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EFFECTS OF DECEREBRATION AND DECORTICATION ON SHIVERING IN THE CAT

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ABSTRACT

The effects of decerebration and decortication on the metabolic intensity of shivering in cats were determined. There was neither shivering nor an appreciable rise in the oxygen consumption rate of chronic decerebrate cats during rapid cooling. The intermittent somatomotor activity that was induced by rapid cooling was occasionally tremulous but it was also evoked by rapid warming and was absent during slow cooling and warming. This suggested that the motor activity of decerebrate cats during rapid cooling was more a generalized avoidance response to nociceptive stimulation than a temperature regulating mechanism. In decorticate cats shivering was depressed three days after surgery, the mean shivering to nonshivering ratio in oxygen consumption rate being 1.6 ± 0.12 (S. D.), while the same ratio before operation was 2.6 ± 0.48 (S. D.). One month after decortication shivering had returned to its pre-operative intensity. This suggested that the net telencephalic influences on shivering could hardly be suppresive, as suggested by some earlier investigators.

PUBLICATION REVIEW

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Director of Research

EFFECTS OF DECEREBRATION AND DECORTICATION
ON SHIVERING IN THE CAT*

SECTION 1. INTRODUCTION

The hypothalamus is recognized by the majority of investigators as responsible for the primary control of shivering. This belief is based on the finding of most observers that decerebrate animals cannot shiver (Bard, 1961; Bard and Macht, 1958; Bazett and Penfield, 1922; Blair and Keller, 1946; DeBarenne, 1920) while decorticate preparations can (Bard, 1961; Aring, 1935; Pinkston et al, 1934). However, two investigators (Dworkin, 1930; Barbour, 1939) have maintained that shivering can occur in decerebrate preparations. If correct, this would imply the primary integration of this tremor is at the lower midbrain or pontile level since all the above investigators concur that shivering is abolished by transection of the caudal pons.

Some investigators (Bard, 1961; Aring, 1935; Pinkston et al, 1934), while recognizing the primary role played by the hypothalamus in shivering, have claimed that the telencephalon is tonically inhibitory with respect to shivering. This was based on the observation that on exposure to cold, shivering appears earlier and is more intense in decorticate as compared to intact homeotherms. This concept may conflict with other reports of shivering induced by hypnotic suggestion (Gessler and Hansen, 1927) and by electrical stimulation of the septum of the forebrain (Akert and Kesselring, 1951; Andersson, 1957). Since shivering can also be suppressed by hypnotic suggestion and by electrical stimulation of a variety of telencephalic loci (Kaada, 1951; McLean and Delgado, 1953; Hemingway et al, 1954), it seemed more likely that the telencephalon could exert both suppressive and facilitating influences on shivering.

Recently in our laboratory, measurements have been made of the metabolic changes during shivering, which is the most quantitative method of measurement of its intensity. Such metabolic studies have been made of decerebrate and decorticate cats before and during cold exposure in order to obtain quantitative data on shivering which will add information useful in resolving these controversies.

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SECTION 2. SUMMARY

Decerebrate cats were found capable of movements in response to rapid body cooling. However, similar movements were evoked by rapid body warming. This suggested the movements were more a generalized avoidance response to nociceptive stimulation than a temperature regulating response. The movements consisted of spasmodic jerks, kicks and running motions and sometimes included tremulous activity. Such tremors appeared to be alternating (i.e. agonists relaxed while antagonists contracted), with limb tremor frequencies of 4-7 cycles/sec. There was no appreciable rise in oxygen consumption rate during this tremulous activity, nor during any of the other observed activities. The tremor of shivering in an intact cat is 9-11 cycles/sec. and involves synchronous agonist-antagonist muscular contractions with a two- to four-fold elevation in oxygen consumption rate. It therefore appears that decerebrate cats cannot shiver and that the neural control of this form of muscular activity must be more rostral than the midbrain. This concept is supported by some but not all investigators who have studied this problem. Those investigations which support the concept are based on studies of animals maintained in relatively good health for many weeks after surgery. Those studies which do not support this concept are based on visual observations of acute decerebrate preparations. Unlike the experiments reported here, they do not contain data on the metabolic effectiveness of movements made by decerebrate preparations in response to cooling.

For the first few days after surgical removal of the telencephalon, cats were found to be autonomically hyperactive -- urinating, defecating, vomiting and "raging" excessively. Classically such hyperactivity is considered a result of removal of the net suppressive influence which the telencephalon is supposed to exert tonically upon the hypothalamus and its subservient functions. However, as measured metabolically, the intensity of shivering was depressed at this stage and did not return to the preoperative level until four weeks after surgery. By the time shivering had returned to its preoperative intensity, the autonomic hyperactivity had abated. Such results imply that the net telencephalic influence on shivering is not solely one of inhibition, as implied by previous investigators, but reflects either a balance of inhibitory and facilitating influences or the absence of any tonic influence. This opinion is in keeping with results of those who have produced and suppressed shivering by electrical stimulation of the forebrain and by hypnotic suggestion. All decorticate cats studied in these experiments could huddle in the cold. This observation has not been discussed in previous literature on the nervous control of body temperature.

SECTION 3. DECEREBRATION STUDIES

Methods

Seven cats were anesthetized with pentobarbital sodium (35 mg/kg I. P.) and decerebrated at the intercollicular level. Figure 1 shows gross aspects of the decerebration, in which the meninges formed the only connection between the prosencephalon and the lower brain. There was widespread thalamic degeneration and damage but an intact tuberal hypothalamus. By preserving the ventral hypothalamus, the hypothalamic-hypophyseal system was spared, as evidenced by the preparation's lack of polyuria. After surgery the preparations were poikilothermic and their body temperatures were maintained artificially at 36° to 38° C by controlling environmental temperature. They were given penicillin intramuscularly and meat and water daily by stomach tube. One to nine days after surgery each animal's oxygen consumption rate ($\dot{V}O_2$) was determined in a closed circuit system over a 20-minute period. During this determination the body temperature was maintained near 38° by keeping the environmental temperature at 30° to 35° C. The body temperature was then lowered rapidly by immersing the cats in cool water for 10 minutes. After cooling, the oxygen consumption rate was redetermined over a 20-minute period. During cooling and the second determination of oxygen consumption rate, somatomotor responses were noted. These responses were compared to those during slow cooling and slow and rapid rewarming.

For determination of $\dot{V}O_2$ before cooling, three successive 20-minute measurements were recorded and the mean value computed. After cooling only one determination was made, to record the $\dot{V}O_2$ as soon as possible after such cooling. During all determinations air and rectal temperatures were continuously monitored with copper-constantan thermocouples.

Results

Somatomotor Responses. Table I summarizes the metabolic and somatomotor responses of the seven cats subjected to rapid cooling one to nine days after decerebration. All of these animals had somatomotor responses to immersion in cold water. These movements consisted of spasmodic twitches, jerks and large amplitude kicks and running movements. These responses were accompanied by an increase in respiratory rate and depth. The violence and frequency of these intermittent movements were greater in the animals tested 5 to 9 days and after surgery than in those tested 1 or 3 days after surgery. Cat No. 7 gave evidence of a slow tremor interspersed between grosser

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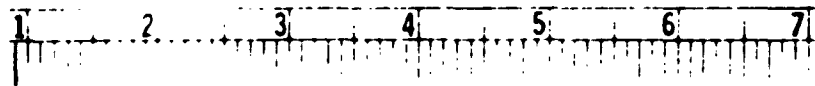
DORSAL VIEW

PARASAGITTAL VIEW

mms.

FIGURE 1. Gross aspects of
decerebrate cat brain (No. 7).

TABLE I: OXYGEN CONSUMPTION RATES OF DECEREBRATE CATS
BEFORE AND AFTER RAPID BODY COOLING

Oxygen Consumption Rates ($\dot{V}O_2$) expressed in mls. O_2 STPD/kg./min., Rectal Temperature (R.T.), Environmental and Water Temperature (E.T. and W.T.) expressed in degrees Centigrade. Weight expressed in kilograms. $\dot{V}O_2$ based on a 20 min. determination in a closed circuit system immediately before and after animal immersion in cool water. ΔR.T./20' is the change in rectal temperature during the $\dot{V}O_2$ determination after immersion. ΔR.T./10'imm. is the change in rectal temperature during immersion in cool water.

Cat No.	Weight Before Surgery	Weight Day Tested	Day After Surgery	Oxygen Consumption Rates and Temperature Measurements										Observations of Somatomotor Activity	
				Before cold stress			During cold stress		After cold stress					During cold stress	After cold stress
				$\dot{V}O_2$	R.T.	E.T.	ΔR.T./10'imm.	W.T.	$\dot{V}O_2$	Dev.%	ΔR.T./20'	E.T.			
5	3.75	3.70	1	6.0	37.5	30	-2.5	10	6.2	+3	-3.5	30		Intermittent twitching	Quiet
6	2.01	2.00	3	8.0	38.0	30	-3.4	10	8.0	0	-3.1	30		As above	As above
7	3.36	2.98	5	5.0	36.0	30	-3.5	10	6.6	+32	-3.0	30		Gross kicking Intermitt. slow tremor-hypervent.	Less frequent kicking and twitching
8	2.70	2.50	5	7.2	38.0	30	-0.5	20	7.9	+10	-5.0	30		Faster tremor no gross movements	Tremor maintained
10	2.70	2.35	5	7.4	36.2	30	-9.2	0	4.3	-42	+0.6	31		Violent intermitt. kicking and running movements-hypervent.	Hypotonic
17	3.45	3.09	5	3.8	35.2	32	-2.0	10	3.1	-18	-0.8	32		As above	As above
22	3.50	2.93	9	3.7	38.0	35	-6.0	5	3.4	-9	0	35		As above	As above

arrhythmic twitches, and cat No. 8 had a faster tremor that, by palpation, resembled shivering. If the body temperatures of the preparations were more slowly lowered by decreasing the environmental temperature to 25° C, no responses were evident even when the body temperatures fell to the same levels attained following immersion in cold water; when the animals were rewarmed by immersion in warm water (40° C) the movements disappeared when the body temperatures reached 36° to 38° C. If the rewarming was rapid (immersion in 50° C water), the animals' responses were similar to those seen during rapid cooling. This suggests that the response the decerebrate animal makes to rapid cooling and rewarming is a nonspecific response. This concept is supported by the fact that similar somatic responses of briefer duration were evoked by other "unpleasant" stimuli such as insertion of a rectal thermometer, pinching the hindlimb, or rapid rotation of the animals.

Metabolic and Rectal Temperature Responses. Table I shows that the oxygen consumption rates before cooling of cats No. 5, 6, 7, 8 and 10 lay within the normal range of intact cats of similar weight (Bard and Macht, 1958). Cats No. 17 and 22 had lower oxygen consumption rates but were particularly enfeebled after surgery. There was little variation in the animals' somatomotor responses during the period of cooling. After cooling, such variations were quite marked during the $\dot{V}O_2$ determinations. Cats No. 5 and 6 made few movements, cat No. 7 kicked intermittently, cat No. 8 maintained the tremor evoked by cooling, and cats No. 10, 17 and 22 became hypotonic although they made violent movements during cooling. The variations in oxygen consumption rate after cooling paralleled variations in somatomotor activity.

The rectal temperatures of cats No. 5, 6, 7 and 8 continued to fall during the period of $\dot{V}O_2$ determination after cooling. This was not the case with cats No. 10, 17 and 22. The rectal temperature of cat No. 10 rose 0.6° C during determination of $\dot{V}O_2$ of 32 per cent over the control rate. This was in keeping with its somatomotor activity after cooling. In contrast, cats No. 17 and 22 were hypotonic during the determination of $\dot{V}O_2$ after cooling and had oxygen consumption rates 50 per cent less than that of cat No. 7. However, the rectal temperature of cat No. 17 fell only 0.8° C, and that of cat No. 22 remained the same during this period.

Discussion

Shivering is a 9-11 c/sec. tremor which increases oxygen consumption rate two- to fourfold (Stuart, 1961). On the basis of this definition none of these animals shivered after decerebration. Even the two cats which displayed tremors had no appreciable elevation in oxygen consumption rate.

Somatomotor responses during rapid cooling were similar to those during rapid warming, insertion of a rectal thermometer and pinching the pinna. They were absent during slow cooling and warming. Thus, it seems that the somatomotor responses of a decerebrate cat to rapid cooling is more a generalized avoidance response to an unpleasant or nociceptive stimulus than a temperature regulatory mechanism.

It is not surprising that such responses include tremulous activity. Jenkner and Ward (1953), Folkerts and Spiegel (1953) and Wycis, Szekeley and Spiegel (1957) have reported tremulous activity in anesthetized cats and monkeys during electrical stimulation of the reticular formation of the midbrain, pons and bulb. If tremor can be produced by a nonspecific stimulus such as electrical stimulation, it is conceivable that nociceptive stimulation could produce the same effect in a decerebrate animal.

The information in Table I is for cats surviving up to nine days after decerebration. Bard and Macht (1958) studied 15 cats that survived 30 to 349 days after decerebration. These animals were poikilothermic and when exposed to cold their rectal temperatures fell as low as 23° C. Spasmodic gross muscle twitches (intermittently tremulous) appeared at rectal tempertures lower than 33° C. This activity failed to arrest the rate of rectal temperature decline. Possibly the conductive and convective heat loss was greater during these movements. Their results appear essentially similar to those presented in Table I.

The wide range of oxygen consumption rates after cooling is considered more a reflection of the difficulty of maintaining these animals in good postoperative health than of variation in the level of brain section. The variations in the rectal temperature of these preparations during and after exposure to cold were of similar magnitude to the variations in metabolic rates. Sometimes the variations were in reverse direction. For example, the $\dot{V}O_2$ of cat No. 7 was 32 per cent higher after than before cooling but the rectal temperature of this cat continued to fall after cooling. On the other hand the rectal temperature of cat No. 10 rose slightly after cooling even though its oxygen consumption was 42 per cent lower than before cooling. This suggests the presence of cutaneous vasoconstriction in cat No. 10. The rectal temperature of cat No. 7 was 32.5° C and of cat No. 10 was 27° C at the beginning of the $\dot{V}O_2$ determination after cooling. Possibly the disparity in cooling loads caused differences in $\dot{V}O_2$ and rectal temperature responses of those two animals. Cat No. 17's temperature after cooling was 32° C, implying a similar cooling load to that imposed on cat No. 7. However, the rectal temperature of cat No. 17 fell but 0.8° C, and the $\dot{V}O_2$ 18 per cent after cooling. A simple explanation is that cats No. 10 and 17 kicked more violently during immersion than did cat No. 7 and consequently were less wet and had less conductive heat loss after cooling. Perhaps the hypothalamic-hypophyseal system was injured to varying extents in these animals.

Endocrine disturbances were not studied after surgery. The endocrine system has been primarily implicated in the temperature regulative capacity of spinal animals by Thauer (1935), Chatonnet (1960) and Bonvallet and Dell (1946).

That none of our animals shivered after decerebration confirms the results of Bard and Macht (1958), Dusser de Barenne (1920), Bazett and Penfield (1922), Bazett, Alpers and Erb (1933) and Keller and Hare (1932). Their results indicated no shivering up to a year after decerebration. All these reports conflict with Dworkin's (1930) and Barbour's (1939) observations of metabolically effective "shivering" in rabbits and cats immediately after decerebration. If shivering was integrated at the pontile or lower level it might be depressed immediately after decerebration and return several days or weeks later when the animal had recovered from surgical trauma. As the reverse was true in Dworkin's results, his conflicting data cannot be adequately explained.

SECTION 4. DECORTICATION STUDIES

Methods

Decortication was performed on 21 cats under pentobarbital sodium anesthesia (35 mg/kg I. P.). For the first three days after surgery these animals were given daily penicillin injections and maintained in a 25° C environmental temperature.

Figure 2 shows coronal planes of the brain of one of these decorticate preparations. It demonstrates that in preserving the medial aspects of the anterior heads of the caudate nuclei, the septum was preserved bilaterally even though the corpus callosum was removed. The fornices were removed but direct paleocortical-diencephalic connections still existed by virtue of an intact right amygdaloid nucleus. The thalamus, hypothalamus and midbrain were undamaged.

Immediately prior to and three days after surgery the resting oxygen consumption rates were determined. One cat was also tested 28 and 470 days after surgery. The necessary apparatus for these determinations is described elsewhere (Stuart, 1961). The shivering oxygen consumption rate was determined after a mild cooling stress that induced shivering at a rectal temperature of 36° to 37° C. This stress consisted of immersing each animal in 10° C water for two minutes and 40° C water for one minute. This was repeated once and finally the animal was immersed in 10° C water for one minute. The rectal temperature of each cat was continuously monitored during $\dot{V}O_2$ determinations.

A. FOREBRAIN LEVEL

B. PREOPTIC-SUPRAOPTIC LEVEL

C. TUBERAL HYPOTHALAMIC LEVEL

D. P. HYPOTHALAMIC-MIDBRAIN LEVEL

FIGURE 2. Frontal sections of decorticate cat brain (No. 14).

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Of the 21 decorticated cats, 10 lived three days or longer, 5 one week or longer, 2 two weeks or longer, and one was sacrificed 570 days after surgery. The most frequent cause of death was aspiration of vomitus. This may have been due to vagal nerve injury during surgery.

The brains of these cats were fixed in formalin for gross and sometimes histological inspection. The animals were not fed between the day of surgery and the time of testing three days later. Three intact cats were also tested in similar fashion before and after a 3-day fast.

Results

The changes in oxygen consumption rate caused by shivering and measured before and after decortication are given in Tables II and III. Ten cats were tested three days after decortication and one of these further tested 28 and 470 days after surgery. All of the ten animals shivered feebly three days after decortication, as indicated by the presence of visible and palpable shivering and elevated oxygen consumption rates. The mean shivering to nonshivering ratio of oxygen consumption rate for the ten cats three days after decortication was 1.6 ± 0.12 (S.D.), range 1.4 - 1.7, while the same ratio before surgery was 2.6 ± 0.48 (S.D.), range 2.1 - 3.8.

After decortication, sham or undirected rage was easily induced by such stimuli as pinching the pinna, inserting a rectal thermometer or rapid body rotation. The animals tended to hyperventilate spontaneously, to have violent fits of gross somatomotor activity (leaping, running) followed by period of complete physical quiescence. Defecation, urination and vomiting were excessive and uncoordinated.

The one animal tested additionally at 28 and 470 days after surgery became less hyperactive in the second week after surgery. He assumed a crouched posture and moved slowly in response to nociceptive stimuli. The resting and shivering oxygen consumption rates at 28 and 470 days after surgery were similar to those values before decortication. This supported the visual observation of continuous and vigorous shivering in response to cooling. The resting and shivering oxygen consumption rates of the one hemidecorticate animal tested 42 days after surgery lay within the normal range. In this animal shivering was of equal intensity and duration on both sides of the body.

Body weights three days after surgery were 8% to 15% below the preoperative weights. As shown in Table IV the range in body weights of three intact cats after a 3-day fast was 6% to 15% below the control weights. However, these animals shivered just as intensely after fasting as before fasting.

TABLE II: RESTING (R) AND SHIVERING (S) OXYGEN CONSUMPTION RATES BEFORE AND AFTER DECORTICATION

Oxygen Consumption Rates ($\dot{V}O_2$) expressed in mls. O_2 STPD/kg./min. and based on closed circuit determinations. Weight expressed in kilograms.

Cat No.	BEFORE SURGERY				3 DAYS AFTER SURGERY				
	Weight	$\dot{V}O_2R$	$\dot{V}O_2S$	$\dot{V}O_2S/R$	Weight	% Weight Loss	$\dot{V}O_2R$	$\dot{V}O_2S$	$\dot{V}O_2S/R$
2	4.59	5.3	20.0	3.8	4.23	8	8.8	12.9	1.5
3	2.77	9.5	25.0	2.6	2.41	13	7.6	10.5	1.4
8	2.98	8.1	18.5	2.3	2.53	15	7.9	12.2	1.5
10	2.29	9.1	19.2	2.1	1.95	15	8.4	14.9	1.8
14*	2.08	9.0	19.6	2.2	1.84	12	7.2	12.2	1.7
15	3.02	13.0	30.4	2.4	2.63	13	8.7	14.4	1.7
18	2.91	8.4	22.8	2.7	2.81	4	7.0	11.6	1.7
19	3.04	9.1	21.6	2.4	2.60	15	7.5	11.7	1.6
20	4.09	9.7	24.3	2.5	3.66	10	7.0	11.0	1.6
21	2.57	7.1	20.7	2.9	2.23	13	7.6	13.0	1.7

* 28 days after decortication $\dot{V}O_2R$ = 7.8, $\dot{V}O_2S$ = 20.2, $\dot{V}O_2S/R$ = 2.6

* 470 days after decortication $\dot{V}O_2R$ = 7.8, $\dot{V}O_2S$ = 28.6, $\dot{V}O_2S/R$ = 2.3

One Hemidecorticate preparation tested 42 days after surgery $\dot{V}O_2R$ = 9.00, $\dot{V}O_2S$ = 19.50, $\dot{V}O_2S/R$ = 2.2

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TABLE III: MEAN SHIVERING (S) AND NON-SHIVERING (R) OXYGEN CONSUMP-
TION RATES ($\dot{V}O_2$) OF 10 CATS BEFORE AND AFTER DECORTICATION

$\dot{V}O_2$ expressed in mls. O_2 STPD/kg./min.

	Before Surgery		3 Days After Surgery		28 Days After Surgery		470 Days After Surgery	
	$\dot{V}O_2R$	$\dot{V}O_2S$	$\dot{V}O_2R$	$\dot{V}O_2S$	$\dot{V}O_2R$	$\dot{V}O_2S$	$\dot{V}O_2R$	$\dot{V}O_2S$
MEAN	8.82	22.20	7.77	12.43	7.72	20.18	7.94	18.55
S.D.	1.94	3.41	1.99	1.35				

	RATIO $\dot{V}O_2S/R$	RATIO $\dot{V}O_2S/R$	RATIO $\dot{V}O_2S/R$	RATIO $\dot{V}O_2S/R$
MEAN	2.58	1.60	2.60	2.33
S.D.	.48	.12		

TABLE IV: RESTING (R) AND SHIVERING (S) OXYGEN CONSUMPTION RATES BEFORE
AND AFTER 3 DAY FAST

Oxygen Consumption Rates expressed in mls. O_2 STPD/kg./min. and based
on 20 minute closed circuit determinations. Weight expressed in kilograms.

	BEFORE FAST				AFTER 3 DAY FAST				
Cat No.	Weight	$\dot{V}O_2R$	$\dot{V}O_2S$	$\dot{V}O_2S/R$	Weight	% Weight Loss	$\dot{V}O_2R$	$\dot{V}O_2S$	$\dot{V}O_2S/R$
A	2.93	7.2	25.2	3.5	2.77	6	4.6	22.1	4.8
B	2.16	5.3	26.0	4.9	1.95	10	7.4	20.3	2.7
C	2.36	5.4	25.2	4.7	2.00	15	5.6	19.0	3.4

Cold-induced huddling was evident in all animals before and after decortication and fasting.

Discussion

These results on a single chronic decorticate cat suggest that the intensity of shivering is normal after decortication but is diminished in the acutely decorticate stage. Bard (1961), Pinkston, Bard and Rioch (1934) and Aring (1935) found that cold-induced shivering appeared with more vigor and less latency of onset after decortication.

In chronic preparations during cold exposure they also observed a faster fall in rectal temperature and a higher skin temperature than in unoperated controls, which suggested that cutaneous vasoconstriction was impaired by decortication. Their observations are based on more chronic decorticate animals than are the present ones but do not have the support of metabolic data similar to those presented in Table II. If their observation of chronic cutaneous vasodilation is valid, it is conceivable that shivering would appear with less latency on exposure to cold after decortication, since the blood temperature should drop more rapidly. Conversely, if shivering is instigated by a change in skin rather than brain temperature, it would be slower in onset after decortication because the skin would be warmer due to the cutaneous vasodilation. From Liebermeister in 1860 to Benzinger in 1960 there have been investigators who believed shivering was initiated by changes in skin temperature, but from Richet in 1892 to Hammel, Hardy and Fusco in 1960, other investigators have shown that shivering can be initiated by either changes in both brain and skin temperature or in brain temperature alone. Our results have been insufficient to determine the latency of onset of shivering in chronic decorticate animals.

The results of Bard (1961), Pinkston, Bard and Rioch (1934) and Aring (1935) suggested that the telencephalon exerted a tonic inhibitory influence on shivering. Kaada (1951) reported the suppression of shivering during stimulation of the exposed orbitofrontal and gyrus genualis regions. McLean and Delgado (1953) reported similar suppression during stimulation of the amygdala and globus pallidus. Hemingway, Forgrave and Birzis (1954) reported the suppression of shivering during septal stimulation. Such results may support the concept of a tonic telencephalic suppression of shivering. On the other hand, our results indicate shivering is of normal intensity in a chronic decorticate cat. This suggests that the telencephalon might tonically exert both a suppressive and a facilitating influence on shivering. This is supported by the results of Akert and Kesselring (1951) and Andersson (1957) who produced shivering during stimulation of the forebrain's septum. Gessler and Hansen (1927) reported the use of hypnotic suggestion to both activate and suppress shivering in humans. Bykov (1957)

in his review of cerebral influences on the internal organs concludes that both the production and dissipation of heat can be conditioned by classical Pavlovian techniques. Thus, the literature affords some evidence that the telencephalon can have both suppressive and facilitating effects on shivering. The question, then, is which effect is greater in the intact animal.

In this regard the shivering response of cats three days after decortication is of interest. As shown in Tables II and III, these animals shivered more feebly even though they were autonomically hyperactive (i. e. excessive vomiting, defecating, etc.). However, they shivered with a more consistent intensity after than before decortication. The standard deviation of $\dot{V}O_2$ shivering/resting was four times less after than before surgery. This sample, although small, invites speculation that there are both suppressive and facilitating telencephalic influences on shivering. In an intact animal on a given day one or the other may be dominant, causing wide variance in the intensity of shivering. When the telencephalon is ablated, such influences are abolished and shivering is then directly related to body temperature and is of more consistent intensity.

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Rpt. AAL-TDR-62-15. EFFECTS OF DECEREBRATION AND DECORTICATION ON SHIVERING IN THE CAT.
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1. Shivering
2. Brain
3. Cats

I. Project 8238-22
II. Contract AF41(657)-344
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The effects of decerebration and decortication on the metabolic intensity of shivering in cats were determined. There was neither shivering nor an appreciable rise in the oxygen consumption rate of chronic decerebrate cats during rapid cooling. The intermittent somatomotor activity that was induced by rapid cooling was occasionally tremulous but it was also evoked by rapid warming and was absent during slow cooling and warming. This suggested that the motor activity of decerebrate cats during rapid cooling was more a generalized avoidance response to nociceptive stimulation than a temperature

regulating mechanism. In decorticate cats shivering was depressed three days after surgery, the mean shivering to nonshivering ratio in oxygen consumption rate being 1.6 ± 0.12 (S.D.), while the same ratio before operation was 2.6 ± 0.48 (S.D.). One month after decortication shivering had returned to its pre-operative intensity. This suggested that the net telen-cephalic influences on shivering could hardly be sup-pressive, as suggested by some earlier investigators.