successive 100 msec from 15 left and 15 right successive trials. DA1 illustrates the distribution when 0 time was screen raising (SC↑). DA2 illustrates the same data replotted with the onset of lever press taken as 0 time (J↑). SA illustrates the response during simple alternation performance. Each curve represents the average of 10 lever presses to the side in question using the lever press time (J↑) as 0 time. Time calibration, 0.5 sec.

alternation task, however, the activity on the simple task was less, and the time interval from the first spike to EMG onset was shorter. Further, on the simple task, fewer spikes were evoked for a right-sided press than for a left-sided press.

Spontaneous activity during delay periods was relatively regular (up to 30 Hz) in about half of the dorsomedial E units. This is illustrated in Fig. 6 in a record of averaged responses. The temporal sequence of this kind of unit activity was not different from that described above. Facilitation of the activity began 100–150 msec after the screen was raised (DA1 diagram) and the spike activity was highest at the time of a lever press (DA2 diagram). This increase in frequency with lever pressing was present during performance on the simple alternation task (SA diagram) as well as on the delayed alternation task.

The present results indicate that the units in the dorsomedial region may be concerned with the initiation of hand movements involved in pressing the levers. This conclusion is based on the fact that spike activity preceded EMG activity regardless of whether the monkey was performing the delayed or the simple version of alternation. Complementing these findings on animals tested on both versions of the task are the results from two monkeys that were trained only on the simple task. The activity of the two units indicated by open circles in Fig. 3 was correlated with voluntary lever pressing irrespective of the side pressed. Figure 8 presents an example of one of the units. Spikes

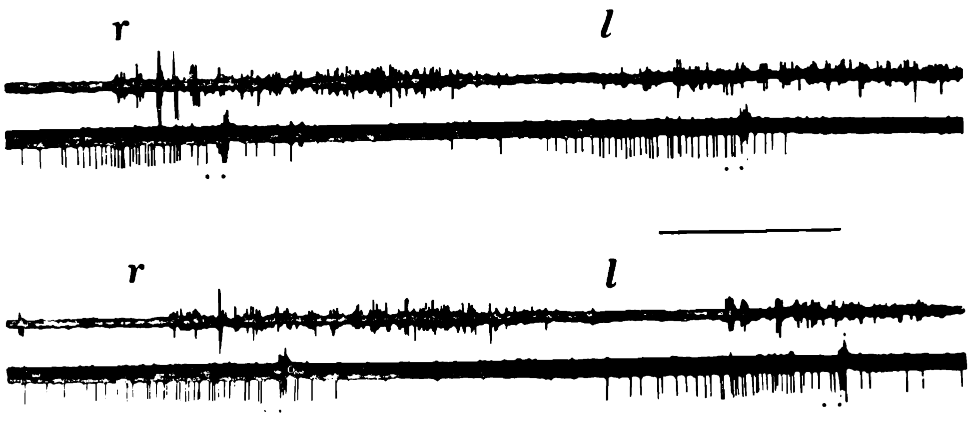

Fig. 8. Activity of a dorsomedial unit during performance on the simple alternation task. The pairs of records are continuous. Right (*r*) and left (*l*) levers were depressed alternately. Upper trace: EMG of the triceps brachii. Lower trace: a unit recorded from the dorsomedial nucleus. This unit is the one indicated by an open circle with an upwardly directed arrow below it in Fig. 3. The two dots below the pairs of traces indicate the time of depression of the lever. Time bar between records, 0.5 sec.

appeared preceding and during the early phases of the triceps EMG activity and stopped just after the lever press was made. The time from the first spike to EMG onset could exceed 200 msec. Although conclusions can not be drawn on the basis of so few cases, these data indicate a need for further investigation of the role of the dorsomedial nucleus in the initiation of voluntary hand movements.

In contrast to the units located in the dorsomedial nucleus, those in ventralis lateralis in one monkey showed an increase in its discharge rate almost simultaneously with the EMG activity during lever pressing.

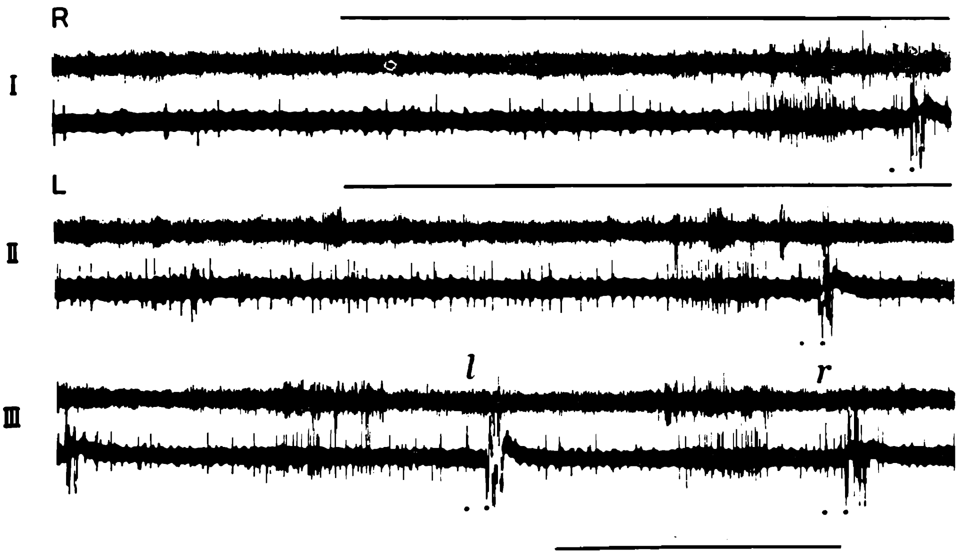

Fig. 9. Activity of a ventralis lateralis neuron during delayed alternation performance (*I-R*, right sided press; *II-L*, left sided press) and simple alternation performance (*III*, *l*—left sided press and *r*—right sided press). Horizontal bars above traces indicate the period during which the screen was raised. The upper trace of each pair is the EMG recorded from the triceps brachii muscle and the lower trace is activity of the unit in the ventralis lateralis. The location of this unit is indicated by a cross in Fig. 1. The two dots below the pairs of traces indicate onset of a lever press. Note that the unit is activated almost simultaneously with the EMG. Time, 0.5 sec.

As shown in Fig. 9, the sumultaneity of unit activity and the EMG occurred regardless of which test (simple or delayed alternation) was being performed and regardless of which lever (left or right) was depressed. Although there were only three such units, the close timing of unit and EMG activity was not observed in other thalamic areas, nor in the prefrontal cortex. This finding is consistent with those of Evarts (1970) who observed that unit activity in ventralis lateralis neurons occurred

TABLE I

Various latency values (in msec) during delayed and simple alternation performance in 11 samples[a]

(Delayed Task)		Sample size	Used hand	Laterality	1 Screen–Lever		2 Screen–Spike		3 Screen–EMG	
No	Units	(L, R)			L	R	L	R	L	R
DM1	5–21–A	(9, 4)	R	C	1156.0±261.8	1450.0±317.0	483.3 ±185.5	475.0±108.3	—	—
2	5–21–B	(7, 4)	R	C	1156.0±261.8	1450.0±317.0	454.3±197.8	667.5±255.4	—	—
3	8– 4–1	(7, 8)	R	C	822.9± 84.3	501.3± 33.0	184.5±111.2	120.0± 60.0	632.9 ± 82.3	328.8 ± 28.9
4	8–14–1	(10, 11)	L	C	642.0± 96.4	629.1± 82.7	(450)	(550)	282.0 ± 38.7	298.2 ± 58.1
5	8–18–2	(3, 5)	L	C	1200.0±332.4	860.0±134.6	(150)	(150)	613.3±273.4	452.0±129.2
6	8–21–1	(16, 14)	L	C	801.9±127.5	746.4± 129.0	(350)	(450)	650.6±107.9	555.0± 91.6
7	8–22	(4, 0)	L	C	882.5±119.9	—	(50)	—	577.5±162.1	—
8	8–18–3	(10, 7)	L	C	1008.0±216.2	738.0±220.0	511.3±193.5	296.7±111.2	540.0±245.9	388.0±137.8
9	5–08	(5, 5)	R	C	1054.0±254.5	1486.0±492.8	558.0±333.3	308.0±178.4	742.0±238.6	1132.0±401.4
	Mean±SD				969.0±181.0	982.6±383.7	438.3±131.4	373.4±185.0	576.9±133.9	525.7±283.8
VL 1	5–51–2	(12, 4)	R	C	1074.2±239.0	1108.8± 83.4	705.8±194.7	718.8± 31.0	718.8±174.1	728.8± 98.6
2	5–43–2	(4, 4)	R	C	870.6±372.2	1045.0±165.2	370.0±150.0	557.0±256.8	327.5± 87.6	482.5± 96.5
Data from previous study (cortex)					917 ±316	1197 ±597	324 ±167	303 ±101	484 ±210	581 ±226

a See legend to Fig. 7 for details.

TABLE II

Various time values (in msec) during delayed and simple alternation performances in 11 samples[a]

(Delayed Task)		Sample size	Used hand	Laterality	4 Spike–Lever		5 EMG–Lever		6 Spike–EMG	
No	Units	(L R)			L	R	L	R	L	R
OM1	5–21–A	(9, 4)	R	C	710.0± 99.6	1035.0±410.5	–	–	–	–
2	5–21–B	(7, 4)	R	C	780.0±267.1	772.5±512.7	–	–	–	–
3	8–04–1	(7, 8)	R	C	512.9±230.0	381.0± 68.6	190.0± 23.9	172.5± 19.2	351.4±173.3	208.8± 55.6
4	8–14–1	(10, 11)	L	C	(90)	(120)	364.0±108.3	330.9± 74.9	–	–
5	8–18–2	(3, 5)	L	C	(1150)	(710)	586.0± 59.1	418.0± 63.1	(560)	(300)
6	8–21–1	(16, 14)	L	C	(550)	(550)	151.3± 50.6	191.4± 78.0	(400)	(350)
7	8–22	(4, 0)	L	C	(830)	–	330.0± 69.6	–	(500)	–
8	8–18–3	(10, 7)	L	C	551.3±173.4	488.0±208.0	468.0± 92.1	390.0±153.4	136.7±209.7	210.0±166.5
9	5–08	(5, 5)	R	C	496.0±155.8	1005.0±482.3	312.0± 48.3	348.4±104.6	–	–
	Mean±SD				610.1±113.8	736.3±264.8	343.1±139.6	308.5± 93.9	244.1±107.4	209.4± 0.6
VL 1	5–51–2	(12, 4)	R	C	368.3±126.3	390.0± 55.2	355.4±135.6	380.0±102.3	13.3± 51.3	10.0± 82.4
2	5–43–2	(4, 4)	R	C	500.0±370.7	487.5±170.8	542.5±286.6	562.5± 93.4	42.5±142.5	75.0±172.1
Data from previous study (cortex)					642 ±333	877 ±543	431 ±248	537 ±329	176 ±176	305 ±181
(Simple Task)					4′		5′		6′	
1	8–04–1	(6, 6)			466.7± 41.1	115.0± 35.0	195.0± 17.1	288.3± 58.1	261.7± 34.4	∞
2	8–14–1	(8, 7)			(100)	(100)	342.5± 89.8	217.1± 86.5	–	–
3	8–21–2	(10, 10)			(550)	(350)	252.0±102.1	181.0± 54.5	(300)	(170)
4	8–22	(4, 0)			(450)	–	332.5± 8.3	–	(120)	–
5	8–18–3	(10, 10)			225.0± 37.5	211.0± 46.3	219.0± 31.5	204.0± 25.7	7.0± 51.9	7.0± 32.1
6	10–08	(4, 3)			660.0± 61.2	596.7±262.3	247.5± 99.8	340.0± 51.0	412.5±136.8	303.3±273.1
	Mean±SD				450.6±178.0	307.6±208.7	264.8± 54.9	246.1± 59.1	227.1±167.4	155.2±148.2
VL 1	5–51–2	(17, 14)			348.8±123.2	314.6±120.9	332.7±124.1	310.0±103.5	16.2± 39.4	11.8± 71.2
Data from previous study (cortex)					625 ±241	434 ±230	425 ±197	529 ±231	264 ±245	58 ±113

( ) : estimated values from averaged responses in spontaneously active units

a See legend to Fig. 7 for details.

during voluntary wrist flexion and extension movements. Thus, the activity of units in ventralis lateralis does not seem to be directly coupled with the initiation of responses in delayed-response tasks but rather with the nonspecific voluntary movement itself.

A summary of the various time values associated with the thalamic units of the present study are shown in Tables I and II, and Table III contains a comparison between similarly obtained mean values for dorsomedial, caudate and prefrontal E units (left-sided and right-sided presses were averaged for Table III). These values were obtained from records

TABLE III

Comparisons of various time values among prefrontal, caudate and dorsomedial units[a]

			Prefrontal		Caudate		Dorsomedial	
1	SCREEN -LEVER	DA	1057 ± 377	(15)	813 ± 109	(7)	981 ± 266	(8)
2	SCREEN -SPIKE	DA	314 ± 113	(15)	290 ± 149	(7)	367 ± 140	(8)
3	SCREEN -EMG	DA	533 ± 151	(13)	497 ± 110	(7)	551 ± 197	(6)
4	SPIKE LEVER	DA	760 ± 345	(15)	514 ± 198	(8)	619 ± 253	(8)
4'		SA	535 ± 216	(11)	337 ± 84	(6)	337 ± 184	(5)
5	EMG LEVER	DA	484 ± 274	(13)	302 ± 162	(8)	327 ± 121	(6)
5'		SA	477 ± 192	(11)	222 ± 29	(6)	249 ± 33	(5)
6	SPIKE EMG	DA	241 ± 130	(13)	212 ± 95	(8)	315 ± 98	(4)
6'		SA	161 ± 159	(5)	116 ± 64	(6)	200 ± 145	(3)

mean ± SD (number) msec

a See legend to Fig. 7 for details.

in the manner illustrated in Fig. 7. The numerals in the Figure correspond to the column headings in the tables and are explained in the figure legend. All values were widely variable. There were no statistically significant differences (t-test, $p > 0.05$) between prefrontal and caudate units, between caudate and dorsomedial units or between prefrontal and dorsomedial units. Some statistically significant differences emerged when the data were broken down for left-sided and right-sided presses, respectively (as shown for dorsomedial units in Tables I and II). For example, there was a significant difference between right prefrontal and right dorsomedial units, and between right and left prefrontal and right and left caudate units with respect to latency from EMG onset to lever pressing on the simple alternation task. The mean values of the prefrontal units were about twice those of the caudate and dorsomedial units. The significant differences could easily be due to the fact that the cortical values included several samples of larger values obtained from a single slowly-behaving monkey.

Although no firm inferences can as yet be drawn as to the causal

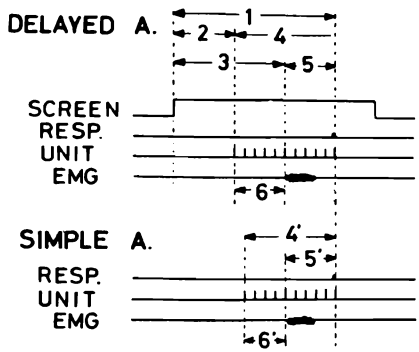

Fig. 7. Diagrammatic explanation of time value measurements in Tables I–III. Numbers refer to columns in the Tables: (1) time from the screen raising to the lever press; (2) time from the screen raising to the first spike activity; (3) time from the screen raising to the onset of EMG activity; (4 and 4') time from the first spike activity to lever pressing; (5 and 5') time from EMG onset to lever pressing; (6 and 6') time from the first spike activity to EMG onset. (From Kubota and Niki 1971.)

chain of events in the transmission of information among the dorsomedial nucleus, the caudate nucleus, and the prefrontal cortex, nevertheless some comments are in order. If information to press the lever in these tasks is transmitted from the thalamus to the cortex, as the anatomical data would indicate, then the dorsomedial nucleus may be a way-station between an unknown visual structure, conveying information that the screen is raised, and the midprincipalis area where interactions with the units there may ensue. The anatomical data suggest (Johnson et al. 1968) that information about the lever press at the midprincipalis area could be transmitted to the caudate nucleus. Since E units were found both in the prefrontal cortex and the caudate nucleus, while D units were found only in the cortex, it is possible that the efferent neuron of the prefrontal cortex is not a D unit but an E unit.

The failure to observe D units both in the dorsomedial and caudate nuclei may indicate that D unit activity is generated independently of the thalamo-cortico-caudate system. How the D unit is activated is not at all understood. It is possible that it may be activated somewhere in paleo-cortical or arci-cortical systems or it may arise from a regenerative circuit within the prefrontal cortex. The functional significance of the D unit is also not known. It is difficult to relate it to mnemonic mechanisms, despite its activation during delays, because no evidence has been found for a different temporal pattern of discharge nor differences in frequency with respect to right-sided and left-sided presses. If D units have effects upon other neurons within the prefrontal cortex, then the effect is most likely to be an inhibition of E unit activity to produce the delay state and thus prevent the E unit from initiating a lever-press response.

As indicated, the main findings of the present study were that the units of the dorsomedial nucleus in the thalamus were active preceding the lever presses whether or not delays were imposed between the trials. These findings are in contrast to those obtained from prefrontal units some of which could be related to the delay phase of the alternation task. Although 9 of the 12 units in the present study were found in the dorsomedial nucleus, their locations were not necessarily confined to the parvocellular division of this nucleus which projects to the mid-principalis prefrontal cortex. The units were located closer to the boundary of the dorsomedial nucleus (*see* Fig. 1) and were difficult to distinguish from those of the nuclei centralis lateralis or centralis ventralis. This finding raises the possibility that the dorsomedial nucleus, as anatomically defined, is not the sole thalamic nucleus involved in mediating delayed-response performance in the monkey. If other thalamic nuclei are so involved, then previous failures to obtained delayed-response deficits in monkeys with lesions confined to the dorsomedial nucleus alone are not inconsistent with the present findings and indeed, the findings of this study may give some basis for understanding these failures.

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