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FRONTAL LOBE SULCI IN THE DOG

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The frontal lobe sulci in the dog are the subject of the present paper. They were previously dealt with by Langley (1882), Ellenberger (1891), Filimonoff (1928), Klimov and Akaievskii (1955), and Adrianov (1959). In contradistinction to the method described by the authors, mentioned above, the microscopic, more accurate observation method has been used in the present paper.

MATERIAL AND METHOD

Series of histological sections from 17 dog brains made up the material used for the investigation. The brains, fixed in formalin, were transected in the frontal plane into 20 or 50 micron thick sections and stained alternately according to the Nissl and Klüver, or Weigert-Wolters methods. From such preparations, figures were drawn of every 50th section (that is, 1 mm distant from each other), magnified 3.5 to 5 times. Additional preparations were drawn in places that might arouse doubts. The drawing accuracy was checked microscopically. Hereafter, the medial and lateral surfaces of the hemispheres were graphically reconstructed on the basis of the drawings. The sulci of both hemispheres were observed separately, the following, classification being introduced: (1) deep sulci, 2.5 to 5.5 mm (e.g., fissura cruciata; (2) shallow sulci, 1.0 to 2.5 mm (most sulci); (3) very shallow sulci, below 1.0 mm (e.g., sulcus rostralis; (4) cryptosulci (cf. Kreiner 1961). By cryptosulci we mean oblong cortical fields in which radiant fibers are scattered and shortend, while layer I is thickened, all these forming a picture with a considerable similarity to the architectonics of the sulcal fields, however, without a concavity, marked on the cortex surface (Figs. 9 and 10).

On the basis of the reconstructed frontal lobe sulci of 17 dog brains, the general scheme of their distribution was determined. Accordingly, an average schematic outline of the medial and lateral surfaces was drawn and all sulci from the 17 dogs investigated, were placed on it with consideration of different variants of their trace. To draw a more clear picture, only the most frequent types of the sulci were taken into account in the final scheme, thus obtaining an average, general scheme of both cerebral hemispheres (Figs. 1 and 8).

The depth and frequency of occurrence, were adopted as a criterion of division into fissures and sulci. Thus, the term, a fissure was applied only to the sulci which are deep (type 1) and stable, both as to their occurrence and course. The remaining ones were called just sulci.

RESULTS

The frontal lobe area was divided into the following regions: (1) medial region (regio medialis), (2) lateral region (regio lateralis), and (3) the region of the anterior composite gyrus (regio gyri compositi anterioris).

Medial region. Fissura cruciata and its prolongation up to sulcus corporis callosi and, further on, the latter sulcus as far as lamina terminalis were adopted as a boundary of the frontal lobe on the medial side.

Sulcus corporis callosi, dorsally surrounding corpus callosum and semicircularly reaching under its anterior section, that is, the genu (Fig. 1), is the most stable (100 per cent) sulcus of the medial aspect of the frontal lobe. This is a shallow or very shallow sulcus. Its depth is almost constant over the entire length, seldom (18 per cent) increasing in the anterior part, situated slightly apart from genu of corporis callosi (Fig. 1, ccal). Sulcus corporis callosi is a continuous sulcus, also regular in shape. It was only in a single case that, on both hemispheres,

Fig. 1. Scheme of the frontal lobe sulci of the medial surface of the left (A) and right (B) cerebral hemisphere. Continuous heavy solid line, unstable sulci. Cryptosulci are marked by crosses

a deviation from the general scheme was recorded, namely, the sulcus, surrounding genu, bifurcated and formed a small fork (Fig. 1B).

A shallow, stable (over 90 per cent), but very irregular in its trace, sulcus, that is, sulcus genualis occurs anteriorly to corpus callosum and sulcus corporis callosi. In most instances, this is a long, arcuate sulcus, surrounding genu of corporis callosi anteriorly and at a certain distance from it; posteriorly, on the dorsal side, it runs parallel to sulcus corporis callosi, reaching as far as over truncus corporis callosi. This part of the sulcus is often divided into 2 to 3 sections (Fig. 2A). According to Klimov and Akaievskii (1955), sulcus genualis is the anterior part of a long cingulate sulcus, sulcus cinguli or sulcus callosomarginalis whose posterior part is formed by sulcus splenialis. In our material, no junction was observed of sulcus genualis and fissura cruciata, mentioned by Langley (1882).

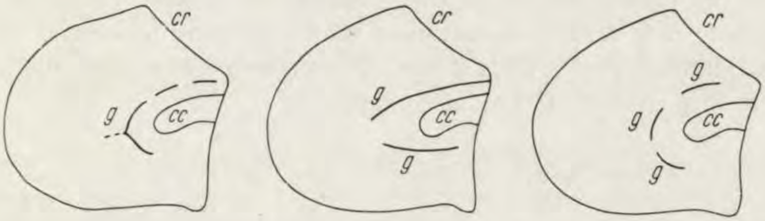

Fig. 2. Types of sulcus genualis

It is not always that sulcus genualis occurs in the form of an arcuate sulcus. Sometimes (12 per cent of all cases), it consists of 2 loose sections that do not connect with each other in the anterior part (Fig. 2B). It happens (35 per cent) to disintegrate into a few short grooves which, only in a general outline, form an arcuate sulcus (Fig. 2C). Hence, difficulties arise in settling the course of sulcus genualis. There is a necessity of microscopic checking of preparations and determining the course of sulcus genualis in relation to the fasciculus cinguli (cingulum). The distance between sulcus genualis and corpus callosum varies depending on the extent of the cingulum fibers. A radial process (Fig. 2A) may occur in the anterior part of sulcus genualis.

Very seldom (18 per cent of all cases), a sulcus, called, sulcus entogenualis (Klimov and Akaievskii 1955, Adrianov 1959), occurs between sulcus corporis callosi and sulcus genualis. In most instances, it forms a sort of a prolongation of the oral process of sulcus genualis, running to the inside of an arc, formed by this sulcus (Fig. 3, entg) but, sometimes, it may also run diagonally.

A long, arcuate sulcus, sulcus ectogenualis (Adrianov 1959, Klimov and Akaievskii 1955) occurs almost always outside sulcus genualis. Its appearance is strongly resembling of that of sulcus genualis, however, sulcus ectogenualis is longer and, in some places, deeper. Sulcus ectogenualis has been recorded in 70 per cent of the specimens examined and, therefore, it is a frequent sulcus (Fig. 3, ectg). Sulcus genualis happens to fall into several cections, sometimes, only slightly outlined, while sulcus ectogenualis occurs as a distinct arcuate furrow.

Below sulcus genualis and sulcus ectogenualis, a very shallow and often barely visible sulcus rostralis (Langley 1882) runs almost parallel to the lower margin of the hemisphere. It may be continuous or divided into a few sections between which cryptosulci occur. Its length also considerable varies (Fig. 3 ros). The presence of s. rostralis has been found in 70 per cent of the dogs examined.

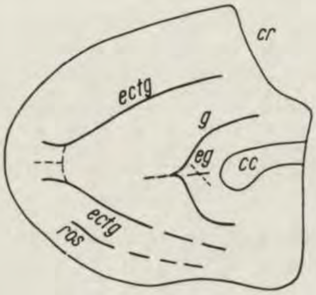

Fig. 3. Types of sulcus ento- and ectogenualis, as well as of sulcus rostralis

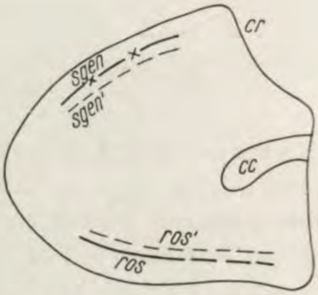

Fig. 4. „Double" sulci, sulcus supragenualis and sulcus rostralis

Above corpus callosum, fissura cruciata runs towards the upper margin of the hemisphere. This is a very stable (100 per cent), deep sulcus, passing from the lateral to the medial surface of the cerebral hemisphere (Figs. 1 and 8 cr).

Posteriorly to fissura cruciata, sulcus praesplenialis (Adrianov 1959) may occur on the medial surface of the hemisphere, while anteriorly, sulcus supragenualis, a stable (81 per cent), short and shallow sulcus runs parallel to the upper edge of the cerebral hemisphere. The latter may occur in a continuous form or divided into several sections (Fig. 4). These sections may be connected with each other by cryptosulci.

In addition to sulci that always occur in most dogs investigated, other, occasionally occurring ones were also found. Thus, for instance, a double sulcus supragenualis occurred in two dogs (Fig. 4). It looked like another sulcus, identical in depth (or somewhat shallower) and length and which runs parallel, below or above the proper sulcus supragenualis. On the other cerebral hemisphere of one of these dogs, there was no sulcus supragenualis at all, a double sulcus rostralis being recorded instead (Fig. 4, sgen). A double sulcus praesplenialis (Adrianov 1959) may also be located in this place.

Lateral region. On the lateral side, the boundary of the dog's frontal lobe runs from the posterior part through fissura cruciata and its prolongation as far as sulcus rhinalis anterior and, further on, along the latter up to the anterior margin of the hemisphere.

A large operculum of the cortex, usually termed, gyrus compositus anterior, has been isolated from this region as an independent entirety. On the outer surface of the hemisphere, fissura cruciata and its prolongation are adopted as a caudal boundary of this section. The so-called fissura praesylvia and, as a matter of fact, its inferior surface apparently constitutes the mediooral boundary.

Fissura praesylvia requires a somewhat more detailed discussion. It is a formation, very different from those we used to call colloquially a fissure. It is of a considerable depth and its walls in turn have several sulci. A few separate folds, specific in structure, may be distinguished in it which, in addition to fissura praesylvia, are only exceptionally met with. Hence, a problem, whether or not fissura praesylvia can be considered a sulcus at all. Perhaps, it should be considered a cortical region, covered with an operculum, formed by gyrus compositus anterior. The acceptance of the former, that is, considering fissura praesylvia to be a fissure is supported primarily by tradition. Fissura praesylvia is a generally recognized name, identified by all authors and thus shown in

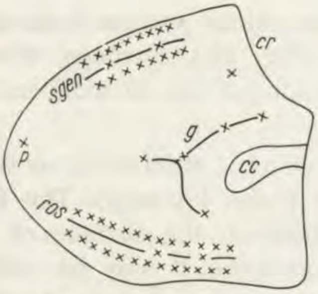

Fig. 5. Distribution of cryptosulci on the medial surface of the frontal lobe

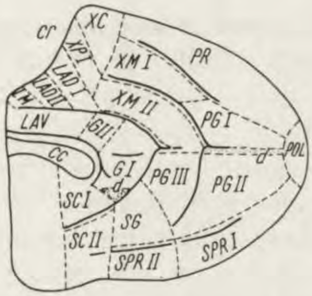

Fig. 6. Course of sulci in relation to the myeloarchitectonic fields on the medial surface of the frontal lobe

all brain atlases. Undoubtedly, much confusion might arise following the introduction of a quite different concept to replace it. Nevertheless, we must not forget the structure of its walls which is fully different from that met with in all other fissures and, therefore, we suggest to introduce a term of a perfissura praesylvia which could emphasize its different structure (a Latin prefix „per" implies something particularly strongly developed) and a certain superiority of this „cleft" to the fissures and folds, hidden in its walls. It should be also stressed that the introduction of the term of perfissura praesylvia does not by any means eliminate the term of fissura praesylvia. The latter continues to denote a fissure, hidden at the very bottom of the perfissura praesylvia (Fig. 9, prs). A fissure, located there, is a formation that does not differ at all from other fissures. Perfissura praesylvia is a very stable (100 per cent of all cases), very deep and long „cleft". Its arcuate, dorsally running trace, penetrates, in the form of a deep crevice, the cerebral hemispheres and separates gyrus compositus.

The following fissures occur on the lateral surface of the area, remaining after the removal of the gyrus compositus anterior. Sulcus proreus (Fig. 8A, pr.) frequently (70 per cent of all cases) occurs anteriorly to fissura cruciata. It is a shallow, short sulcus with cryptosulci sometimes forming its prolongation. Sulcus proreus may run almost parallel to the anterior edge of the hemisphere (very seldom) or in the horizontal plane.

Another sulcus, also shallow and short like sulcus proreus runs above and parallel to it but more posteriorly (Fig. 8A). Perhaps, this is a section of sulcus proreus formed by its division and not an independent sulcus.

A medial wall of perfissura praesylvia on which 2 sulci occur as well, has also been included in the lateral region (regio lateralis). The first of these sulci (Figs. 7A and 10) runs just beneath the surface of the hemisphere and, on lifting slightly gyrus compositus, it may be visible. In the present paper, this sulcus is called, sulcus supraorbitalis. Another sulcus (Figs. 7A,a and 10) is more deeply hidden under gyrus compositus and, sometime, it may terminate in a small fork. Both these sulci are almost equal in length, but the latter, marked „a" in the Figure, happens to be shorter.

Fissura rhinalis anterior runs below perifissura praesylvia. This sulcus is deep (type 1), long, continuous or, rather seldom, broken into separate, loose sections. Cryptosulci, occurring between them, were found in 20 per cent of all the animals examined. In the anterior part of the brain, fissura rhinalis anterior turns slightly downwards and separates

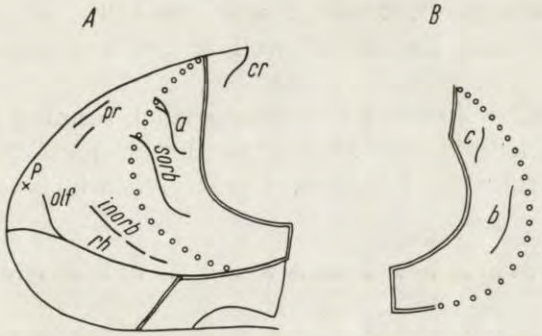

Fig. 7. A. Lateral region (regio lateralis). Gyrus compositus and bulbus olfactorius removed. The wall of perfissura praesylvia with internal sulci. B. Medial surface of gyrus compositus

bulbus olfactorius. Also, it forms a dorsally running branch, termed as sulcus olfactorius (Fig. 9). This branch occurs in all cases.

Between sulcus supraorbitalis and fissura rhinalis anterior a single sulcus only, that is, fissura interorbitalis (Langley 1882) is situated. This is a very shallow (type 4) and short sulcus, described by Ellenberger (1891) as sulcus frontalis. It occurs in 60 per cent of all cases on both hemispheres, in 30 per cent, only on the left and in 10 per cent, only on the right hemisphere (Fig. 8A,B).

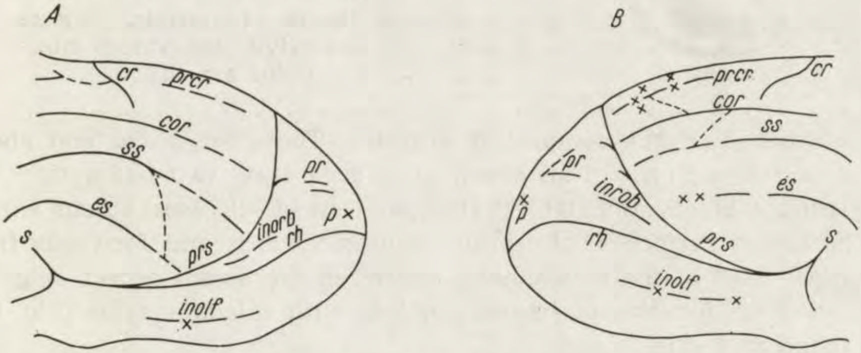

Fig. 8. Scheme of the frontal lobe sulci on the lateral surface of the left (A) and right hemisphere (B)

Below fissura rhinalis, in the area identified as allocortex, only one, anonymous cryptosulcus occurs (Fig. 9), sometimes, slightly deepened and forming a very shallow sulcus, it is covered by the olfactory bulb.

The region of the anterior composite gyrus constitutes a large cortical operculum with which perfissura praesylvia is laterally covered. The anterior composite gyrus, together with caudally adjoining parts of neighboring gyri, and the lateral wall of perfissura praesylvia belong to this part.

Two very shallow (type 4), anonymous sulci, running parallel to each other along the longitudinal axis of the brain (Figs. 7B, b, c, and 9), occur in the lateral wall of perfissura praesylvia which constitutes a medial surface of gyrus compositus anterior. These are short and stable (occur in 100 per cent of all cases) sulci, separating two flat gyri.

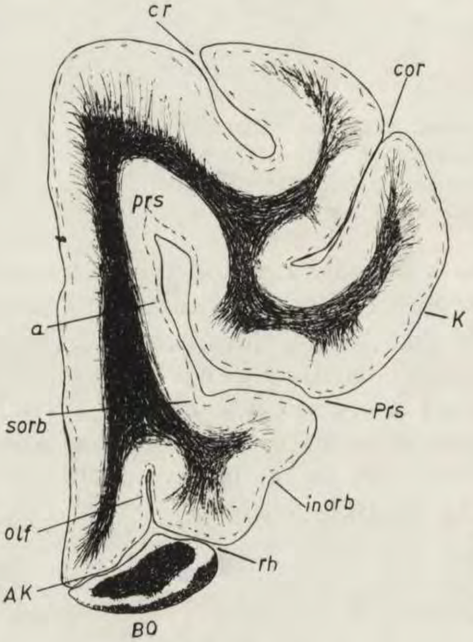

Fig. 9. Frontal section through the cerebral hemisphere. Perfissura praesylvia, fissura praesylvia and sulcus olfactorius are shown

Fissura cruciata, the stablest (100 per cent of all cases) sulcus which, on the dorsal surface of the brain, runs sidewards and forwards from the upper edge of the hemisphere, occurs on the dorsal aspect of gyrus compositus. A junction of fissura cruciata with sulcus ansatus (Fig. 8A) was found in a single case.

Fissura coronalis runs laterally to fissura cruciata. This is a deep and stable (occurs in 100 per cent of all cases) sulcus but with a considerably varying track. On the basis of the material investigated, the following types of sulcus coronalis have been differentiated: (1) a deep, long, continuous sulcus, running rostrally to fissura cruciata (70 per cent of all cases); (2) it is connected with sulcus suprasylvius (20 per cent of all cases) by means of a radiant process, processus acominis (Adrianov 1959); (3) connected with sulcus praecruciatus (one case).

Sulcus praecruciatus (Fig. 8A,B) runs anteriorly to fissura cruciata, mostly almost parallel to the upper edge of the hemisphere. This is a shallow, mostly slightly outlined sulcus, continuous or divided into 2—3 parts. When a distinct sulcus was absent, cryptosulci were found instead, occurring particularly on the left hemisphere.

The anterior part of sulcus suprasylvius (100 per cent of all cases) is a very stable sulcus. It runs parallel to fissura coronalis towards the anterior part of the brain. Its length varies. It may terminate just behind fissura cruciata, as well as run toward the anterior part of the brain. As it has already been mentioned above, a connection was found of sulcus suprasylvius with fissura coronalis (20 per cent of all cases). In the 10 dogs examined, sulcus suprasylvius bifurcated; by means of one of these branches it can be connected with sulcus ectosylvius (Fig. 8A).

Fig. 10. Scheme of a cryptosulcus

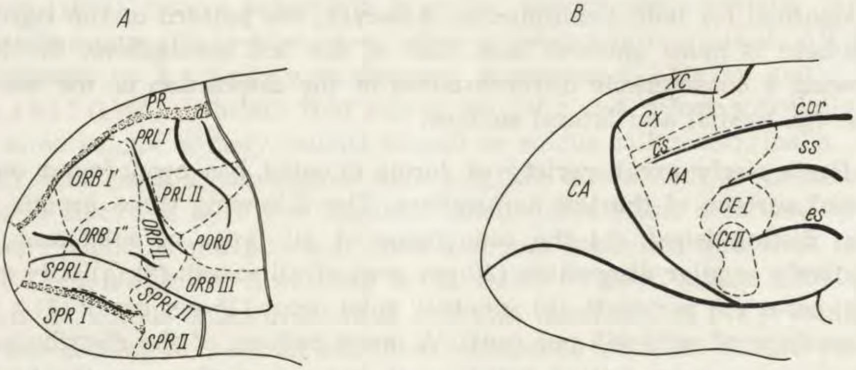

Fig. 11. Course of sulci in relation to the myeloarchitectonic fields on the lateral surface of the hemispheres. A, after the removal of gyrus compositus, B, prior to te removal of gyrus compositus

Sulcus ectosylvius anterior (100 per cent of all cases) is a long, arcuate, continuous sulcus, running, in the area discussed, by a slight arc to the lower part where it becomes shallow and terminates just over the edge of perfissura praesylvia which makes up an apparent, medio-oral boundary of gyrus compositus.

Cryptosulci whose presence can be detected only by means of a microscope, supplement the pattern of sulci, macroscopically visible on both the medial and lateral surface. The greatest accumulation of cryptosulci occurs in the dorsal aspect, namely: in the region of sulcus supragenualis on the medial surface and in the region of sulcus praecruciatus on the lateral surface, as well as on the ventral aspect, namely: in the region of sulcus rostralis on the medial surface. In addition, cryptosulci occur occasionally in a place where the regular sulcus is broken, thus forming a sort of its prolongation (e.g., sulcus genualis, Fig. 5). On the lateral surface, cryptosulci mostly constitute the prolongation of sulcus ectosylvius. Cryptosulci have also been found in the walls of other sulci, primarily those of fissura coronalis and fissura rhinalis. More cryptosulci were observed on the left hemisphere. On the medial surface, cryptosulci, occurring on both sides of sulcus supragenualis and sulcus rostralis, are slightly deepened which may result in a shallow sulcus, formed in this place. Probably, the „double" sulci, (Fig. 5) are formed in this way.

Comparison of both hemispheres. The final pattern of sulci is basically identical for both hemispheres. However, the pattern of the right hemisphere is more uniform than that of the left hemisphere, the latter showing a considerable differentiation of the disposition of the sulci on both the medial and lateral surface.

Particularly great variety of forms of sulci has been found on the medial surface of the left hemisphere. The following three groups have been distinguished: (1) the occurrence of all types of sulci and their relatively regular disposition (20 per cent of all cases); (2) (a) only stable sulci occur (15 per cent), (b) „double" sulci occur (15 per cent); (3) a typical pattern of sulci (45 per cent). A mean pattern of the distribution of the sulci has been settled within each group and then, on the basis of the 3 schemes obtained, a final, mean scheme for the left hemisphere was derived (Fig. 1A). It was found that differences may occur in the pattern itself of particular sulci, for instance, sulcus genualis may be more distinctly outlined on one hemisphere than on the other and may occur in a more typical form.

The left hemisphere shows greater differentiation also on the lateral surface. This primarily pertains to fissura coronalis almost all variants of which, mentioned above, concern precisely the left hemisphere.

Cryptosulci also occur more often and are more clearly seen on the left hemisphere. Cryptosulci are in certain regions frequently limited to one hemisphere which may result in the occurrence of „double" sulci also on one hemisphere, of instance, sulcus supragenualis. Sulcus rostralis may also occur on one hemisphere only, more often on the left than on the right.

DISCUSSION

The microscopic method allowed us (1) to establish the existence of the cryptosulci and (2) to investigate the brain tissue inside the sulci of the frontal cortex. It appeared that „internal" sulci occur in almost all deep sulci. These are either regular, or cryptosulci. Most „internal" sulci (as much as 5) have been found in the inferior surface of the depth of the so-called fissura praesylvia. In this connection, a problem arose whether or not this is a regular sulcus at all and, to designate the so-called fissura praesylvia perfissura praesylvia, emphasizing the fact that independent sulci and gyri occur inside it. „Internal" sulci also occur in fissura rhinalis (2 of them) and in fissura coronalis (also 2).

So far, the nomenclature with regard to the sulci of the frontal lobe cortex has been highly heterogeneous. Thus, for instance, in Langley's papers (1882), fissura praesylvia is called, fissura supraorbitalis. Sulcus frontalis occurs (Ellenberger 1891) as fissura interorbitalis. All sulci are termed by Langley as fissures. Moreover, Klimov and Akaievskii (1955) maintain that sulcus genualis and sulcus splenialis are the same sulcus, namely, sulcus cinguli or sulcus callosomarginalis.

In some cases, an ambiguous nomenclature is met with in the descriptions of sulci and gyri. For instance, sulcus olfactorius, described in the present paper, is not univocal with a sulcus described and thus called by Ellenberger. According to Ellenberger, sulcus olfactorius occurs on bulbus olfactorius while a sulcus, described in the present paper has nothing in common and is not connected with the olfactory bulb. The differences in the nomenclature of sulci and gyri are summarized in Tables I and II.

The pattern of frontal lobe sulci in the dog established on the basis of the present investigation basically coincides with that elaborated thus far, but it is extended by recognizing the cryptosulci. It is interesting that the left hemisphere shows a predominance over the right hemisphere in both the number of sulci and cryptosulci and in their differentiation.

It is worth while considering the pattern of sulci in relation to the myeloarchitectonic fields (Kreiner 1961, 1962). Figs. 6 and 11A,B show that on the medial surface, sulcus genualis makes up a boundary

Ta

Langley (1882)	Ellenberger (1891)	Filimonoff (1928)	Akaievskii and Klimov (1955)
callosal fissure	—	—	sulcus corporis callosi
genual fissure	sulcus genualis	fissura genualis	sulcus genaulis
crucial fissure	fissura cruciata	fissura cruciata	fissura cruciata
—	—	sulcus ectogenualis	sulcus ectogenualis
—	—	sulcus entogenualis	—
rostral fissure	sulcus rostralis	fissura rostralis	—
—	—	—	—
precrucial fissure	fissura praecruciata	fissura praecruciata	—
coronal fissure	sulcus coronalis	fissura coronalis	sulcus coronalis
sylvian fissure	fissura Silvia	fissura Sylvii	sulcus Sylvii
ectosylvian fissure	fissura ectosylvia	fissura ectosylvia	sulcus ectosylvius
suprasylvian fissure	fissura suprasylvia	fissura suprasylvia	sulcus suprasylvius
supraorbital fissure	fissura praesylvia	fissura praesylvia	sulcus praesylvius
rhinal fissure	sulcus rhinalis	fissura rhinalis	sulcus-basalis s. rhinalis
olfactory fissure	fissura olfactory	sulcus olfactorius	—
interorbital fissure	sulcus frontalis	—	—
interolfactory fissure	fissura intraolfactoria	—	—
prorean fissure	fissura prorea	fissura prorea	—
—	—	—	—
—	—	fissura diagonalis	—
—	—	fissura polaris	—

between the areas LM, LAD II, LAD I and LAV, and also between XM II, PG III, SG, SC II and G II, G II, CS I.

The areas, XM I and PG I are separated by sulcus ectogenualis from XM II and PG II from PG III. Sulcus rostralis is a boundary sulcus between SG and SPR, as well as between PG II and SPR I. Sulcus suprable I

Adrianov and Mering (1959)	Singer (1962)	Dziurdzik
sulcus corporis callosi	sulcus corporis callosi	sulcus corporis callosi
sulcus genualis	—	sulcus genualis
fissura cruciata	sulcus cruciatus	fissura cruciata
sulcus ectogenualis	sulcus genualis	sulcus ectogenualis
sulcus entogenualis	—	sulcus entogenualis
sulcus rostralis	—	sulcus rostralis
—	—	sulcus supragenualis
sulcus praecruciatus	—	sulcus praecruciatus
sulcus coronalis	sulcus coronaris	fissura coronalis
sulcus Sylvii	sulcus sylvius	sulcus Sylvii
sulcus ectosylvius	sulcus ectosylvius	sulcus ectosylvius
sulcus suprasylvius	sulcus suprasylvius	sulcus suprasylvius
sulcus praesylvius	sulcus praesylvius	perfissura praesylvia
sulcusrhinalis	fissura rhinalis	fissura rhinalis
—	—	sulcus olfactorius
sulcusinterprorealis s. sulcus intraorbitalis	—	sulcus intraorbitalis
—	—	sulcus intraolfactorius
sulcusproreus	sulcusintraproreus	sulcus proreus
—	—	sulcus supraorbitalis
sulcus diagonalis	—	—
—	—	crypto-sulcus polaris

genualis makes up a boundary between the area PR and XM I and, partially PG I. Sometimes, the boundaries of the areas run independently of the sulci. Sulcus entogenualis is not a boundary between any areas.

Particular attention has been paid to sulcal fields, that is, regions with slightest myelinization, usually marked by „d". It came out that

Table II

Langley (1882)	Ellenberger (1891)	Adrianov and Mering (1959)	Singer (1962)	Dziurdzik
prorean conv.	gyrus proreus	gyrus proreus	gyrus genualis	gyrus proreus
subprorean conv.	gyrus subproreus	—	gyrus rectus	gyrus subproreus
genual conv.	gyrus cinguli	gyrus genualis	—	gyrus genualis
supracallosal conv.	gyrus fornicatus	gyrus cinguli	gyrus cinguli	gyrus cinguli
—	gyrus genuatus	—	gyrus paraolfactorius	—
dentate conv.	—	—	—	—
—	—	gyrus fornicatus = gyrus cinguli + gyrus genualis	—	—
—	—	gyrus cruciatus anterior	gyrus frontalis	gyrus praecruciatus
anterior limb of the sigmoid gyrus	gyrus centralis anterior	pars anterior gyri sigmoidei s. gyrus cruciatus ant.	gyrus sigmoideus	gyrus cruciatus
anterior Sylvian	gyrus sylviacus ant.	gyrus Sylvius anterior	gyrus sylvius	gyrus Sylvius anterior
anterior ectosylvian	gyrus ectosylvius	gyrus ectosylvius	gyrus ectosylvius	gyrus ectosylvius
coronal conv.	gyrus coronalis	gyrus coronalis (pars ant. g. suprasylvii)	gyrus suprasylvius	gyrus coronalis
uncinate	gyrus pyrifomis	—	—	—
prorean	gyrus supraorbitalis	—	gyrus frontalis	gyrus proreus
subprorean	gyrus subroreus	—	—	gyrus subproreus
orbital lobe	gyrus frontalis s. gyrus orbitalis	gyrus proreus	gyrus proreus	gyrus orbitalis
—	—	gyrus orbitalis	—	—
—	gyrus compositus	—	—	pars anterior gyrus ectosylvius
—	gyrus sigmoideus (pars ant. gyri compositi)	—	gyrus coronalis	g. sylvius + g. ectosylvius + g. coronalis + + g. cruciatus
—	—	—	gyrus subcallosus	—

the subareas G Id and PG IId (Kreiner 1961) coincide with sulcus genualis and sulcus ectogenualis (Fig. 6).

After the removal of the gyrus compositus anterior (Fig. 11A), it is seen that the myeloarchitectonic areas are related to the sulci as follows. Sulcus proreus constitutes the boundary between the fields ORB I' and PR. Fissura rhinalis separates ORB III and a part of ORB II from the allocortex, while sulcus olfactorius, which is its branching, separates ORB I' from SPRL I. The fields SPRL I and SPR I are separated by an anonymous cryptosulcus. The myeloarchitectonic areas, PRL I, PRL II and PORD (Fig. 11A), are located in the medial wall of perfissura praesylvia and, through sulcus supraorbitalis, border on the field ORB II. Area PORV borders on area ORB II. The sulcal subareas „d" coincide, on the lateral surface, with sulcus proreus and an anonymous criptosulcus, separating area SPRL from area SPR I.

The following myeloarchitectonic areas occur on the surface of gyrus compositus: XC, CX and CS. They all are located posteriorly to fissura cruciata. Area CS borders on area KA and sulcus suprasylvius makes up a boundary with area CE I. Area CE II, reaching as far as fissura rhinalis anterior is situated below area CE I. Area CA extends along the anterior section of perfissura praesylvia.

SUMMARY

Frontal histological sections from 17 dog brains were a subject of microscopic observations. Sulci were classified as to their depth and frequency of occurrence. Thus, the following depths of sulci were distinguished: (1) deep sulci, 2.5 to 5.5 mm, (2) shallow sulci, 1 to 2.5 mm, (3) very shallow, below 1 mm, and (4) cryptosulci. There are the following frequencies of the occurrence of sulci: (1) stable, occurring in about 100 per cent, (2) frequent (70 per cent), (3) rare (50 per cent), and (4) very rare (below 50 per cent).

A new term, perfissura praesylvia has been introduced to name the sulcus which, thus far, was called, fissura praesylvia. Perfissura praesylvia is much deeper, several other sulci run over its walls and a few separate gyri with a specific structure may be distinguished. A term, fissura praesylvia has been left to denote a sulcus which makes up a bottom of perfissura praesylvia.

Particular attention has been paid to cryptosulci, that is, cortical areas with the sulcus type structure (Kreiner 1961) but without any distinct concavity which would be outwardly marked in this place. The greatest accumulation of cryptosulci occurs in the dorsal part in the region of sulcus praecruciatus (on the lateral surface) and sulcus sup-

ragenualis (on the medial surface). Besides, they occur as a prolongation of other sulci. The comparison of both hemispheres shows that the left one is more differentiated as to the distribution of its sulci, although general schemes of both hemispheres are very similar.

ABBREVATIONS

a, anonymous sulcus in the medial wall of the perfissura praesylvia
AK, anonymous crypto sulcus
b, anonymous sulcus in the lateral wall of the perfissura praesylvia
Bo, bulbus olfactory
c, anonymous sulcus in the lateral wall of the perfissura praesylvia
C, area sulci centralis
CA, area composita anterior
cc, corpus callosum
ccall, sulcus corporis callosi
CE I, II, area composita ectosylvia
CJ, area composita interna
cr, fissura cruciata
cor, fissura coronalis
CS, area composita sigmoidea
CSL, area composita sigmoidea lateralis
CX, area composita praecruciata
ectg, sulcus ectogenualis
entg, sulcus entogenualis
es, sulcus ectosylvius
FMC, area fissurae callosomarginalis
FK, area fissurae coronalis
FPS, area fissurae praesylviae
FRh, area rhinalis
FS, area fissurae splenialis anterioris
G I, II, area genualis I, II
g, sulcus genualis
inolf, sulcus intraolfactorius
inorb, sulcus intraorbitalis
K, crypto sulcus
KA, area coronalis anterior
KM, area coronalis medialis
LAD, area limbica dorsalis
LAL, area limbica anterior
LAV, area limbica anterior ventralis
LM, area limbica media
olf, sulcus olfactorius
ORB, area orbitalis
p, crypto-sulcus polaris
PG II, area pregenualis
POL, area polaris
PoC, area postcentralis
PORD, area paraorbitalis dorsalis
PORV, area paraorbitalis ventralis
PR, area prorealis
PR b, area prorealis medialis
PR c, area prorealis lateralis
pr, sulcus proreus
PRC, area praecentralis
PrCJ, area praecentralis interna
PrCL, area praecentralis lateralis
prcr, sulcus praecruciatus
Prs, perfissura praesylvia
prs, fissura praesylvia
PRL I, area prorealis lateralis I
PRL II, area prorealis lateralis II
rh, fissura rhinalis
ros, sulcus rostralis
S, sulcus Sylvi
SC I, II, area subcallosa I, II
GS, area subgenualis
sgen, sulcus supragenualis
sorb, sulcus supraorbitalis
SPR I, II, III, area subprorealis
SPRL I, II, area subprorealis lateralis
ss, sulcus suprasylvius
XC, area praecruciata centralis
XL, area praecruciata lateralis
XM, area praecruciata medialis
XPI, area praecruciata posterior

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MYELOARCHITECTONICS OF THE AMYGDALOID COMPLEX OF THE DOG

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This paper deals with the myeloarchitectonics of the amygdaloid complex of the dog and it is a continuation of the topographical study of Maksymowicz (1963).

The study was carried out on the basis of a series of frontal sections of a dog brain, stained by the Weigert method, and another series of frontal sections stained by the Klüver-Barrera method. The results were checked using two sagittal series stained by the Weigert and the Klüver-Barrera methods and one horizontal Weigert series. A total of five series were used for this study.

The division of the amygdaloid complex into nuclei was based on the cyto- and myeloarchitectural differences. Attention was given to the direction, stainability and arrangement of fibres in the particular nuclei. The course and similarity, if any, of the fibres made it possible to draw conclusions concerning their origin.

The amygdaloid complex consists of nuclei differing in both the size of cells and in their myeloarchitectural structure. It is situated above the ventromedial portion of the pyriform lobe, extending from the level of the anterior commissure orad nearly as far as the ventrocaudal pole of the cerebral hemipshere.

Orally, the amygdaloid complex borders on the substantia innominata and it clings to the external capsule laterally. The medial surface of the complex makes the lateral wall of the inferior corner of the lateral vetricle and, dorsally, it comes into contact with the optic tract, putamen and internal capsule. Its posterior portion neighbours on the hippocamus over a fairly large area. Eight nuclei can be distinguished in the amygdaloid complex: 1) the basal nucleus (Figs. 1, 2, 3, 4,...11, 13, and 14), 2) the medial nucleus (Figs. 1, 2, 7,...11, and 15), 3) the central nucleus (Figs. 1, 3, 3, 4,...11, and 16), 4) the cortical nucleus (Figs. 1, 2, 3, 4,...12, and 17), 5) the nucleus of the lateral olfactory tract (Figs. 1, 2, 12, and 18), 6) the intercalate nuclei (Figs. 3, 7,... and 19), 7) the lateral nucleus (Figs. 1, 2, 3,...11, and 20), and 8) the putaminal nucleus (Figs. 1, 2, 6,...11, and 21).

Generally, this division agrees with the divisions applied by other authors (Gurdjian 1928, Craige 1925, Humphrey 1953, Young 1936, Maksymowicz 1963).

MYELOARCHITECTONICS

The amygdaloid complex has numerous and various connexions. It is connected with the preoptic area and the hypothalamus by means of the stria terminalis and with the lemniscus diagonalis Brocae through the substantia innominata. Besides, it has connexions with the hippocampus and the external capsule. Orally it is connected with the lateral olfactory tract, dorsally with the putamen, and ventrally with the pyriform cortex.

Basal Nucleus and Longitudinal Association Fascicle (Figs. 1, 2, 3, 4,...11, 13, and 14)

The basal nucleus occupies the middle of the complex and forms about 21 per cent of the volume of this formation (Maksymowicz 1963). It is intimately connected with the hippocampus and the stria terminalis. Orally it is connected with the substantia innominata. It has connexions to the other nuclei of the amygdaloid complex as well.

Laterally the basal nucleus comes into contact with the lateral nucleus, merging with it without any distinct boundary. Medially it borders on the medial nucleus, from which it is separated by a flat bundle of fibres of the supracommissural part of the stria terminals, accompanied by some fibres coming from the hippocampus. They run sagittally to the substantia innominata, and part of them deviate towards the ventral portion of the basal nucleus.

The longitudinal association fascicle separates the basal nucleus from the overlying central nucleus. It consists exclusively of fibres coming from these two nuclei. Ventrally and medially to the basal nucleus is the cortical nucleus, separated from the former by a loose and faint bundle of fibres. This bundle is the extension of the ventral portion of the supracommissural part of the stria terminalis, situated between the basal and the medial nuclei. It runs towards the lateral portion of the cortical nucleus to disperse within it.

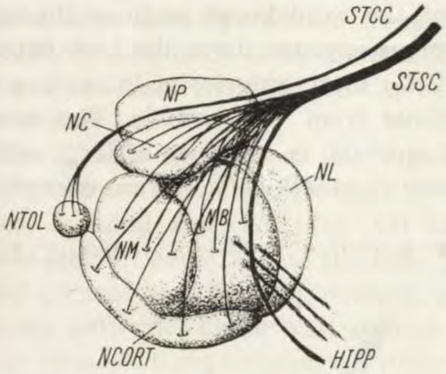

Fig. 1. A diagram of connexions of the amygdaloid complex with the stria terminalis and hippocampus, medial view

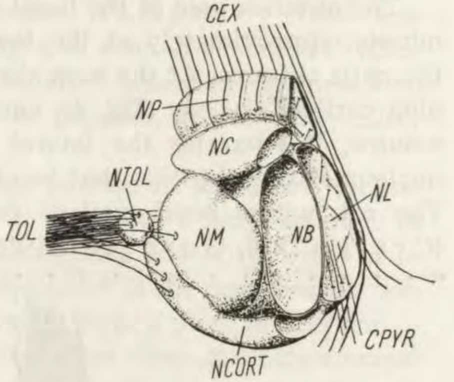

Fig. 2. A diagram of connexions of the amygdaloid complex with the external capsule, pyriform cortex and olfactory tract, medial view

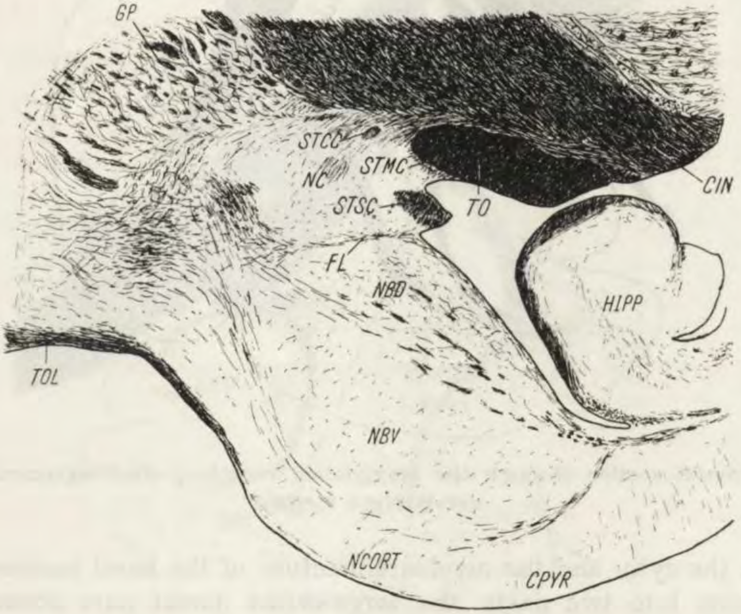

Fig. 3. Sagittal cection through the amygdaloid complex, semi-diagrammatic. Klüver-Barrera method

The anterior pole of the basal nucleus borders on the substantia innominata, approximately at the level of the caudalmost sections through the optic chiasma. At the back the nucleus appears above the here extending cortical nucleus (Fig. 4), and a little more anteriorly, increasing in volume, it separates the lateral nucleus from the vetricle. The basal nucleus of the dog, like that in other animals, is made up of large cells. The rat, whose basal nucleus consists of small cells, is an exception (Craige 1925, Gurdjian 1928).

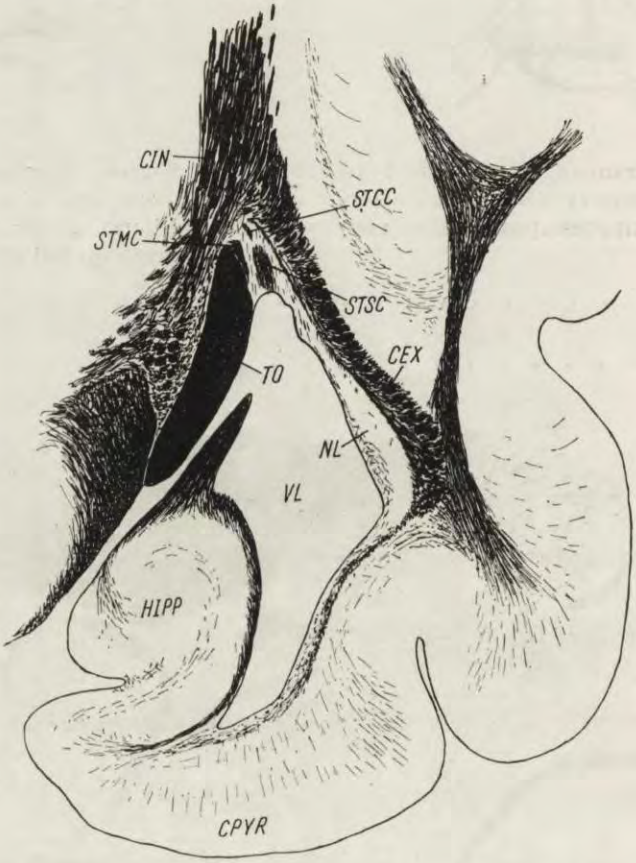

Fig. 4. Frontal section through the amygdaloid complex, semidiagrammatic. Klüver-Barrera method

Both the cyto- and the myeloarchitecture of the basal nucleus permit its division into two parts: the large-celled dorsal part abounding in fibres and the ventral part built of smaller cells and containing a smaller number of fibres. This division agrees with the observations of Jansen (1953), who distinguishes a large-celled lateral part and a small-celled medial part of the basal nucleus in the whale. Humphrey (1953) also finds a large-celled part situated larerally and a small-celled part lying medially in this nucleus of the bat. The separate treatment of these two parts of the basal nucleus seems to be to the purpose, because they differ in character.

The fibrous network of the large-celled portion of the basal nucleus is very dense. It is characterized by the presence of a large number of fibres, forming fascicles (Fig. 13) extending caudodorsally with more or less distinct deviations to the side. They appear in the posterior portion of the nucleus and, running anterad, scatter to form a more or less homogeneous network. These well-stained fibres come from the hippocampal gyrus. Some of them terminate within the nucleus, the others pass through it anterad and mix with the fibres of the substantia innominata. The dorsal part of the basal nucleus is strongly connected with the longitudinal association fascicle, which sends off numerous fibres running in mediocaudal, dorsocaudal, and laterocaudal directions and dispersing within the nucleus. Besides, in the inside of the nucleus there are some delicate fibres running in bundles from the supracommissural part of the stria terminalis

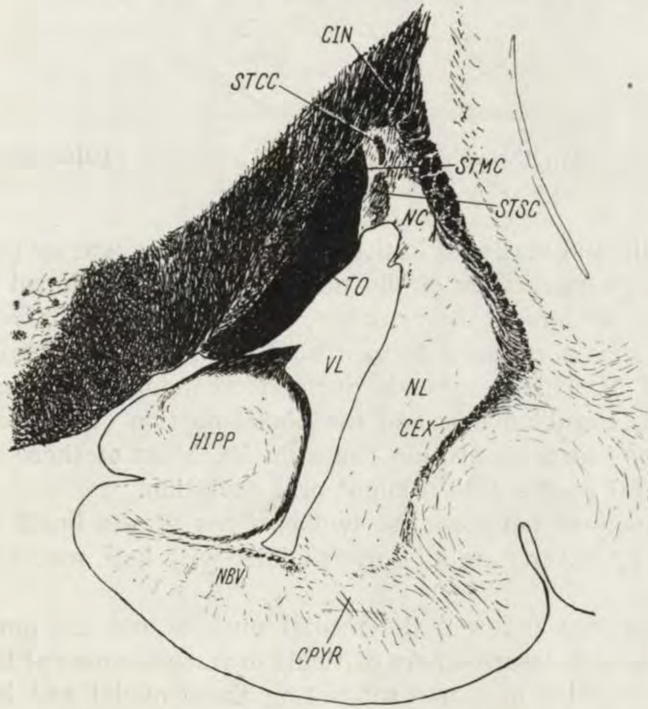

Fig. 5. Frontal section through the amygdaloid complex, semidiagrammatic. Klüver-Barrera method

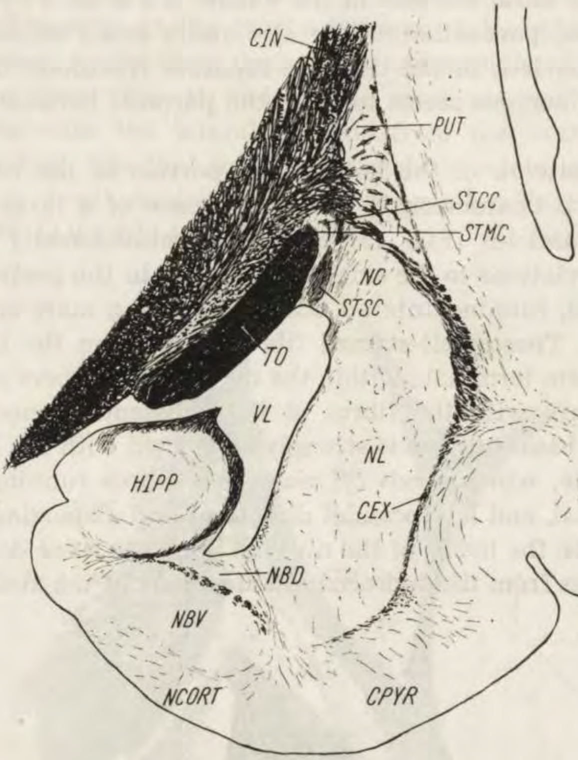

Fig. 6. Frontal section through the amygdaloid complex, semidiagrammatic. Klüver-Barrera method

dorsoventrally and scattered in the nucleus. In the posterior portion, where after the disappearance of the medial nucleus the dorsal part of the basal nucleus borders on the ventricle, the fibres of the supracommissural part of the stria terminalis form a kind of matted sheat on its surface (Figs. 5 and 6). Their course is dorsolaterocaudal. The faint boundary between the lateral nucleus and the dorsal portion of the basal nucleus is crossed by fibres connecting these nuclei. Most of these fibres show a ventrolateral course with a slight oral deviation.

The connexions between the two portions of the basal nucleus are represented by fibres running dorsocaudally with both medial and lateral deviations.

The connexions between the medial nucleus and the portion of the basal nucleus here described are difficult to trace because of the compactness of the bundles of fibres separating these nuclei and belonging to the supracommissural part of the stria terminalis. Although there are some fibres entering the medial nucleus laterally or from the side of the

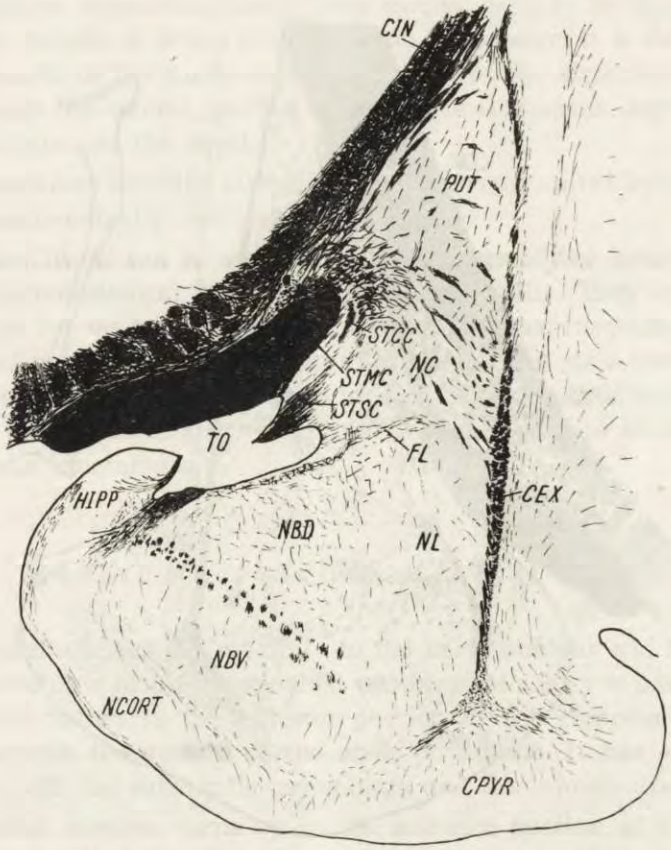

Fig. 7. Frontal section through the amygdaloid complex, semidiagrammatic. Klüver-Barrera method

basal nucleus, but they may take rise in the basal nucleus as well as in the stria terminalis. It is only in the anterior portion, where the number of fibres of the stria terminalis decreases, that some distinct fibres, running lateromedially and connecting both nuclei, can be traced.

The longitudinal association fascicle is less compact (Figs. 7 and 8), and for this reason it is easy to observe some fibres in it, extending dorsocaudally and connecting the central nucleus with the dorsal portion of the basal nucleus. The systems of fibres mentioned above mix with each other inside the nucleus, presenting a very distinctive myeloarchitectural picture.

The small-celled ventral portion of the basal nucleus is poorer in fibres than the dorsal portion. Its cells are smaller and stain less intensely (Figs. 2, 6, 7, 8, and 14).

Fibres running from the supracommissural part of the stria terminalis

Fig. 8. Frontal section through the amygdaloid complex, semidiagrammatic. Klüver-Barrera method

are also found in this portion of the basal nucleus. They form fascicles and extend dorsocaudally. In addition, in the ventral portion the bundle of fibres of the supracommissural part of the stria terminalis is dispersed fan-like, giving rise to fibres running dorsolaterally, of which some terminate in the ventral portion of the basal nucleus and the others reach the cortical nucleus lying below.

A few bundles of fibres with a dorsocaudomedial course pass from the substantia innominata towards the inside of the basal nucleus. They may be seen in the proximity of the boundary with the dorsal portion of the basal nucleus. Still less numerous fibres run caudoventrally from the hippocampal gyrus.

On the boundary with the cortical nucleus situated ventromedially to the small-celled portion of the basal nucleus, as well as above it, there are thick fibres connecting both these nuclei. Square to them there is a loose wide bundle of fibres extending caudomedially. It is the prolongation of a bundle of the supracommissural part of the stria terminalis and tends towards the lateral portion of the cortical nucleus, separating the cortical nucleus and the basal.

The connexions with the lateral nucleus are represented by a few fibres running medioventrally and mediolaterally.

Few thick fibres can be seen among the fibres of the anterior portion of the supracommissural part of the stria terminalis. They extend sagitally through the ventral portion of the basal nucleus; they come from the hippocampal gyrus pass orad among the fibres of the stria terminalis and can be traced as far as the substantia innominata. Also the fibres emerging orad from the inside of the ventral portion of the basal nucleus run to the substantia innominata.

Medial Nucleus (Figs. 1, 2, 7,...11 and 15)

The medial nucleus lies medially to the basal nucleus and forms 4 per cent of the volume of the amygdaloid complex (Maksymowicz 1963). It is situated rather in the anterior portion of the complex and shows connexions with the system of the stria terminalis. It has also distinct connexions with the substantia innominata and the lateral olfactory tract.

The medial nucleus turns up in the anterior portion of the complex almost exactly where the inferior corner of the lateral ventricle disappears. The optic tract marks out the medial boundary of the nucleus in the upper part and the medial surface of the cerebral hemisphere in the lower part. Ventrally, the medial nucleus neighbours on the cortical and, laterally, it is separated from the basal nucleus by a flat bundle of the commissural part of the stria terminalis. It comes into contact with the central nucleus dorsolaterally and with the substantia innominata orally, whereas its caudal portion merges with the hippocampal cortex without any visible boundary.

In the whole bulk of the medial nucleus its fibres have a more or less exact dorsoventral course.

The mere vicinity of the bundle of the supracommissural part of the stria terminalis may indicate its connexion with the nucleus. A myeloarchitectural analysis reveals the presence of fibres derived from this bundle. They pass dorsomedially orad, increasing in number in the ventral portion of the nucleus. A bundle of fibres runs dorsoorally, parallel to the medial sur face of the medial nucleus, which is at the same time the surface of the cerebral hemisphere. It is particularly well seen in the posterior portion of the nucleus and the fibres making up the bundle can be traced up to the place where the stria terminalis breaks up into particular parts.

In the anterior portion of the nucleus there are some dorsomedio-caudally extending fibres coming from the lateral olfactory tract. The fibres connecting the medial nucleus with the substantia innominata show a similar course.

Inside the nucleus, in the neighbourhood of the optic tract, there are some thick well-staining fibres (Figs. 9 and 10), which resemble the fibres of the optic tract and seem to run off its surface. They take their rise in the stria terminalis, to be exact, in the part connecting it with the stria medullaris (Young 1936). These fibres do not terminate within

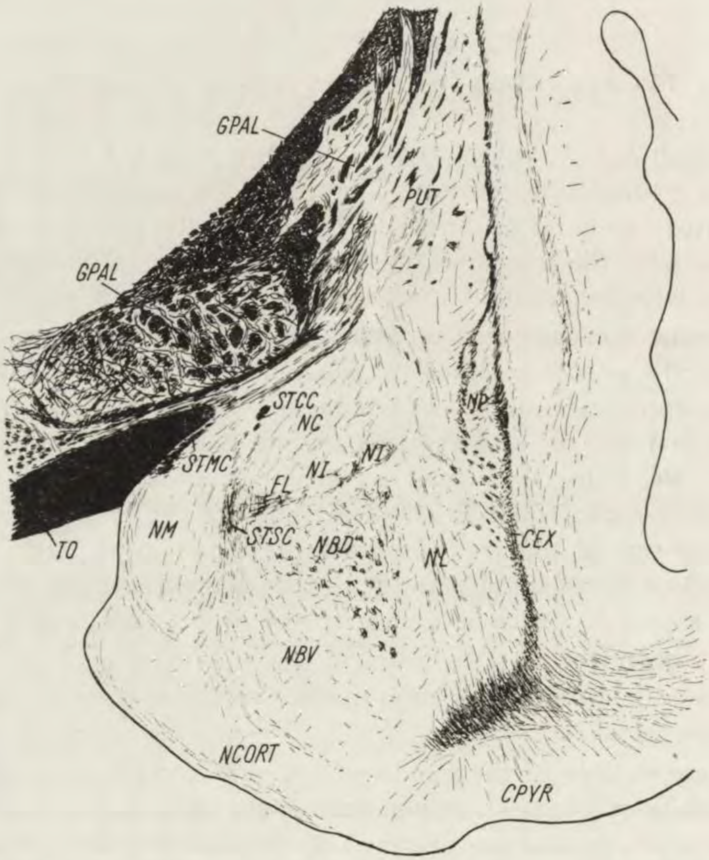

Fig. 9. Frontal section through the amygdaloid complex, semidiagrammatic. Klüver-Barrera method

Fig. 10. Frontal section through the amygdaloid complex, semidiagrammatic. Klüver-Barrera method

the nucleus, but pass dorsomedioorally in front of the optic chiasma to disperse in the preoptic area.

The medial nucleus is connected with the other nuclei of the amygdaloid complex, especially with the underlying cortical nucleus. Running dorsomedially the fibres connecting these both nuclei pierce through the mass of fibres in the ventral portion of the medial nucleus. Some fibres passing dorsomedioorally from the central nucleus enter the medial nucleus dorsally.

The fibres of the supracommissural part of the stria terminalis make it difficult to detect the connexion between the medial nucleus and the basal; nonetheless, orally, where the fibres of the stria become looser, single fibres connecting these nuclei are visible among them.

Central Nucleus and Nucleus E
(Figs. 1, 2, 3, 4,...11 and 16)

The central nucleus is situated dorsally to the basal nucleus and forms about 12 per cent of the volume of the amygdaloid complex (Maksymowicz 1963). In the dorsal portion its cells are mixed with those of the putamen. Medially and ventrally it passes into the medial nucleus, there being no distinct boundary between them, and orally joins the substantia innominata. A group of larger cells can be distinguished within it, sometimes called nucleus E (Völsch 1910).

Fig. 11. Frontal section through the amygdaloid complex, semidiagrammatic. Klüver-Barrera method

The central nucleus occupies the dorsal portion of the amygdaloid complex and appears in its posterior portion above the medial nucleus. Orally, it reaches to the substantia innominata. Below the central nucleus is the basal nucleus separated from the former by the fibres of the longitudinal association fascicle. Ventromedially the central nucleus borders on the medial nucleus. Dorsally it merges with the putamen.

The central nucleus is built of small cells similar to the cells of the medial nucleus. In its medial portion there is a group of larger cells, particularly well seen in the Nissl preparations and described by Völsch (1910) as well as by Maksymowicz (1963) as the nucleus E. As far as its myeloarchitecture is concerned, this group does not differ from the remaining part of the nucleus and for this reason it is treated here as its part.

Inside the nucleus there are many fibres running from its rear and top portions orad and laterad. These fibres are especially numerous in the dorsal portion. They form a system extending from above the internal capsule and accompanying three compact systems of the stria terminalis.

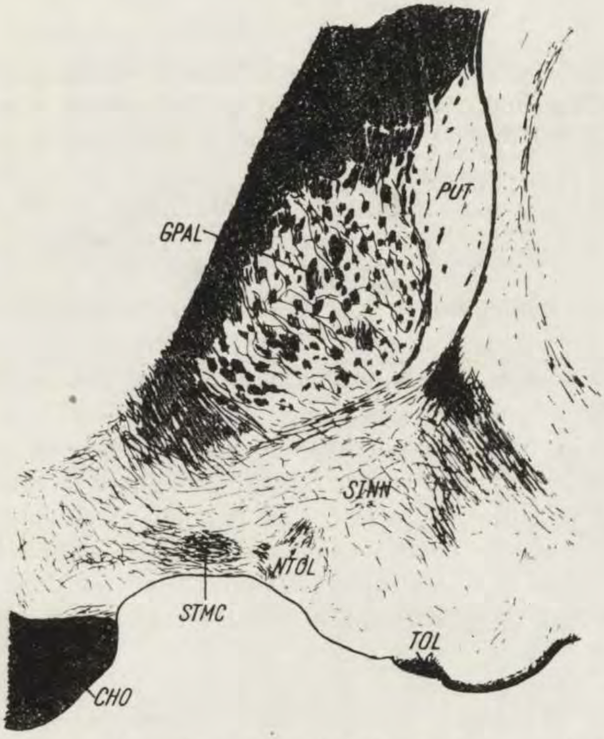

Fig. 12. Frontal section through the amydaloid complex, semidiagrammatic. Klüver-Barrera method

The system of fibres directed sagittally within the central nucleus is an important one. Its fibres are more numerous in the vicinity of the longitudinal association fascicle, which, together with the course of the fibres, points to their coming from this very fascicle.

The supracommissural part of the stria terminalis passes trough the caudomedial portions of the nucleus and, before turning ventrad between the basal and the medial nuclei, sends off a few bundles directed dorsomedially and spreading radially within the nucleus.

Some bundles of fibres pass dorsolaterally through the dorsal portion of the central nucleus from the internal capsule to the external capsule.

Thick fibres running dorsomedioorally penetrate through the longitudinal association fascicle and connect the central with the basal.

There are strong connexions between the central nucleus and the putamen. They are represented by many fibres extending dorsomedioorally and forming fairly large accumulations at places.

Cortical Nucleus (Figs. 1, 2, 4,... and 17)

The cortical nucleus lies in the ventromedial portion of the amygdaloid complex. It constitutes a medial extension of the pyriform cortex and surrounds the amygdaloid complex on the outside. Its size is about 22 per cent of the volume of the complex (Maksymowicz 1963). The cortical nucleus receives fibres from the stria terminalis as well as from the lateral olfactory tract. It is a continuation of the pyriform and the hippocampal cortex, with which it merges without any distinct boundaries.

The cortical nucleus is a flat nucleus prolongating the pyriform cortex and lying on the surface of the amygdaloid complex. Its cells do not show a pyramidal shape characteristic of the cortex. They are rather club-like and multiangular and form superficial layer. This layer becomes loose in its inner portion and in arrangement resembles the other nuclei of the complex rather than the distinctly stratified pyriform cortex. In addition, the pyriform cortex is much more compact than the supercical layer of the cortical nucleus. The cortical nucleus has also specific connexions, in which it differs from the cortex. It is, for instance, lacking in efferent fibres showing a radial arrangement so characteristic of the cortex.

Above the cortical nucleus and somewhat laterally to it lies the ventral portion of the basal nucleus. The boundary between them would be difficult to mark out, unless there was a rare bundle of mediocaudal fibres, which is a prolongation of the system of the supracommissural part of the stria terminalis towards the lateral portion of the cortical nucleus.

Dorsally the cortical nucleus borders on the medial nucleus. These two nuclei are separated from each other by a bundle of fibres directed dorsoventroorally, which turns off the surface of the medial nucleus

Fig. 13. Dorsal portion of the basal nucleus, myeloarchitectonics. Weigert method

Fig. 14. Ventral portion of the basal nucleus, myeloarchitectonics. Weigert method

Fig. 15. Medial nucleus, myeloarchitectonics. Weigert method

Fig. 16. Central nucleus, myeloarchitectonics. Weigert method

towards the bundle of the supracommissural part of the stria terminalis dispersing in the ventral portion.

The caudalmost portion of the nucleus is to be seen between the hippocampus on the medial side and the pyriform cortex on the lateral side. The boundary of the cortical nucleus both with the hippocampus and with the pyriform cortex is very indistinct.

Orally the cortical nucleus reaches the substantia innominata and borders on the nucleus of the lateral olfactory tract. The surface of the cerebral hemisphere is the medioventral boundary of this nucleus.

The cortical nucleus has clear-cut connexions with the system of the supracommissural part of the stria terminalis.

3*

It scatters above the dorsal surface of the nucleus giving rise to a large number of fibres spreading fan-like dorsomedioorally and terminating inside the nucleus. Part of them pass along the boudary with the basal nucleus to the lateral portion of the nucleus.

The connexions with the medial nucleus are represented by fairly numerous dorsomediooral fibres, many of which come from a bundle present on the surface of the medial nucleus.

Thick dorsocaudal fibres, diverging both laterad and mediad, as well as a system of fibres oriented dorsolaterocaudally extend from the ventral portion of the basal nucleus towards the cortical nucleus.

The essential system of fibres in the cortical nucleus is that of fibres running orad. These fibres, showing a tendency to form bundles in the anterior portion, are well visible in all parts of the nucleus as a not very compact layer at some distance from the external surface of the nucleus (Fig. 17). They probably have origin in the lateral olfactory tract.

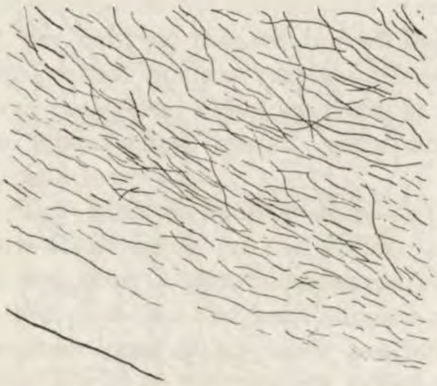

Fig. 17. Cortical nucleus, myeloarchitectonics. Weigert method

Fig. 18. Nucleus of the lateral olfactory tract, myeloarchitectionics. Weigert method

The nucleus is flat and its structure fully justifies the name, though there are evident differences between it and the pyriform cortex (appearance of cells, arrangement of fibres, connexions).

Nucleus of the Lateral Olfactory Tract
(Figs. 1, 2, 12 and 18)

The nucleus of the lateral olfactory tract is the foremost nucleus of the amygdaloid complex. It is a small accumulation of cells (0.5 per cent of the volume of the complex, Maksymowicz 1963) differing from the surrounding substantia innominata in the density of the fibrous network and in the size of cells. Orally it receives fibres from the lateral olfactory tract, whereas the fibres of the commissural part of the stria terminalis enter it caudally and dorsally.

The nucleus of the lateral olfactory tract is very small and it projects orad beyond all the other nuclei. It is built of middle-sized cells and forms a compact globular mass, well visible against the background of the substantia innominata abounding in fibres. In the dog the structure of this nucleus is uniform. No such parts can be distinguished in it as have been found by Gurdjian (1928) in the rat and by Young (1936) in the rabbit. Orally and laterally a large number of fibres run from the lateral olfactory tract towards the nucleus.

The commissural part of the stria terminalis disperses in the vicinity of the dorsal surface of the nucleus of the lateral olfactory tract. Its fibres enter the nucleus to form a system characterized by its dorsoventromedial course. Besides, there is a bundle of fibres passing from the stria terminalis, but it reaches the nucleus by another way. It is smaller and its fibres extend dorsomedially. Some caudodorsal fibres coming from the cortical nucleus appear in the vicinity of the dorsal boundary of the nucleus of the lateral olfactory tract.

Intercalate Nuclei (Figs. 3, 7,...11 and 19)

Between the basal nucleus and the medial nucleus as well as between the basal and the central and also among the fibres of the substantia innominata there are accumulations of small cells with a small number of fibres.

The intercalate nuclei are represented by a few accumulations of small cells disposed in various places of the amygdaloid complex as well

Fig. 19. Intercalate nucleus, myeloarchitectonics. Weigert method

Fig. 20. Lateral nucleus, myeloarchitectonics. Weigert method

as in the substantia innominata. Flat intercalations among the fibres of the supracommissural part of the stria terminalis and amidst the longitudinal association fascicle. are the most important of them.

Sanides (1957) considers the intercalate nuclei in man to be fragments broken off the islands of Calleja and finds them scattered throughout the corpus striatum. A similar situation can be found in the dog.

The accumulations of cells of the intercalate nuclei always occur in contact with the accumulations of fibres, which may point to their associative nature. However, the small amount of fibres in the accumulations of the intercalate nuclei is typical. Only passig fibres are seen in the Weigert sections. It is silver sections that reveal the presence of non-myelinated thin fibres ending in particular accumulations. This fact as well as the presence of glial satellites accompanying particular cells proves their indubitable neuronic nature.

Lateral Nucleus (Figs. 1, 2, 4,...12 and 15)

The lateral nucleus, situated laterally to the basal nucleus, extends along the whole complex occupying 34% of its volume (Maksymowicz 1963). Together with the overlying putaminal nucleus it makes up a group of nuclei which are not connected directly with the stria terminalis.

The lateral nucleus occupies the lateral portion of the amygdaloid complex. Laterally it is bounded throughout its lenght by the external capsule, separating it from the claustrum and the pyriform cortex. Medially it borders on the inferior corner of the lateral ventricle and, somewhat more orally on the basal nucleus. The boundary with the basal nucleus is very indistinct. Dorsally the lateral nucleus is separated from the putaminal nucleus by a bundle of fibres. It extends farthest to the back of all the nuclei of the amygdaloid complex. Its caudal portion is visible between the lateral ventricle and the external capsule, and its oral portion neighbours on the substantia innominata.

The lateral nucleus is built of medium-sized cells. In the lateral portion, adhering to the external capsule, the cells seem to be larger and stain better.

The latteral nucleus does not show any direct connexions with the stria terminalis, but it is strongly tied with the external capsule by means of two systems of fibres directed laterocaudally and dorsomedially.

The well-stained fibres coming from the pyriform cortex are most numerously represented in this nucleus. They run in a compact mass and are particularly abundant in the medioventral and ventral portions of the nucleus. Orally these fibres reach the substantia innominata.

In the caudal region where the nucleus neighbours on the ventricle there is a compact network of fibres running dorsomedioorally, lateromedioorally and dorsoventroorally. The fibres connecting the lateral nucleus with the basal pass across the boundary between these nuclei, extending ventrolaterally.

The connexions with the cortical nucleus are represented by a few fibres oriented dorsomedially and dorsomediocaudally.

A branch of the external capsule makes it difficult to trace the fibres connecting the lateral nucleus with the putaminal. The fibres which might maintain connexion between these nuclei extend in the same direction as those coming from the external capsule.

Young (1936) distinguishes two parts of the lateral nucleus of the rabbit: a small-celled anterior part and a posterior part built of larger cells. Johnson (1959) finds the same in the guinea pig. In the dog the putaminal nucleus might be homologous with the anterior part of the lateral nucleus. Its position in relation to the external capsule, the putamen, and the remaining part of the lateral nucleus seems to support this presumption. The cells of the putaminal nucleus resemble the cells of the lateral nucleus, especially those situated nearer to the external capsule. In so far as their myeloarchitecture is concerned, these nuclei are alike, as well.

Putaminal Nucleus (Figs. 1, 2, 6, 11, and 21)

The putaminal nucleus is a small formation; it occupies 3% of the volume of the amygdaloid complex (Maksymowicz 1963). It lies dorsally to the lateral nucleus, pressed in between the putamen and the external capsule and surrounded by the branches of the latter on all sides.

The putaminal nucleus, small and triangular in cross sections, is made up of medium-sized cells resembling those of the lateral nucleus. Myeloarchitecturally these nuclei are also similar only that the putaminal nucleus is lacking in connexions with the other structures except for the external capsule. The putaminal nucleus differs evidently from the putamen. Its cells are larger and stain better and the fibrous network is less dense and devoid of bundles characteristic of the putamen. This indicate that the putaminal nucleus belongs to the amygdaloid complex.

In the putaminal nucleus there are two systems of fibres, the course of which is here similar to that in the external capsule. They run lateroorally showing a tendency to form bundles or dorsomedially, and are more abundant in the marginal portions, that is to say, in the proximity to the external capsule. A small number of thick dorsomedial fibres from the ventral region of this nucleus pass towards the lateral nucleus. Their

Fig. 21. Putaminal nucleus, myeloarchitectonics. Weigert method

course is identical with that of the fibres coming from the external capsule.

The putaminal nucleus has been distinguished in the dog by Maksymowicz (1963). It was not mentioned in other studies, though it is well visible both in the drawings and in the photographs.

The putaminal nucleus may be homologous with the anterior part of the lateral nucleus observed by Young (1936) in the rabbit, and by Johnson (1959) in the guinea pig.

Connexions of the Amygdaloid Complex

The amygdaloid complex is connected directly with many adjacent structures: the putamen, hippocampus, substantia innominata and via the stria terminalis with the preoptic area and hypothalamus. It has connexions with the internal capsule through the external capsule.

A small number of fibres, leaving the amygdaloid complex orad, joins the lemniscus diagonalis Brocae. Some nuclei (the nucleus of the lateral olfactory tract, the cortical nucleus, and the medial nucleus) receive fibres from the lateral olfactory tract.

The *stria terminalis* is the main pathway leading to the amygdaloid complex. Young (1936) distinguishes the following components of the stria terminalis of the rabbit: a) the supracommissural component, coming out of the amygdaloid complex and after going round the internal capsule passing orad above the anterior commissure; b) the commissural component, emerging from the nucleus of the lateral tract and after covering the same way as the other components passing over together with the fibres of the anterior commissure to the other hemisphere and tothe amygdaloid complex of the oppoiste side; c) the preoptic component dispersing in the preoptic area; d) the stria medullaris component tending with the fibres of the stria medullaris towards the habenula, and e) the amygdalo-hypothalamic tract joining the cortico-hypothalamic tract.

Fox (1943) finds simlar components in the cat. He established that the supracommissural and the preoptic components reach the same region by different ways and suggests to call them the preoptic-hypothalamic component. Besides, basing on the degeneration picture obtained by the Marchi method he indicates the efferent nature of the stria terminalis in relation to the amygdaloid complex .

In the dog, the stria terminalis leaves the amygdaloid complex as a trifid bundle, the particular parts of which take rice in different regions of the complex (Fig. 1).

The commissural part of the stria terminalis is dispersed in the nucleus of the lateral olfactory tract. It corresponds to the portion called by Young the commissural component. The part connecting the stria terminalis with the stria medullaris corresponds to the stria medullaris component and it does not end in the amygdaloid complex but extends orad as far as the substantia innominata.

The supracommissural part of the stria terminalis corresponds to the portion which Young calls the supracommissural component. A large number of its fibres, especially those showing a medial deviation, reach the hippocampal gyrus. The remaining fibres turn between the medial nucleus and the basal, forming a well-visible bundle, the fibres of which run to both parts of the basal nucleus, to the cortical nucleus and to the medial nucleus.

Besides the fibres of the supracommissural part of the stria terminalis, in the flat bundle between the medial nucleus and the basal nucleus there are thick well-stained fibres extending in the sagittal direction from the hippocampal gyrus to the substantia innominata, but they are very few as compared with the fibres of the stria terminalis. Part of them deviates to the ventral portion of the basal nucleus.

A mass of loose fibres runs parallel to the three compact bundles of the stria terminalis from above the external capsule towards the amygdaloid complex. They terminate in the central nucleus.

The *longitudinal association fascicle* corresponds to the formation described in the literature as the lateral association budle (Gurdjian 1927, Crosby 1917, Fox 1940, 1943). Whereas in the cat (Fox 1940) it passes in the form of a compact bundle towards the hypothalamus, in the dog it is not so well developed and disperses as soon as it reaches the substantia innominata. As in the cat (Fox 1943), the longitudinal association fascicle of the dog does not join the lateral nucleus. It is composed exclusively of fibres from the adjacent nuclei, the dorsal portion of the basal nucleus, and the overlying central nucleus. The mediocaudodorsal, orolaterodorsal, and medioorodorsal systems of fibres as well as the systems of fibres running lateral and medial from the anterior region can be distinguished in it.

In the medial region the fibres of the longitudinal association fascicle mix with those of the supracommissural part of the stria terminalis.

Connexions with the Hippocampal Gyrus and the Substantia Innominata

The hippocampal gyrus sends out numerous fibres to the basal nucleus. The division of this nucleus into two parts seems to depend just upon their relation to the hippocampus. Even in the caudalmost region of the nucleus the compact bundles of fibres coming from the hippocampus evidently separate both its portions (Figs. 3, 5 and 7). More orally a vast majority of these fibres penetrate into the dorsal portion and only few turn ventrad. They greatly increase the density of the fibrous network of the dorsal portion, facilitating its distinction from the ventral portion.

The substantia innominata is a region filled with loosely arranged cells, among which many fibres run mostly in the ventrooral direction, situated in front of the amygdaloid complex (Figs. 1 and 2). The posterior part of the substantia innominata directly adjoining the amygdaloid complex is often described as the anterior amygdaloid area (Brodal 1937). In the dog this area does not differ from the remaining parts of the substantia innominata (Maksymowicz 1963) and, consequently it is treated here as one of them.

The nuclei of the amygdaloid complex send out a large number of fibres orad. They mix with the fibres of the substantia innominata and pass through the lemniscus diagonalis Brocae to the septum.

The *lateral olfactory tract* reaches the region of the anterior portion of the amygdaloid complex orally. Its fibres run to the nucleus of the lateral olfactory tract as well as to the cortical and the medial nuclei.

DISCUSSION

The nuclei of the amygdaloid complex form a fairly compact whole and are connected with each other by means of numerous fibres. However, they differ in myeloarchitecture and in connexions.

The amygdaloid complex may be divided into two groups of nuclei on the basis of their relation to the stria terminalic and to the external capsule (Fig. 1).

The first group consists of the lateral nucleus and the putaminal nucleus. These two nuclei differ from the rest in their lack of connexions with the stria terminalis, whereas they are strongly connected with the external capsule.

The putaminal nucleus much resembles the lateral nucleus in structure. Two systems of fibres coming from the external capsule and showing a course similar to that of the fibres in the lateral nucleus can be seen in it.

In the lateral nucleus, besides the systems corresponding to those in the putaminal nucleus, there are many fibres passing from the base of the external capsule triangular in cross sections. They are fibres connecting the lateral nucleus with the pyriform cortex (Figs. 4—12).

To the group of nuclei described above we must oppose the group connected with the stria terminalis but not with the external capsule. This group includes the basal nucleus, the medial nucleus, the central nucleus, the cortical nucleus, and the nucleus of the lateral olfactory tract.

The nucleus of the lateral olfactory tract is the only formation of the amygdaloid complex that connects with the commissural part of the stria terminalis. In addition, it receives fibres from the lateral olfactory tract.

The other nuclei, i.e., the basal, medial, central, and cortical nuclei, are connected with the supracommissural part of the stria terminalis.

The basal nucleus has connections with the hippocampal gyrus. The ventral portion of this nucleus receives a very few fibres from the hippocampal gyrus; insteated, these fibres are numerous in the dorsal portion. Besides, some fibres emerge from the dorsal portion and, together with the fibres coming from the central nucleus, form the longitudinal association tract, which next disperses in the substantia innominata. The ventral portion of the basal nucleus seems to have no connexions except for those with the stria terminalis and some poor ones with the hippocampal gyrus.

The central nucleus is connected with the putamen. Besides the fibres of the supracommissural part of the stria terminalis, the central nucleus contains many fibres from a loose system accompaying the compact systems of the stria terminalis.

The cortical nucleus and the medial nucleus, similarly to the nucleus of the lateral olfactory tract, in addition to the fibres of the supracomissural part of the stria terminalis receives some fibres from the lateral olfactory tract.

The interlacate nuclei differ obviously from all the other nuclei. They are built of much smaller cells than the cells of the nuclei described above. They are always situated among fairly large accumulations of fibres, both the fibres of the stria terminalis and those of the longitudinal association fascicle. No paths leading to the intercalate nuclei can be distinguished; they are connected only with the surrounding accumulations of fibres.

SUMMARY

The amydgaloid complex of the dog consists of eight subcortical nuclei in the region of the pyriform lobe. These nuclei, generally corresponding to those found in other animals, are as follows: 1) the basal nucleus, connected with the supracommissural part of the stria terminalis as well as with the hippocampus and the substantia innominata; 2) the medial nucleus, connected with the stria terminalis and the lateral olfactory tract as well as with the substantia innominata; 3) the central nucleus, being in contact with the overlying putamen and connected with the stria terminalis and the substantia innominata; 4) the cortical nucleus, having strong connexions with the supracommissural part of the stria terminalis and sending fibres out to the lateral olfactory tract; 5) the nucleus of the lateral olfactory tract, receiving fibres from the commissural part of the stria terminalis and sending some fibres out to the lateral olfactory tract; 6) the intercalate nuclei, the accumulations of fine neurons among bundles of fibres, presumably centres of association; 7) the lateral nucleus, connected with the external capsule by two systems of fibres and with the pyriform cortes by one system and sending fibres out to the substantia innominata; and 8) the putaminal nucleus, so far described only by Maksymowicz (1963), connected with the external capsule.

The lateral and the putaminal nuclei form a group differing from the other nuclei in their connections with the external capsule and in their lack of connexions with the stria terminalis. All the other nuclei are connected with the stria terminalis. The basal nucleus characterized by its connexions with the hippocampus should be distinguished among them. The nucleus of the lateral olfactory tract and the cortical and the medial nuclei are connected with the lateral olfactory tract. The central nucleus has connexions with the putamen.

ABBREVIATIONS

CIN, capsula interna,
CEX, capsula externa,
CHO, chiasma opticum,
CPYR, cortex pyriformis,
FL, fasciculus longitudinalis associationis,
GPAL, globus pallidus,
HIPP, hippocampus,
NB, nucleus basalis,
NBD, nucleus basalis pars dorsalis,
NBV, nucleus basalis pars ventralis,
NC, nucleus centralis,
NCORT, nucleus corticalis,
NL, nucleus lateralis,
NM, nucleus medialis,
NP, nucleus putaminalis,
NTOL, nucleus tracti olfactoris lateralis,
NI, nuclei intercallati,
PUT, putamen,
STCC, stria terminalis pars commissuralis,
STSC, stria terminalis pars supracommissuralis,
STMC, stria terminalis pars ad striam medullarem,
SINN, substantia innominata,
TOL, tractus olfactorius lateralis,
TO, tractus opticus,
VL, ventriculus lateralis.

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THE PRECOMMISSURAL HIPPOCAMPUS IN THE DOG

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In looking at frontal sections from different mammals' brains, a dense group of cells, vertically disposed in the area of the genu of the corpus callosum, is seen in the medial aspect of the hemisphere. These cells are more susceptible to the staining with the Nissl method than those of the adjacent cortical areas which causes this area to be easily observable even without the use of a microscope. This area is part of the hippocampal formation. Its presence in the anterior portion of the brain may be understood in the light of the phylogenetic development. In the aplacentalia which have not yet the corpus callosum, the hippocampal formation makes up a continuous entirety and occupies the central part of the medial aspect of the cerebral hemisphere. The corpus callosum, bilaterally connecting the neocortical areas, occurs in higher mammals. This is related with the reduction of a large frontal portion of the hippocampus to a thin strip of nerve cells adjoining the corpus callosum. On the dorsal side of the corpus callosum, the indusium griseum is situated along the longitudinal cerebral fissure and an area, described as the precommissural hippocampus (other names of this area may also be met with, such as, tenia tecta, anterior part of the hippocampus, anterior hippocampal cortex or, hippocampal rudiment) is located ventrally to the genu and the rostrum of the corpus callosum.

MATERIAL AND METHOD

The present paper is based on observations of seven continuous series of the dog brain sections. Three series of sections, stained by the Weigert-Wolters method (frontal, horizontal and sagittal) and transected every 50 μ, as well as four series, stained by the Klüver-Barrera and Nissl method (two frontal, one horizontal and one sagittal) and transected every 20 μ were used for observations.

RESULTS

Observations. The precommissural hippocampus in the dog makes up a ventral continuation of the indusium griseum with (Fig. 2) which it is connected in its frontodorsal part. Dorsally, the precommissural hippocampus reaches the genu and the rostrum of the corpus callosum. Oroventrally, it borders on the neocortex and, posteriorly, the anterior part of the hippocampus reaches the anterior part of the septohippocampal nucleus. Ventrally, in its most developed part, sometimes, it reaches the nucleus accumbens septi.

The precommissural hippocampus in the dog, as observed in the sections of the sagittal series (Fig. 6), has a shape, approaching that of a right-angled triangle whose shorter leg is situated horizontally below the corpus callosum and in the orocaudal line, while its longer leg (joining the former in its posterior end) runs vertically towards the bottom of the brain and its hypotenuse forms an arc, drawn between the

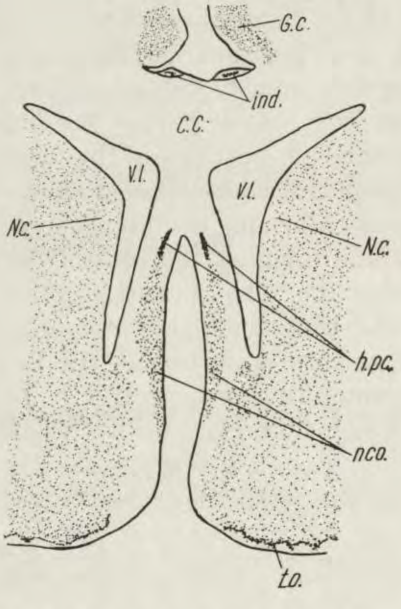

Fig. 1. Semischematic frontal section of the frontal area of the precommissural hippocampus in the dog, transected at the level of the genu of the corpus callosum. From the section stained by the Nissl method

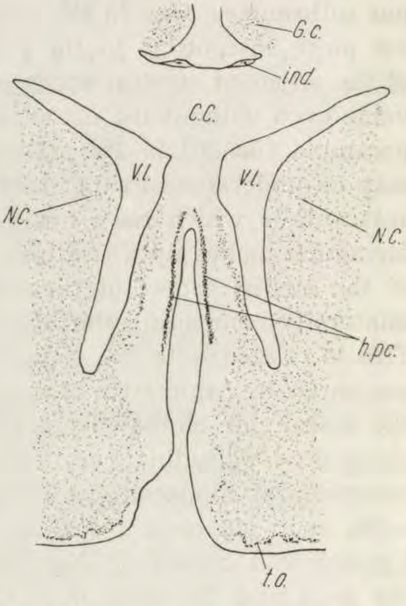

Fig. 2. Semischematic frontal section of the frontal area of the precommissural hippocampus in the dog, transected at the level of the genu of the corpus callosum. From the section stained by the Nissl method. The section is located about 2 mm posteriorly

ends of these two lines, the concavity of this arc being directed towards the right angle. The horizontal (Fig. 4) leg of this triangle is about 2.5 mm long, the vertical one, about 4 mm. (Fig. 2). In some specimens, the area of the precommissural hippocampus is elongated, its right angle becoming obtuse and then, the vertical leg is ventrocaudally directed.

The anterior hippocampal cortex forms a distinct continuation of the indusium griseum. The latter is a layer of cells of the hippocampal origin, situated on the dorsal aspect of the corpus callosum. The fiber bundles, striae longitudinales Lancisii, run together with them. All this system makes up a connection of the rudimentary parts of the hippocampus, situated in the anterior part of the brain with the hippocampus proper. In the anterior part, the indusium griseum encircles the genu of the corpus callosum and reaches the subcallosal gyrus where it is connected with the precommissural hippocampus (Fig. 6). In its posterior part, the indusium griseum encircles the splenium of the corpus callosum and runs ventrally, reaching the external layer of the hippocampal gyrus.

Any boundary between the indusium griseum and the precommissural hippocampus is lacking. These parts are similar to each other to such an extent that some authors treat them as a whole, calling them, a hippocampal rudiment (Ranson 1959).

Cells, typical of the cellular layer of the cornu Ammonis, are found both in the indusium griseum and in the precommissural hippocampus. The indusium griseum consists of oval cells, elongated and flattened by the adjoining fiber bundles, striae longitudinales Lancisii. Sometimes, round cells are also met with (Fig. 6a). Variform cells may be found in the precommissural hippocampus layer. In addition to oval and round cells, predominant in numbers, there are pyramidal and elongated, arcuate cells. The pyramidal cells are similar to the pyramidal layer of the cells of the cornu Ammonis. In some series of frontal sections of the dog brain, a layer of a few cells, strongly compressed and flattened by the expanding corpus callosum may be seen in the dorsal part of the anterior hippocampal cortex below the corpus callosum. These cells are elongated and, sometimes, arcuate cells with their arc branches pointed downwards, are also met with in this area. The remaining cells of the precommissural hippocampus are located below this group of cells. They make up a compact layer of cells, tightly adjoining each other. These cells are withdrawn from the frontal aspect of the brain, somewhat approach the deeper parts of the hemisphere and are disposed parallel to it.

On the frontoventral and ventral side, the precommissural hippocampus borders on the neocortex. This boundary is not clearly outlined and these formations mildly pass from one to the other. The compact layer of the hippocampal rudiment loosens towards the cortex and over more cells appear which are less stainable. The cells of the neocortex are situated nearer the medial aspect of the hemisphere than the cell layer of the hippocampal rudiment. The neocortical cells do not form groups (Figs. 1, 2, 4) but they are scattered all over the cortical part, except for a place where a layer of the association, that is, superficial, fibers of the cortex are located. In the area, occupied by the anterior part of the hippocampus, this layer is very thin. It is only (Fig. 3) a few fibers, running dorsoventrally, that are located in this place. Such conditions are observed only along a short ventral section of the hippocampal rudiment. Above, over these fibers, there are the fibers, striae longitudinales Lancisii, with an orocaudal track, which, in the anterior part of the hippocampal rudiment, turn upwards, reaching the dorsal aspect of the corpus callosum.

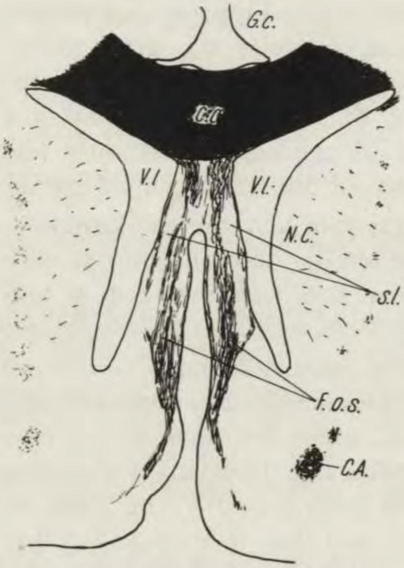

Fig. 3. A drawing of the section, stained by the Klüver-Barrera method. The section plane corresponds with Fig. 2

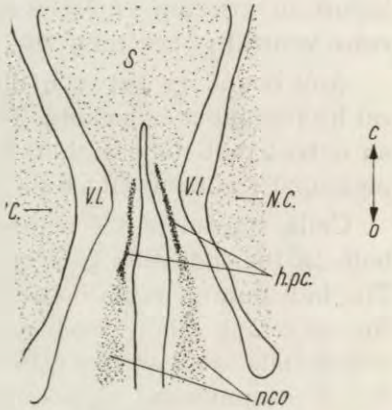

Fig. 4. Semischematic horizontal section at the level of the precommissural hippocampus in the dog (slightly below the genu and rostrum of the corpus callosum). From the section, stained by the Nissl method

In the posterior part, the precommissural hippocampus borders on the septohippocampal nucleus (Fig. 6). In the dog, this nucleus is situated in the medial line of the brain and, in its mediocaudal part, it contacts an identical nucleus of the opposite side. According to Miodoński (unpubl.), it belongs to the septum and, therefore, it was omitted in the present paper.

Connections. On the dorsal side of the corpus callosum, the fiber bunches, striae longitudinales Lancisii run together with the indusium griseum. They were described in the dog by Horodyska (1959) who distinguished among them two striae, that is, stria lateralis and stria medialis (Fig. 6). According to Horodyska's observations, stria medialis runs over the surface of the corpus callosum more medially and stria lateralis — along the edge, nearer the cingulate gyrus and is separated from the corpus callosum by a cell layer of the indusium griseum. Both these bundles encircle the genu of the corpus callosum and pass downwards to the hippocampal rudiment part, situated there.

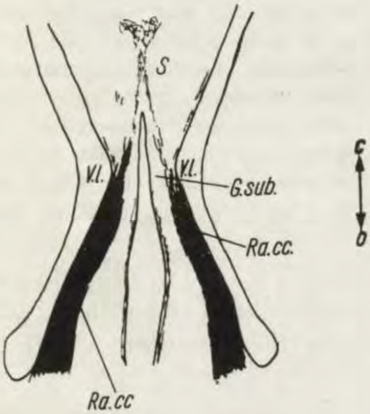

Fig. 5. Horizontal section in the plane as in Fig. 3a. A drawing, made on the basis of the Klüver-Barrera section, supplemented from the Weigert section

Stria medialis encircles the genu of the corpus callosum (Figs. 5 and 6) and, on its ventral side, runs towards the rostral lamina. A part of the fibers of the stria medialis ramify among the cells of the precommissural hippocampus, the remaining ones, reaching the septum pellucidum, become intermixed with its fibers. Horodyska has also observed that the bundles of fibers which frontally penetrate the genu of the corpus callosum branch forth from the main bunch of the stria medialis but their further trace is difficult to determine by means of the anatomical methods.

Stria lateralis, similar to the former bundle, encircles the genu of the corpus callosum, passes downwards and reaches the precommissural hippocampus. It is in this place, that most of its fibers terminate and only a few of them reach the septum pellucidum. According to Horodyska, the striae longitudinales Lancissii reach the hippocampus pro-

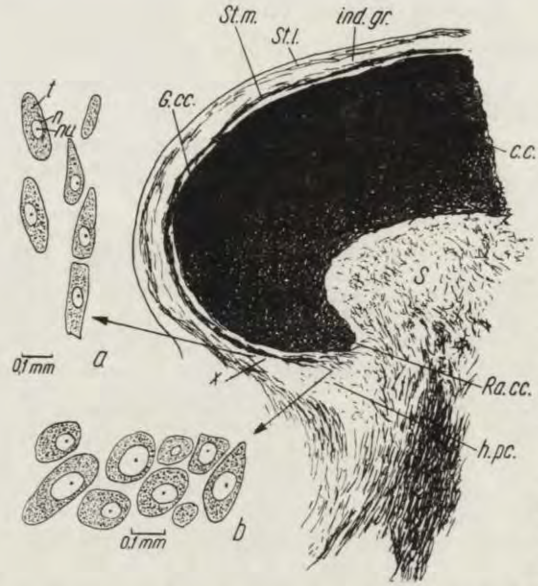

Fig. 6. Sagittal section of the superficial part of the cerebral hemisphere in the dog in the area of the genu of the corpus callosum. A drawing, made on the basis of a section, stained by the Weigert-Wolters method. Cytoarchitectonic samples prepared from the Nissl sections (transected in the sagittal plane). (a) Cells of the indusium griseum; (b) Cells of the anterior part of the hippocampus

per. Stria lateralis penetrates the hippocampal gyrus, while stria medialis ramifies into the cornu Ammonis or, subiculum. Striae longitudiales are considered to be the routes, leading to the hippocampus (Pitha 1959).

DISCUSSION

Anatomically, the precommissural hippocampus appears a relatively well elaborated structure. Numerous neuroanatomists focused their attention on it when dealing with the olfactory system or the telencephalon. However, the elaborations considerably differ from each other since the trace of the precommissural hippocampus is different in various species and, besides, many authors apply their own terminology to this area. The cytoarchitectonic criterion was used in most papers. According to Filimonoff (1949), the precommissural hippocampus in the dog reaches ventral parts of the olfactory bulb. A similar range of the anterior hippocampal rudiment was determined by Lauer (1949) for the Macacca mulatta and for the giant panda (*Ailuropoda melanoleuca*). The hippocampal rudiment of the rabbit (Young 1936) reaches the olfactory tubercle, terminating somewhat posteriorly to the olfactory bulb. As a matter of fact, such an extensive range of the hippocampal rudimentary remainders in the animals, mentioned above, is hardly probable. In our observations, we could not confirm Filimonoff's view since in the examined series of the dog brain sections, the trace of the anterior parts of the hippocampus is considerably shorter. An accurate myeloarchitectonic examination of this area in other species may, also in them, show another trace of the hippocampus. Humphrey (1936) found that the precommissural hippocampus in the bat, *Tadarida mexicana*, has a short trace and it descends vertically below the genu of the corpus callosum, reaching only slightly anteriorly with its ventral part. However Humphrey used silver staining for fibers and therefore, she could obtain a somewhat different picture of the anterior hippocampal rudiment.

The hippocampal formation is also related with the indusium griseum and the septohippocampal nucleus. If the former group of cells, mentioned above, is a part of the hippocampal rudiments, the assignment of the septohippocampal nucleus remains indetermined. Miodoński (unpublished) assigned this nucleus to the group of septal nuclei. Humphrey (1936) reckoned it, however, among the hippocampal rudiments.

According to classical investigations the precommissural hippocampus, indusium griseum and striae longitudinales Lancisii were assigned to the olfactory system of the brain. As to the physiological functions of this area, no data are available in the literature.

ABBREVIATIONS

c, caudalis
C. A., anterior commissure
c. c., corpus callosum
F. o.s., olfactory — septal fibers
G. cc., genu of the corpus callosum
G. c., cingulate gyrus
G. sub., subcallosal gyrus
h.pc., precommissural hippocampus
ind., indusium griseum
n., nucleus
nco., neocortex
nu., nucleolus
o, oralis
R. cc., rostrum of the corpus callosum
Ra. cc., radiation of the corpus callosum
S, septum
S. l., nucleus septalis lateralis (pars anterior)
st. l., stria longituddinalis lateralis
st. m., stria longitudinalis medialis
t, tigroid (Nissl bodies)
t. o, olfactory tubercle
vl., lateral ventricle
X., approximate trace of the boundary between the indusium griseum and the precommissural hippocampus.

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AN INVESTIGATION OF THE RELATIONS BETWEEN SALIVARY AND MOTOR RESPONSES DURING INSTRUMENTAL PERFORMANCE[1]

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The original investigations of animal learning were performed by students of either solely classical conditioning or of solely instrumental learning, this depending upon in which laboratory the scientist was working. Consequently, there was little fruitful interaction between the instrumental and classical schools of thought at this stage, particularly in the realm of theory. This is still true to some extent.

The early studies of Konorski and Miller (1930, 1933, 1936) introduced methods whereby the relations between classical and instrumental responses could be studied. While the general conclusion to be drawn from their experiments is that the salivary CR and the instrumental movement run usually *pari passu*, some of their experiments suggested that these two processes may not be isogenous.

For example, in one experiment these authors established in a dog a classical fod CR to a sporadic stimulus (CS +) using a 15-second CS-US interval, while another stimulus (CS−) was differentiated by non-reinforcement. In the next stage of the experiment, CS+ and CS− were never presented while the dog was trained to lift his foreleg in order to obtain immediate food reinforcement. After this instrumental response was well established, CS+ and CS− were presented against the background of continual performance of the instrumental leg movement. The results of this procedure were that upon presentation of CS+ the

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[1] This research was conducted while G. D. Ellison held a United States Public Health Service postdoctoral fellowship (MH 16, 185) at the Nencki Institute of Experimental Biology, Warsaw, Poland. The present address of G. D. Ellison is Department of Psychology, University of California, Los Angeles, Calif., U.S.A.

dog immediately stopped performing the trained movement and stared intently at the food bowl, salivating copiously. On the contrary, the presentation of CS− barely affected instrumental responding, although the salivary response to it was insignificant (Fig. 1).

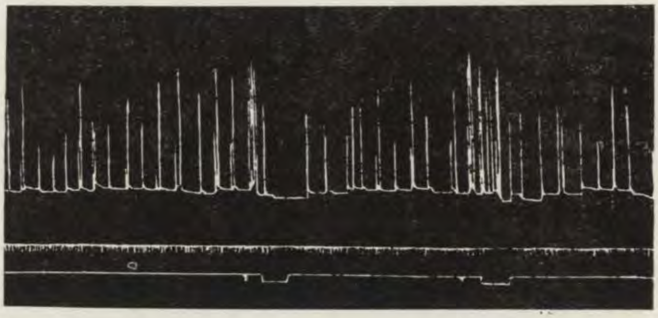

Fig. 1. The effects of a classically-trained CS+ and CS− on sporadic paw-lifting for food and on salivation. (From Konorski and Miller 1936). The markers are, from the top down: paw movements, salivation in drops, and CS. The buzzer was trained classically as CS+, and it elicits increased salivation and decreased paw movements. The metronome (M60) was classically trained as CS−, and it elicits decreased salivation and increased paw movements

In another experiment, a dog was first classically conditioned by Konorski and Miller to two stimuli, a CS+ and a CS− as in the previous case. In the second part of this experiment, this dog was trained to perform an instrumental leg-lifting response whenever a third CS, the instrumental CS, was presented. When the previously trained CS+ and CS− were presented after this training, there was no transfer of the instrumental response to CS+, but good transfer to CS−.

In later experiments by Konorski and Wyrwicka (1950), it was further established that it is extremely difficult to transform a CS which has previously been trained by classical conditioning methods into an instrumental CS. These experiments indicated that, with the same CS-US interval, the instrumental response is always stronger to an originally instrumentally-trained CS than to a CS which was originally classically reinforced and then transformed into instrumental.

On the basis of these experiments, it can be concluded that there is a certain antagonism between the classical food CS, to which the animal must simply wait for food, and the instrumental response, where he must work for food. The exact nature of this antagonism has remained obscure, however.

Opposed to the antagonism revealed in the above experiments were the results of other experiments by Konorski and Miller (1936) where only instrumental training procedures were used with a CS-US interval long enough to allow an examination of the conditioned salivary response, using Pavlov's methods. The results of such experiments were that in a well-trained animal the salivary and motor responses ran, as a rule, *pari passu*. In general, the stronger the instrumental response, the more copious was salivation and *vice versa*. The two responses showed generally similar courses during differentiation, and tended to occur closely correlated in time.

However, a close examination of the relations between the two responses can reveal that this parallelism, although often present, is not an absolute rule. Occasionally the instrumental response is not accompanied by salivation, or salivation to the instrumental CS is not accompanied by the instrumental response. These discrepancies were clearly seen in a study by Konorski and Wyrwicka (1952), where acute extinctions of various instrumental conditioned stimuli were conducted. In these experiments, it was found that extinction of a strongly „motogenic" CS (i.e., one which produces an intense instrumental response) had a strong inhibitory aftereffect upon a weakly „motogenic" CS, while the contrary was not true.

More recently, a number of studies have appeared in which the experimental schedules of reinforcement have been varied and the relations between salivation and the instrumental response have been further studied. It has been found, by Shapiro (1961), by Kintsch and Witte (1962), and by Ellison and Williams (1962), that when a food reward is presented under a fixed-interval schedule of reinforcement (cf. Ferster and Skinner 1957) a good temporal parallelism of the instrumental and the classical salivary response is found. With such a schedule, the first instrumental response made by the animal a fixed interval after the preceding food presentation is rewarded with food; under this schedule both salivation and instrumental responding occur nearly parallely just prior to the time of food availability, with the instrumental response perhaps slightly preceding the salivary response—a result which could be due solely to differences in recording latency between the two responses.

With another type of experimental schedule, „differential reinforcement of low rates", the animal is rewarded for low rates of responding. For example, if no instrumental responses have occurred during the previous 60 seconds, an instrumental response is followed immediately by food. However, repeating the instrumental response in less than 60 seconds is not rewarded. With such a schedule, both Shapiro (1962) and

Williams (1963) have found that the onset of the salivary CR consistently precedes the occurrence of the instrumental response. Insofar as this very complicated schedule of reinforcement fosters the development of unrecorded behavior which occurs prior to the recorded instrumental response, this result would not be at all incompatible with a strict parallelism between instrumental and salivary responses (see, e.g., the discussion by Shapiro 1962).

In a third type of schedule („fixed ratio"), a number of consecutive instrumental responses have been required of the dog in order to obtain food. The results with this procedure have differed with different experiments. Wolf (1963) reported a strict parallelism between instrumental and salivary responding with this schedule; a small increase in salivation followed each instrumental response. Ellison and Williams (1962), on the other hand, found that after prolonged training, salivation began only after about one-half of the 33 required responses had been performed. The results of Kintsch and Witte (1962) appear to confirm this latter finding, suggesting that the salivary response and instrumental responding may be partially dissociated when a long sequence of responses is required of the animal. The differing results on fixed ratio schedules seem to depend upon differences between the experimental procedures used by the different experimenters. In the experiments performed by Wolf, the instrumental CR consisted initially of a single movement, which was immediately reinforced by food. This single movement was firmly established and only then was the number of movements required for food increased. This was done relatively rapidly, so that the animals had no opportunity to acquire a true fixed ratio CR. On the other hand, in the experiments of Ellison and Williams fixed ratio responding was trained over a long period of time.

The results of all of these investigations may be summarized as follows: it seems clear that the degree of concomitance of the classical and instrumental response in alimentary conditioning depends upon the experimental procedure. In particular, if a CS has been presented many times under the classical CR schedule, its tendency to elicit an instrumental response is either little or none. On the other hand, if a CS has been presented for a long time under the instrumental CR training procedures, it elicits a strong instrumental response, while its salivary effect may be small or insignificant. The question of whether or not the instrumental response can be totally separated from the salivary response, and if so what the necessary conditions for such a separation are, has not been answered heretofore. The experiments presented in this paper were desigend to elucidate this problem.

I. SEPARATION OF INSTRUMENTAL AND CLASSICAL CS

MATERIAL AND METHODS

Subjects. The subjects were naive mongrel dogs with ages ranging from one to three years and weights from 10 to 15 kg. The instrumental training was begun on five dogs, but one of these developed strong neurotic symptoms and was discarded from the experiment proper. This dog will be reported separately. Successful experiments, then, were obtained from four dogs.

Apparatus. The method of collecting the saliva from the parotid duct was similar to that described by Sheffield (1957), involving the chronic cannulation of the intact duct with polyethylene tubing. This operation was not performed until all initial pretraining was completed and the dogs were performing well on the instrumental schedule.

The recording method involved a rigid tubing system ending with a No. 24 hypodermic needle fixed 60 cm. below the level of the conditioning stand. Drops from this needle were pierced by a second needle mounted immediately beneath the first needle, and this brief contact served to fire a thyratron tube which in turn operated the recording pen.

The experiments were carried out in the standard soundproofed Pavlovian chamber used in this laboratory. The dog, standing on the conditioning platform, could be monitored visually by E through a viewing window and could be heard or spoken to by E through a 2-way communication system. All stimuli within the chamber (lights, buzzers, and metronomes) were electrically operated by E from without. The experimental stimuli varied for different dogs, as will be described later.

The reinforcement used was a portion of boiled meat and bread cubes soaked in broth. The feeder consisted of a large disk containing a number of filled dishes which could be rapidly rotated into place by means of electrical control. The feeding schedule was arranged so that each S had a daily meal of meat and bread several hours after each daily session; as a consequence the dogs were always in good appetite during the experimental session but their normal body weight did not fall appreciably during the experimental training.

Experimental sessions were scheduled once daily six times weekly. The intervals between trials within sessions varied from one to five minutes, but usually varied only between three and four minutes.

The experimental manipulandum consisted of a clear plexiglass lever, 25 cm. wide, which projected 12 cm. through a slot cut in a clear plastic box. Depressions of this lever operated a microswitch, the output of which was used as the response criterion. The box rested on the conditioning stand floor to the right of the food tray, so that the animal was forced to turn slightly away from the food dish in order to efficiently press the lever. The normal response seen was a rapid striking of the lever with the right paw.

Pretraining. The dogs were first trained to eat from the feeder, and were then trained classically with a one-second CS-US interval to a conditioned stimulus, henceforth called classical conditioned stimulus. For dogs 1, 2, and 3, this stimulus was the sounding of a door buzzer which was mounted out of sight beneath the food tray; for S 4 it was a flashing 100-watt light bulb mounted in front of the conditioning stand at approximate eye level. This stimulus always overlapped several seconds with the presentation of food.

After this training was completed (4—5 days with about 14 trials per day) the experimental manipulandum was installed on the conditioning stand with a small box made of wire screening and filled with meat attached to the lever. When the subjects attempted to eat this meat and were prevented from doing so by the screening, they began to paw at the screening. These paw movements were reinforced with a brief presentation of the classical conditioned stimulus followed immediately by operation of the feeder. After one or two days of such training the wire box could be removed and paw movements to the nonbaited lever reinforced.

After a few additional days of this constant reinforcement training, a second stimulus, henceforth called the instrumental CS, was introduced. Now only those lever presses which occurred in the presence of the instrumental CS were reinforced (with the classical CS, followed by food). For Ss 1, 2, and 3, the instrumental CS was the lighting of a lamp mounted inside the transparent manipulandum; for S 4 it was the sounding of a door buzzer mounted in front of the food tray. The intervals between successive presentations of the instrumental CS were subsequently slowly lengthened to several minutes as training progressed. Finally, the number of presses required to produce the classical CS, and the CS-US interval during the classical CS, were gradually increased to 9 presses and 8 seconds, respectively. A typical trial at the end of training would, therefore, consist of onset of the instrumental CS, 9 lever presses, offset of the instrumental CS and onset of the classical CS, food presentation 8 seconds after the classical CS onset, and about 5 seconds overlap of the classical CS and food. The salivation operation was performed after each individual subject was performing well on this final schedule.

RESULTS

Instrumental responding during the CS. Throughout the duration of training, there was good instrumental responding during the instrumental CS; the mean duration of the instrumental CS (including the latent period and the time required to make the 9 presses) was 6.0, 4.5, 4.0 and 6.0 seconds, respectively, for subjects 1, 2, 3, and 4 at terminal training. After the initial latent period lever pressing began at a high rate and continued with an occasional pause until 9 presses had been recorded and the classical CS was turned on. The dogs would then quickly stop responding and turn to stare at the food bowl. Occasionally, Ss 2 and 4 would become impatient while waiting for food and would change position restlessly, sometimes standing up on the foodtray. This occurred rarely, and they would never perform the instrumental response during such episodes. It should be emphasized that it was not necessary to differentially reinforce non-responding during the classical CS. At no time was reinforcement withheld or delayed because of responding during the classical CS. In other words, the classical CS reflexly elicited non-responding throughout training.

Instrumental intertrial responding. Responding in the absence of either the instrumental or the classical CS occurred to an appreciable extent early in training, but gradually declined and, while it never completely reached zero for all of the dogs, it was clearly insignificant in comparison to the instrumental CS responding for all dogs, and was virtually non-existent in two of the dogs.

Salivation during the classical CS. The classical CS regularly elicited a salivary response, although the latency of this response and the total volume varied considerably from trial to trial. However, irrespective of what was the total amount secreted, the rate of salivation, being insignificant at the outset of the classical CS, increased towards the end of the CS-US interval.

Salivation during the instrumental CS. Early in training, a small salivary CR would frequently occur during the operation of the instrumental CS. This could take one of several forms: it sometimes occurred during instrumental responding, sometimes only during non-responding, and sometimes during both. As training progressed, the amplitude and frequency of these responses gradually decreased, as did intertrial salivary responding.

In two of the dogs (Ss 1 and 2), it was possible to demonstrate across one entire session during some stage of training a significant ($p < 05$) decrease in rate of salivation during the instrumental CS as compared with a control period just prior to the onset of the instrumental CS. This inhibitory effect became gradually less apparent as the intertrial salivation progressively decreased over training. Late in training, on those trials where salivation did occur just prior to the onset of a trial, this inhibitory effect could again be seen.

On some other trials, a small amount of salivation occurred during the instrumental CS, but in a manner so as to be negatively correlated with lever-pressing. On a typical trial where this effect was observed, the dog would begin to lever-press during the instrumental CS, stop after 4 or 5 presses and look toward the food bowl, only then begin to salivate, and finally return to complete the ratio with a rapid decline in salivation. This effect was quite striking to any observer accustomed to thinking of salivation as a sluggish, long-latency response, and accustomed to the usual positive correlation between salivation and instrumental responding.

A complete daily record (11 consecutive trials) of one day on which these two inhibitory phenomena were observed is presented in Figure 2 for S 1. It can be seen that on trials 2, 3, 5, and 6, lever-pressing and salivation are negatively correlated. It can also be seen that considering the session as a whole, the mean rate of salivation is less during the instrumental CS than during a comparable control period just before each trial. This effect was most noticeable in the dog shown, but was observed to some extent in other dogs.
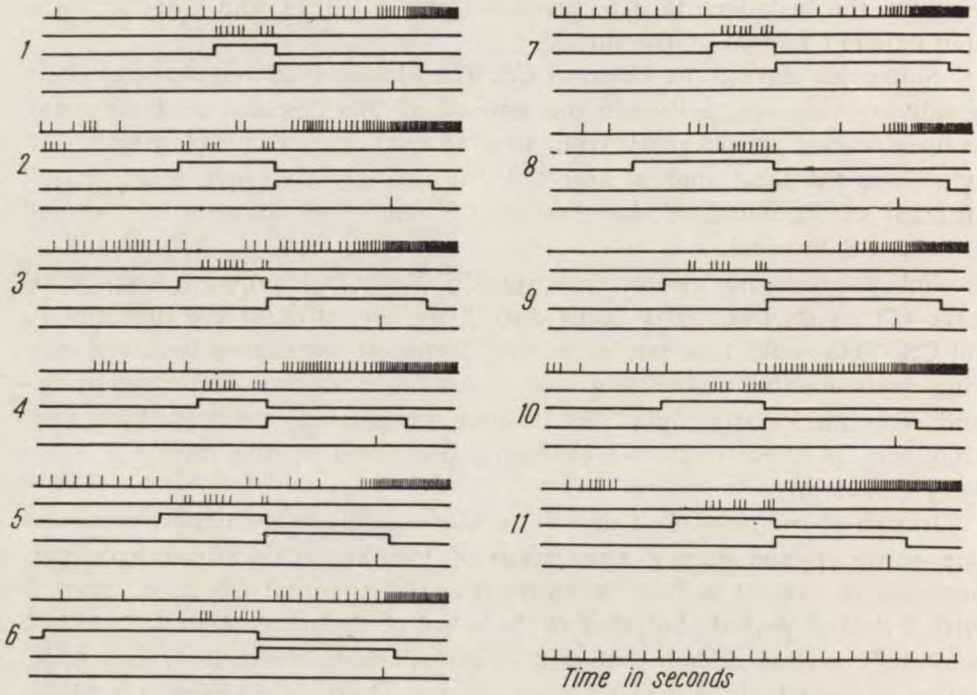
Fig. 2. A complete daily record (11 consecutive trials) of S 1 before terminal behavior had been reached. The stimulus markers are, from top down: salivary drops; lever-presses; the instrumental CS; the classical CS; food presentation. A decrease in salivary rate upon presentation of the instrumental CS can be seen on trials No. 1, 3, 4, 5, 7, 10, and 11. Salivary drops and lever presses are negatively correlated on trials Nos. 2, 3, 5, and 6

Typical results later in training are shown in Figure 3. This figure presents a representative series of 5 consecutive trials taken from the records of each dog at terminal performance. These records show rapid and sustained lever-pressing in each dog to the instrumental CS accompanied by low levels of salivation, and a lack of lever-pressing to the classical CS accompanied by a high rate of salivation. An averaged curve for each dog over one such terminal session is shown in Figure 4.

II. IMMEDIATE FOOD REINFORCEMENT OF THE INSTRUMENTAL CS

MATERIAL AND METHODS

After the above experiments had been completed, further training was given to Ss1 and 3. In this further training, the instrumental CS was followed immediately by food after the ratio of 9 lever-presses was performed. The classical CS

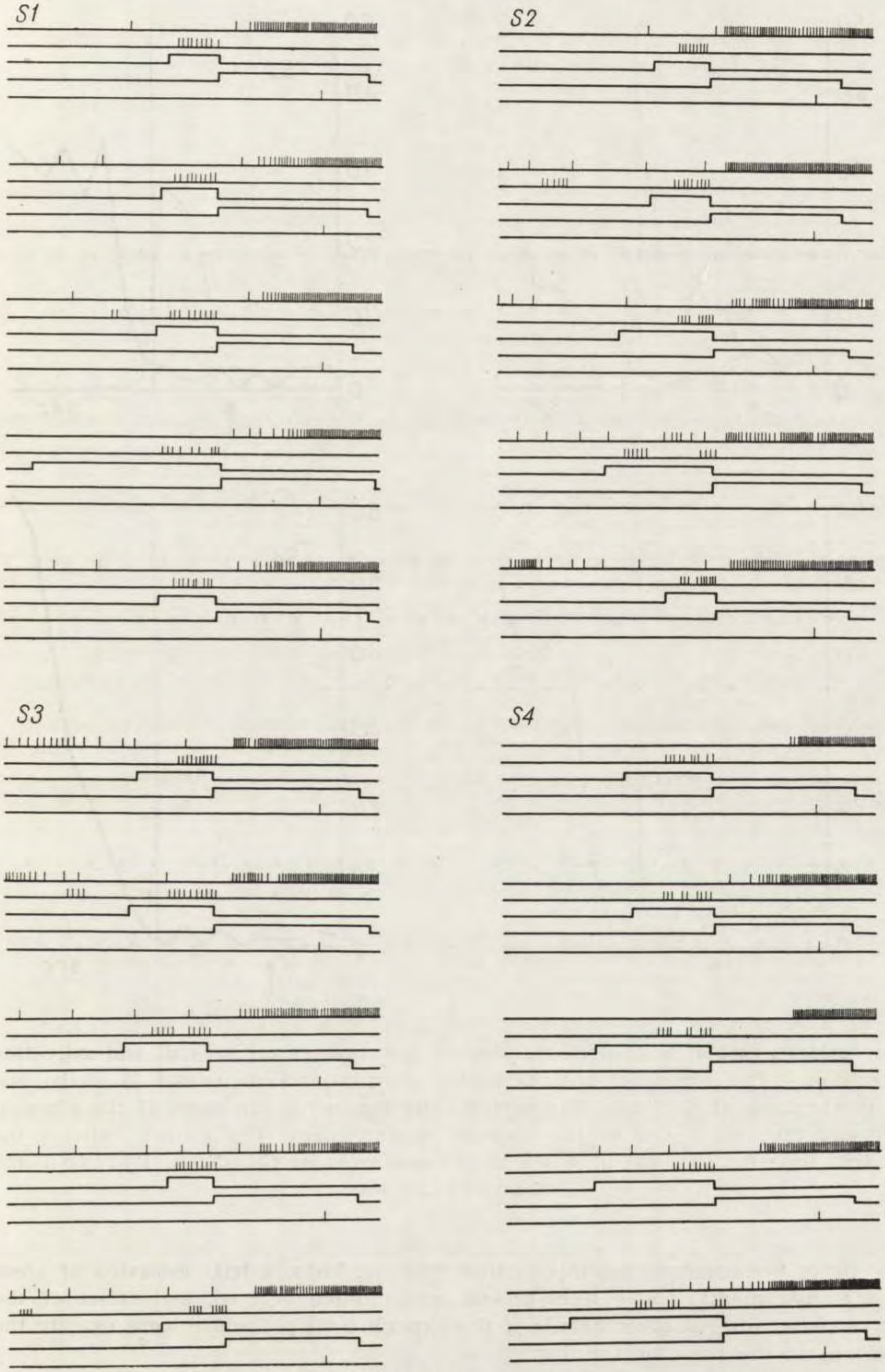

Fig. 3. A representative series of 5 consecutive trials taken from each dog's records at terminal training. Stimulus markers and time marker as in Figure 2

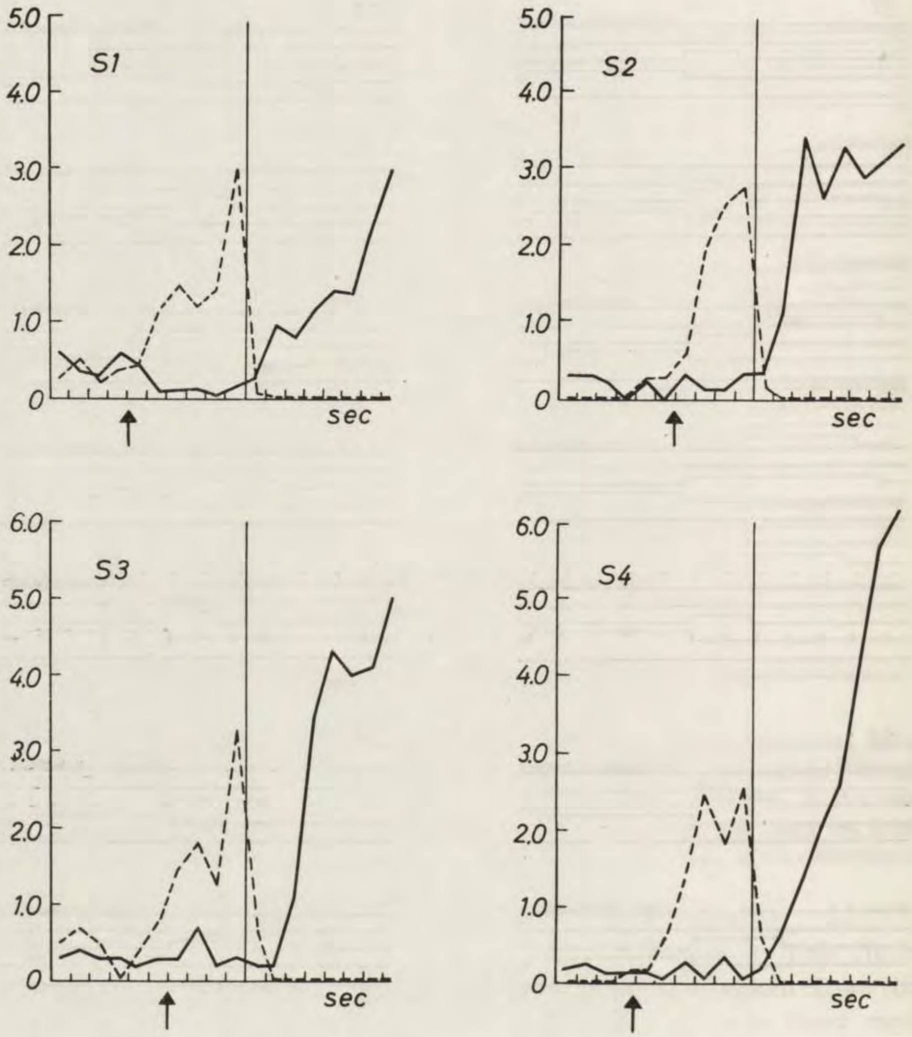

Fig. 4. Mean rate of lever-pressing (dashed line, presses per second) and salivation (continuous line, drops per second) during a typical session (about 15 trials) late in the training of each dog. The vertical line represents the onset of the classical CS, and the curves end at the time of reinforcement. The arrows indicate the median time (in seconds) of onset of the instrumental CS. (From Ellison and Konorski 1964)

was never presented during this further training. Thus, a trial consisted of onset of the instrumental CS, 9 lever-presses, presentation of food, and offset of the instrumental CS. All other details of the experimental procedure were exactly the same as in the previous training.

RESULTS

For the first few days following the introduction of this immediate reinforcement, neither the salivary nor the motor behavior showed any appreciable change. The first change noted, after about 4 days and 60 trials, was that the animals began to pause more frequently in lever-pressing, turn and look at the food bowl, and salivate. This behavior had been observed occasionally during delayed reinforcement training, but the frequency of these pauses increased greatly after the immediate reinforcement training.

After a total of 8 days of immediate reinforcement training (about 120 trials) the lever-pressing behavior was quite similar to that typically found with immediate reinforcement. The first few lever-presses were often emitted before any salivary CR occurred, an effect previously reported for fixed ratio responding (Ellison and Williams 1962). Then a pause in responding would usually occur and salivation would begin, continuing to the time of reinforcement. The responses toward the end of the ratio were almost invariably accompanied by salivation. The results after at least 9 days of training are shown in Figure 5. It can be seen that anticipatory salivation and lever-pressing occur generally at the same time.

While this concomitance between the two behaviors was being established, the instrumental behavior changed markedly. Whereas the be-

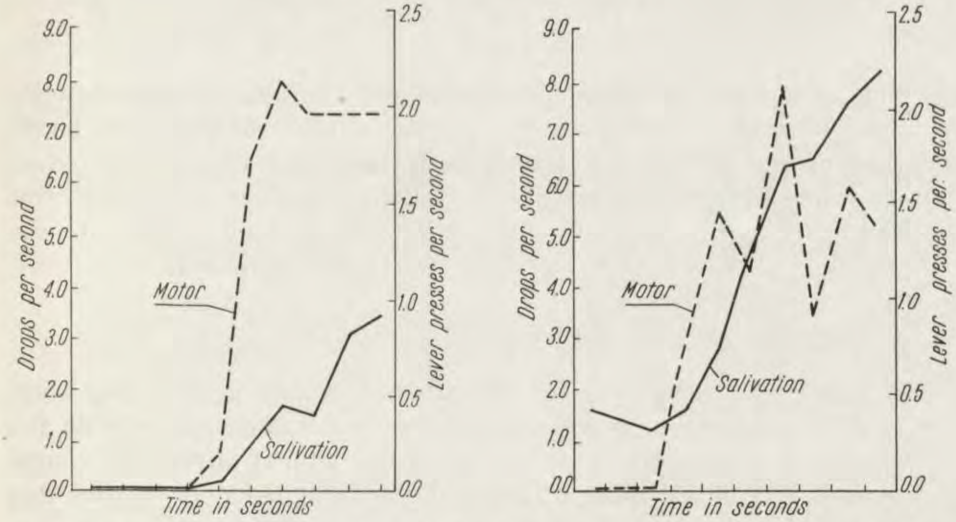

Fig. 5. Concomitance of salivation and lever-pressing after immediate reinforcement training. The curves end at the time of food delivery. On the left is the data of S 1; on the right, S 3

havior of these dogs at the termination of the original training (delayed reinforcement) usually consisted of a short pause between onset of the instrumental CS and onset of lever-pressing, and then a sustained bout of lever-pressing, the typical behavior with immediate reinforcement became one of short bouts of lever-pressing with glances at the food-bowl between each bout. In other words, the average rate of lever-pressing and the average number of presses between pauses declined. Relevant data are shown in Table I. S 1 generally had a short latency of lever-pressing at the end of delayed reinforcement training, and this latency remained unchanged. However, the average number of pauses in lever-pressing of one second or greater greatly increased after the introduction of immediate reinforcement. The latency to first lever-press was lowered in by the introduction of immediate reinforcement, but the average number of pauses during pressing was again increased.

Table I

A comparison of instrumental behavior before and after immediate reinforcement training. Means of 44 consecutive trials at the end of delayed reinforcement training and 44 consecutive trials at the end of immediate reinforcement training

Animal	Delayed	Immediate
Mean latency of first lever-press (in seconds)		
S1	1.43	1.44
S3	3.23	2.48
Mean number of pauses (of one second or longer) per trial		
S1	0.61	2.19
S3	0.79	1.80
Average time (in seconds) required to complete ratio of 9 presses		
S1	5.32	6.31
S3	8.00	7.95

III. UNSUCESSFUL EXPERIMENTS

As noted previously, the results obtained from the fifth dog were totally different from those reported above; this was connected with the experimental neurosis which developed in this animal during the course of training. A detailed description of the general behavior of this dog and its experimental data follows.

The dog was trained in the same manner as those described above, with buzzer as the instrumental CS and a flashing lamp as the classical

CS. The initial training was uneventful, and the behavior of the dog during pretraining was quite similar to that of the other dogs: to the instrumental CS, barking, general motor excitement, and vigorous instrumental movements were observed, while to the classical CS the dog rapidly quieted down and remained immobile, staring at the food bowl. About the time of the salivary operation this dog began to become more and more restless in the experimental chamber, and this situation progressively grew worse as further training progressed. On about half of the experimental days he completely refused to eat while in the chamber. He grew reluctant to come to the experiment, and when on the stand he struggled violently. His salivary CR became smaller and more variable even though he would continue to perform the instrumental movements correctly. After attempts to retrain this animal with a shortened CS-US interval for the classical CS failed, he was discarded. Examples of his salivary and instrumental behavior are shown in Fig. 6.

The trials shown are taken from assorted days during training, and were selected to provide a fair sample of the various types of trials which occurred. The last trial is representative of terminal performance. Du-

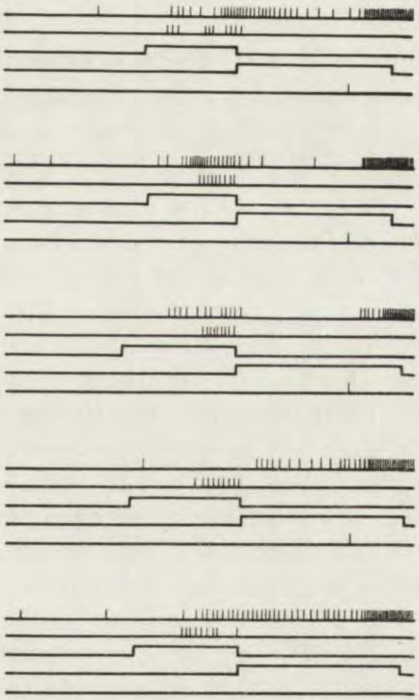

Fig. 6. Five trials representative of the general behavior of S 5. Signal markers and time scale as in Fig. 2

ring the instrumental CS on such trials, the dog would stare at the food--dish while making paw movements with the right forepaw. Because he was not attending to the lever, about half of these movements were abortive and consisted of merely pawing the air. Upon onset of the classical CS, he would usually cease lever-pressing, but would not look for food, rather moving about aimlessly, biting at his leash and his salivary recording fistula, and climbing up on the food tray. Extensive attempts to form a good classical CR to the flashing lamp failed, and this resistance to conditioning surely was the cause of the failure of the experiment.

DISCUSSION

The original hypothesis of Konorski and Miller (1933, 1936) proposed that classical and instrumental conditioned responses are inherently linked, in that an instrumental response can be established when, and only when, its proprioceptive feedback becomes a classical food CS. It was similarly proposed that extinction of this classical CR to the proprioceptive feedback should lead to the extinction of the instrumental response.

This hypothesis implies that (1) proprioceptive feedback from a trained movement is indispensable for the formation of an instrumental CR, and (2) that the performance of an instrumental movement should invariably be followed by salivation.

Knapp et. al. (1958), Jankowska (1959), and Górska and Jankowska (1961) have recently provided evidence showing that proprioceptive feedback from a limb is not indispensable for the preservation, or even establishment, of an instrumental CR. This evidence would constitute a refutation of the above hypothesis unless it were assumed that intercentral feedback could be substituted for the peripheral feedback (cf. Konorski 1962). However, the finding that in instrumental conditioning salivation does not necessarily follow the instrumental movement and that the parallelism between the two responses is often far from being precise seems to cast doubt on even this weaker version of Konorski and Miller's general thesis. Indeed, unless it is assumed that systems of classically conditioned CR's other than that measured by salivation exist, the demonstration that salivation, the traditional exemplar of the classical CR, can be uncorrelated or even negatively correlated with instrumental performance would cast doubt on any theory which attempted to correlate the two types of responses (e.g., Mowrer 1960).

Sołtysik (1960), on the basis of Konorski and Miller's earlier studies of alimentary CR's, has proposed that while a classical CR based on the consummatory feeding act may be considered as a consummatory CR, instrumental responding is the effect of an entirely different CR—the drive CR. The present data are in agreement with this separation of the drive CR on the one hand and the consummatory CR on the other, and allow us to clarify in more detail the particular effects of each of these CR's.

In the investigations of instrumental performance carried out by the behavioristic school, instrumental responding has usually been considered as being energized by the drive state of the animal (Hull 1943, Miller 1951, Sheffield unpublished, and Spence 1956). This drive can be classically conditioned, and results in motor arousal (Sheffield and Campbell 1954). Many neurophysiological studies, such as the studies of the effects of hypothalamic stimulation in waking animals initiated by Hess (1949) and the later ablation studies, such as that of Anand and Brobeck (1951) have provided a precise physiological meaning of the term „drive". Later studies by Miller (1957) and by Wyrwicka et. al. (1959) have shown that the instrumental food response can be indeed faithfully driven by the hunger drive produced artificially by stimulation of the lateral hypothalamus. Thus, the evidence for a drive CR seems adequate.

If the hyperactivity representative of the pure drive CR is adaptive for seeking food, quietness when food is very close at hand is also adaptive for the hunting carnivore. Just such behavior was observed during the classical CS. The existence of a consummatory CR, as distinct from the drive CR, can be inferred from several different observations. The main effect was, of course, the conditioned salivary response. A second effect was the inhibition of both lever-pressing and general activity which occurred upon presentation of the classical CS. This inhibition was correlated with an intense staring at the food bowl, and was similar to that reported originally by Konorski and Miller. The classically conditioned consummatory reflex must be very well established in order to observe this effect. In several experiments (Shapiro and Miller 1963, Bower and Grusec 1964) where presentation of a positively reinforced CS resulted in an increase in instrumental responding, the consummatory CR was probably not so strongly established.

Heretofore, the question of whether or not the conditioned hunger drive directly elicits salivation had remained unanswered. The results reported above definitely indicate that salivation does not belong to the repertory of the direct effects of the conditioned hunger drive.

The question of why a clear separation of the hunger CR and the consummatory CR was possible in our experimental situation arises. Although a complete answer to this question requires further experimentation, the following factors seem to be relevant:

(1) The lever which the animals were required to press was situated on the right side of the feeder, so that the dog had to turn about 45 degrees in order to perform the trained movement. The question is open as to whether a similar lack of salivation during the instrumental responding would have been obtained if the movement had not implied turning away from the feeder, as is the case when the trained movement entails placing the foreleg on the food-tray or lifting the hindleg. It seems quite likely that the clear-cut antagonism (as distinct from the separation) between instrumental responding and salivation seen in at least two of our dogs is attributable to this factor. Just as turning toward the food bowl is certainly and important component (both proprioceptive and visual) of the compound classical CS, turning away from the bowl must make the CS compound less potent.

(2) Spatial contiguity between the classical CS and the place of feeding may contribute to the purity of the classical CR and the lack of its contamination by the instrumental CR.

(3) However, while the two preceding factors might have played an auxiliary role in the success of our experiment, the decisive role was certainly played by the two-segment character of our procedure: the instrumental CS was separated from the time of food presentation by the firmly established classical CS. The decisive character of this factor is clearly shown by the demonstration that when the instrumental CS was immediately followed by food, the salivary and instrumental responses occurred in parallel. The normal process of inhibition of delay in salivary conditioning was heightened in our experiments by the sequential nature of our CS'i (the so-called „masking" of the first stimulus by the second). This was crucial for a full separation of the two responses in our experiments.

Previous investigations of the interrelations between the salivary CR and instrumental responding have indicated a complex relationship between these two responses. The reasons for this become clearer when viewed in the light of our experiments. While the hunger CR, which is responsible for instrumental performance, and the consummatory CR, which is responsible for the salivary response, can be produced by two different stimuli, as was the case in our experimental procedure, they can also be elicited by the same stimulus, as is the case in the majority of earlier experiments. In fact, when the instrumental CS is regularly and closely followed by food, it becomes ipso facto a signal of food—i.e., a classical CS. The more classical its character, the more copious is the salivary response, and the poorer may be its motogenic power; on the other hand, the stronger its instrumental character, the stronger is its motogenic capacity and the poorer the salivary response (cf. Ellison and Konorski, in press). It should be recalled that if the food reinforcement closely follows the performance of the trained movement, the proprioceptive feedback from this movement will certainly become a classical food CS, as is shown by the experiments using the salivary-motor experimental procedure. Although this effect is a usual by-product of instrumental learning, it does not seem to be an indispensable condition for the formation of the instrumental response.

Finally, the contradictory results obtained from our fifth dog need some comment. From the description of this dog's behavior it seems clear that the dog developed a heavy experimental neurosis, with all of the typical symptoms described long ago by Pavlov and confirmed by many others. In this category belong such symptoms as: motor excitement, a tendency to escape from the stand, erratic and unpredictable CR's, and frequent refusals to eat food in the experimental chamber. The fact that the neurotic behavior developed immediately after the insertion of the polyethylene tube into his salivary duct suggests that this operation produced some discomfort to which the animal could not habituate. On the other hand, it should be noted that the instrumental CS often produced not only the instrumental response but also salivation in this dog. Since the instrumental CS for this dog was a buzzer (a strong stimulus) and the classical CS was a lamp (a weak stimulus), it seems likely that both the drive CR and the consummatory CR were conditioned to the first simulus. Thus, the animal expected food immediately after the buzzer, and the additional stimulus interspersed between the buzzer and food may have become the cause of the neurotic symptoms.

SUMMARY

1. Dogs were trained on an experimental schedule with the following final result: to a stimulus called the instrumental CS, the animal was required to perform 9 lever-presses, whereupon the stimulus was turned off and another stimulus, called the classical CS, was presented. Eight seconds after the onset of the classical CS the dog was given food.

2. With this schedule the instrumental and classical conditioned responses appeared to be virtually completely seperated. The animals performed the trained movement without salivation in response to the

first segment, and salivated without performing the movement in response to the second segment.

3. In some dogs a clear antagonism between the classical and the instrumental conditioned response was observed. The lever-pressing coincided with the cessation of salivation and salivation coincided with the cessation of motor responding.

4. When further training was given with the instrumental CS reinforced immediately by food, the salivary and motor response began to occur parallely, as is the case in the typical salivary-motor training procedure.

5. The significance of these results for the interpretation of the relationship between classical and instrumental CRs is discussed.

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THE INFLUENCE OF STIMULUS INTENSITY ON THE EFFICACY OF REINFORCEMENT IN DIFFERENTIATION TRAINING[1]

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It is widely accepted that the ease of differentiation training is primarily related to the discriminability of the stimuli presented. However, little attention is usually paid to the fact which stimulus from the pair serves as the positive conditioned stimulus[3]. As far as stimulus intensity differentiation is concerned, in which the training of a CR to the CS(+) is followed by the extinction of the CR to the CS(−), different results might be expected, depending on whether the strong or the weak stimulus from the pair is used as the CS(+). Experimental evidence on brightness differentiation (Antoinetti 1950) and recent data on auditory differentiation (Moore 1964) are in favour of Hull's prediction (1952), who suggested less difficulty with a differentiation in which the strong stimulus from the pair serves as the CS(+), than with a differentiation in which the CS(+) is a weak stimulus. The theories of Pavlov and Konorski, which seem to predict greater generalization from a stron-

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[3] We follow the terminology that the conditioned stimulus associated with the presentation of the unconditioned stimulus (independently whether the reinforcing agent is atractive or aversive) is called a positive one or CS (+), and the conditioned stimulus not „reinforced" by a presentation of the unconditioned stimulus is called a negative one or CS (—).

ger to a weaker stimulus than from a weaker to a stronger stimulus, would predict the opposite results.

The aim of this study was to retrace the course of differentiation training of two auditory intensities, depending on whether the stronger or the weaker stimulus was used as the CS(+). The technique used was developed by Estes and Skinner (1941) and labelled as a conditioned emotional response (CER) training. During the preliminary training, the experimental situation becomes the conditioned stimulus for bar-pressing behavior which is followed by food reinforcement. When the CER acquisition starts, the compound consisting of the experimental situation and the CS(+) is followed by electric shock (evoking fear responses interfering with bar-pressing for food), whereas the experimental situation alone is not related with shock and as before is associated with food reinforcement. The CER acquisition involves, in fact, the discrimination of two drives, one related to the whole experimental situation, and the second related to the CS(+). When the CS(−) is introduced, the subject (S) learns to inhibit the fear response, which is at first generalized to the CS(−) from the CS(+). This extinction of fear allows the S to bar-press for food during the negative trials. Thus, with regard to the fear response as a determining factor, the training follows the „differentiation" paradigm, because the fear CR is continuously evoked by the CS(+) but becomes extinguished to the CS(−).

It has previously been shown that the CER method is very suitable for parametric studies of the CS intensity function (Kamin and Brimer 1963, Kamin and Schaub 1963). We expected that having a long CS-US interval, commonly used in CER studies, and the opportunity to measure the behavior during intertrial intervals (ITI) we would obtain more information on the course of differentiation training.

MATERIAL AND METHODS

Subjects and apparatus. The Ss were 20 experimentally naive male hooded rats from the McMaster Univ. colony, approximately 6.5 mo. of age at the beginning of the experiment. The apparatus consisted of 8 standard Grason-Stadler operant-conditioning units, with relay, timer, and counter systems providing for automatic programming and recording. The CSi were white noise from a Grason-Stadler Model 90IA noise generator, delivered to the experimental box via a loudspeaker. To maintain constant day-to-day noise levels, the volume dial of the noise generator was set at a fixed position and standard resistors were connected in series with the generator and speakers as required by the experimental design. The mean background noise level of the experimental boxes, with exhaust fans operating, was 62 db measured by a General Radio sound survey meter. Two white noise intensities were used, 80 db and 50 db, measured with the fans disconnected, both were clearly audible through the background noise of the blowers. The US was electric shock provided by a Grason-Stadler Model EI064GS generators. Shock generators were set at „1.0 m.a.", but the current acctually delivered to the grid-floor with the representative male rat in the circuit was about .85 ma. according to an estimate made by Annau and Kamin (1961). The circuit was of the constant type (high voltage, high resistance), which minimized the effect of changes in the rat's resistance on current flow. The shock presentation was of 0.5 sec. duration, and a grid scrambler prevented avoidance of the shock during that period as long as the S was in contact with the grid, walls, or lever.

Experimental design. Prior to any training the Ss were randomly distributed into two experimental groups, 10 Ss each. The experiments were run in three squads counter-balanced between experimental groups. The experimental units were not completely counter-balanced between groups. Both experimental groups had exactly the same treatment in all stages of the experiment except for the white noise intensities used as positive and negative CSi. For Group 1 the termination of 80 db white noise CS coincided with the US application and the termination of the 50 db white noise did not, whereas for Group 2 these relations were reverse. Each CS was presented four times during the two hours daily experimental session, onset of the stimuli terminated with US („positive trials") were at 18.5, 53.5, 74.5, and 92.0 min., and onsets of stimuli not terminated with US („negative trials") at 29.0, 43.0, 61.0, and 106.0 min. after beginning of the session. The CSi durations were 3 min. throughout the whole experiment.

Preliminary training. The Ss were reduced to 75% of ad lib. body weight, and maintained at that weight throughout the experiment, daily portions being given immediatelly after the experimental session. An initial presentation of 40 „free" food pellets on an 1-min. variable interval (VI) schedule („magazine training") was immediatelly followed by a period with a continous reinforced schedule until 120 food pellets were delivered in a single session. Then followed five daily 2-hr. sessions of bar pressing under a 2.5-min. VI food-reinforcement schedule, resulting in acquisition of stable on-going bar-pressing behavior for food. The reinforcement was standard 45 mg Noyes food pellets.

Pretest day. On the next day after preliminary training, CSi were presented in the appropriate time and order both without the US application. The food-reinforcement schedule and the application of the CSi were programmed independently throughout the whole experiment.

CER acquisition and differentiation training. The CER training begun next day after the pretest day, and continued for five days. Only positive trials were presented during this stage of the experiment. During the differentiation training, which begun on the next day, both positive and negative trials were applied.

Measures. For each trial numbers of bar presses were counted independently for 3 minutes before the CS onset (pre-period), and for two 90 secs. periods during the action of the CS (CS-period). The magnitude of the CER was measured by computing the „suppression ratio" described by Annau and Kamin (1961). The ratio is $\frac{B}{A+B}$ where B represents number of bar presses emited during the 3-min. CS-period, and A — number of bar presses during the pre-period also of 3-min. duration. Thus, a ratio of 0 indicates complete suppression of the bar-pressing behavior during the CS, while .50 indicates no effect of the CS on bar-pressing rate. If not indicated otherwise, the ratio was computed for each S and each trial independently. „Daily" ratios were computed for each S by summating responses during the appropriate time intervals in a single session for the four positive and the four negative trials independently. If necessary, suppression ratios were computed for each half of the CS-period independently, and then a product of 2 times the number of bar presses in the given half of the CS-period was used as B in the formula mentioned above. For testing the hypothesis whether or not application of the CS was evoking any changes in the on-going bar-pressing behavior, a comparison of the numbers of responses during the pre-period and the CS-period was done for a given experimental group using the Wilcoxon matched-pairs signed-ranks test (Siegel 1956). The criterion used as an index of the differentiation was: two consecutive days without overlapping in suppression ratios between positive and negative trials in each session independently. In such a case the Mann-Whitney U statistic (Siegel 1956) has value 0, considering suppression ratios for four positive and four negative trials as independent „samples". Probability of occurence of such a behavior by chance in a single session is as small as $p=.014$ (one-tailed test). The differentiation training lasted until the S reached criterion, but no longer than for 20 sessions.

RESULTS

Pretest day. The first presentation of the white noise interfered with bar-pressing and the median of the ratios for the first 90 secs. of the first presentation was .27 in the Group 1 (80 db stimulus), and .45 in the Group 2 (50 db stimulus). This effect was only shortlasting and the medians of the ratios in the second half of the first stimulus presentation equal .50 for both groups.

Daily suppression ratios computed for each stimulus intensity and individual Ss independently ranged from .43 to .60. Comparison of these ratios for different white noise intensities within each group (Wilcoxon matched-pairs test), as well as for the same intensity in different groups (Mann-Whitney test) showed no difference.

CER acquisition. The median daily suppression ratios in consecutive sessions are given in Fig. 1 for Group 1 and in Fig. 2 for Group 2. In accordance with previous studies (Kamin and Schaub 1963), acquisition of the CER was more rapid with stronger CS (80 db, Group 1) than with weaker CS (50 db, Group 2). When daily ratios for both groups were compared, already on the second day of the CER acquisition experimental groups differed in amount of suppression ($p < .02$ and this difference remained significant on the $p < .02$ level throughout the whole CER acquisition period (Mann-Whitney test, two-tailed).

As far as Group 1 alone is concerned, the first statistically significant change in the number of bar presses was observed on the sixth CS-US presentation (the second day of CER training), and suppression remained significant on all further trials of the CER acquisition period.

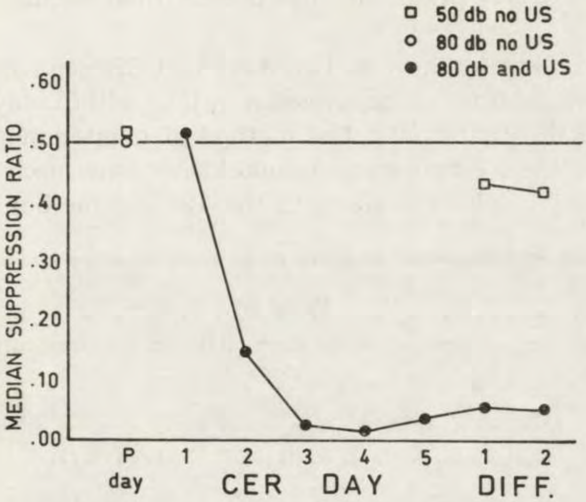

Fig. 1. Median daily suppression ratios during the P-day, CER acquisition, and differentiation training in the Group 1

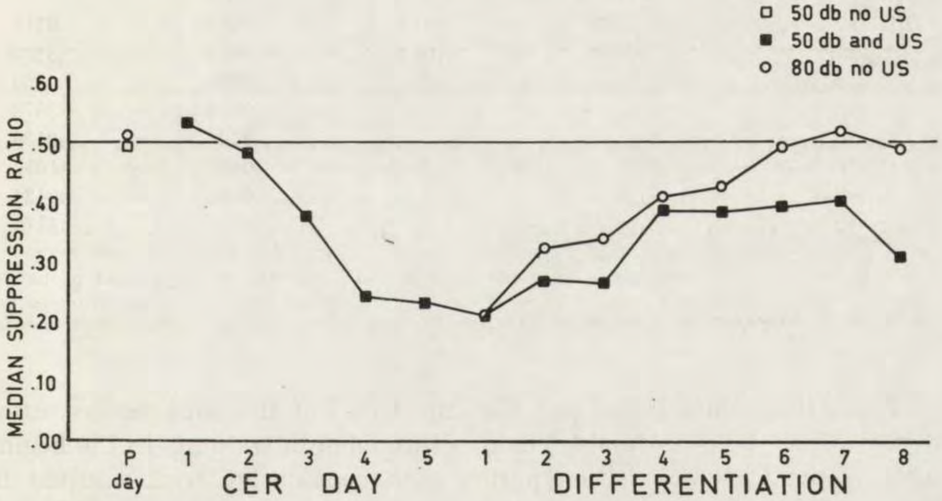

Fig. 2. Median daily suppression ratios during the P-day, CER acquisition, and differentiation training in the Group 2

In Group 2 the 50 db CS did not evoke significant changes in the number of bar presses until the 9th presentation. However, the following three trials of the third session failed to show significant suppression and only during the last two days of CER training there were significantly lower numbers of bar presses during the CS than during the pre-period in each trial.

In Group 2 even in the last two days of CER acquisition there was considerable variability of suppression ratios within days with better suppression in the first trials. The method of nonparametric trend analysis suggested by Fergusson (unpubl.) has been used for estimation of this data and results are given in the Table I for both experimental groups[4].

Table I

Trend analysis of the suppression ration over trials within consecutive experimental sessions

Days of training	Group 1		Group 2	
	80 db CS (+)	50 db CS (–)	50 db CS (+)	80 db CS (–)
P-day	– p = .4502	– p = .7490	– p = .5892	– p = .0238
CER 1st	+ .0136	.	0 1.0000	.
2nd	+ .0001	.	+ .1388	.
3rd	+ .2460	.	+ .7948	.
4th	0 1.0000	.	– .0090	.
5th	– .0124	.	– .0032	.
Diff. 1st	– .0628	– .1616	– .0702	– .0114
2nd	– .0930	– .1616	– .0536	– .3222
3rd	.	.	– .8886	– .3788
4th	.	.	– .0024	– .3078
5th	.	.	– .2802	– .0124
6th	.	.	– .0022	– .1032
7th	.	.	– .0124	– .0424
8th	.	.	– .1586	– .3270

In the body of the table there are given signs of the S statistic and two-tailed probabilities associated to them. The sign "+" means that the CS results in greater suppresion in the last trials, and sign"—" denotes smaller suppression toward the end of a given experimental session.

From these data it is clear that the trend of the suppression ratios over trials shows considerable changes throughouth training. In the beginning of the CER acquisition period each consecutive trial resulted in better suppression. In Group 1 this trend was significant during the 1st and the 2nd acquisition days and indicate rapid shaping of the CER. However, after the suppression ratios reached asymptote, the trend chan-

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[4] The method developed by Fergusson (unpubl.) employs the S statistic as used by Kendall in the definition of a coefficient of rank correlation, *tau*. The null hypothesis was tested against the two-tailed research hypothesis that a monotonic (increasing or decreasing) trend in amount of suppression over consecutive trials within a given experimental session exists.

ged its direction in both experimental groups. In the end of the CER acquisition, as well as during differentiation training, better suppression was observed in the beginning of the experimental sessions. This trend reached significance in several cases in both groups, but in terms of median suppression ratios these changes were more pronounced in Group 2 than in Group 1 (compare Table III).

The long CS-US intervals usually used in CER studies permit us to test whether or not there were any changes in number of bar presses during the action of the CS. Numbers of bar presses for each S and session were cumulated over four trials for the first and for the second half of CS-US interval independently. As seen from Table II, beginning from the 2nd day of CER training the Ss in Group 2 generally showed smaller number of bar presses in the first than in the second half of the CS-period and these differences reached significance toward the end of the CER training ($p < .05$ for the 4th, and $p < .02$ for the 5th day: Wilcoxon matched-pairs test, two-tailed). Analogous analysis for Group 1 is meaningless because of nearly perfect suppression in all Ss, but according to the median values shown in Table II the tendency is rather the opposite one.

Table II

Median numbers of bar presses per min. emitted during the first (a) and during the second (b) halfs of CS-periods in consecutive days of training

	CER acquisition days										Differentiation days			
	1st		2nd		3rd		4th		5th		1st		2nd	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b
Group 1														
positive trials	11.4	11.7	1.9	1.7	.4	.1	.2	.1	.4	.2	.9	.8	.9	1.2
negative trials*	12.5	11.9	6.4	16.7	15.5	14.0	13.1	15.2	15.2	14.9	5.4	7.6	7.9	9.2
Group 2														
positive trials	12.0	11.8	9.5	10.7	5.5	8.7	1.7	2.8	1.3	2.0	2.3	3.7	2.7	3.7
negative trials*	9.6	10.8	7.9	8.5	9.0	10.1	9.2	9.2	9.2	9.8	3.0	2.7	2.0	4.1

Scores underlined with a single line differ at $p < .05$ level, with a double line — at $p < .02$, and with a triple line — at $p < .01$ level (two-tailed).

* Scores given in these rows mean for the CER acquisition period "dummy trials" (see explanation in the text).

Differentiation training.

Group 1. In the case when 80 db CS is followed by shock and 50 db CS is not, the differentiation is quite easy. Seven Ss reached the required criterion during the first two days, and the remaining — after 3, 9, and

12 days of training. It means that for the most of the Ss there was no overlap in amount of suppression between positive and negative trials from the very beginning of the differentiation training. The statistic used as the differentiation criterion does not tell us whether or not the 50 db CS results in any decrease in number of bar presses; it tells us only whether changes in negative trials are smaller than in positive ones and permits to measure degree of overlap. Data shown in Table III demonstrate that the first presentation (after the CER acquisition) of the 50 db CS results in considerable suppression of ongoing behavior (median ratio equals .16), whereas in the next negative trials changes evoked by the CS(−) presentations were small (by the second application median ratio equals .44).

Table III

Median suppression ratios in each trial during the last day of the CER acquisition and the beginning of the differentiation training

Days:	CER 5th day				Diff. 1st day				Diff. 2nd day			
Trials:	1	2	3	4	1	2	3	4	1	2	3	4
Group 1												
80 db CS (+)	$\underline{\underline{\underline{0}}}$	$\underline{\underline{\underline{0}}}$	$\underline{\underline{\underline{.05}}}$	$\underline{\underline{\underline{.04}}}$	$\underline{\underline{\underline{.01}}}$	$\underline{\underline{\underline{.04}}}$	$\underline{\underline{\underline{.04}}}$	$\underline{\underline{\underline{.14}}}$	$\underline{\underline{\underline{.04}}}$	$\underline{\underline{\underline{.02}}}$	$\underline{\underline{\underline{.10}}}$	$\underline{\underline{\underline{.06}}}$
50 db CS (−)*	.49	.52	.50	.50	$\underline{\underline{\underline{.16}}}$	$\underline{\underline{.44}}$	.41	$\underline{\underline{\underline{.45}}}$	$\underline{\underline{\underline{.42}}}$	.46	$\underline{\underline{.43}}$	.47
Comparison within "pairs" p<	.01	.01	.01	.01	.02	.01	.01	.01	.02	.01	.05	.01
Group 2												
50 db CS (+)	$\underline{\underline{\underline{.11}}}$	$\underline{\underline{\underline{.28}}}$	$\underline{\underline{\underline{.23}}}$	$\underline{\underline{\underline{.25}}}$	$\underline{\underline{\underline{.06}}}$	$\underline{\underline{\underline{.23}}}$	$\underline{\underline{\underline{.26}}}$	$\underline{\underline{\underline{.27}}}$	$\underline{\underline{\underline{.03}}}$	$\underline{\underline{.22}}$	.43	$\underline{\underline{\underline{.36}}}$
80 db CS (−)*	.54	.52	.53	.50	$\underline{\underline{\underline{.07}}}$	$\underline{\underline{\underline{.17}}}$	$\underline{\underline{\underline{.19}}}$	$\underline{\underline{\underline{.27}}}$	$\underline{\underline{\underline{.29}}}$	.37	$\underline{\underline{.36}}$	$\underline{\underline{.26}}$
Comparison within "pairs" p<	.01	.01	.01	.01	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.02	n.s.

Scores underlined with a single line denote suppression significant at $p < .05$ level, with a double line — at $p < .02$, and with a triple line — at $p < .01$ level (two-tailed).

* Scores given in these rows mean for the 5th day of CER acquisition "dummy trials" (see explanation in the text).

To analyze the generalization of suppression from 80 db to 50 db CS, a method similar to that used for testing significance of suppression during CER acquisition stage was used. This analysis shows that differences in numbers of bar presses just before and during the presentation of the 50 db CS, although small, were quite consistend and in six out of eight negative trials of the first two days of differentiation training the suppression was statistically significant. This information is given in Table III for both experimental groups. Median suppression ratios shown for the 5th CER acquisition day in the row labeled „negative trials" mean so called „dummy ratios". Thiese ratios were calculated for corresponding time intervals, when no negative CS was given and indicate that there were no systematic changes in numbers of bar presses before the 50 db CS was applied.

One may wonder whether the 7 Ss which reached differentiation criterion without any additional training showed such a generalization of suppression to the negative stimulus. The same test applied to them only showed that suppression was significant in the first and the second negative trials both in the first and the second day of differentiation training.

The order of positive (+) and negative (−) trials was as follow: +, −, −, +, −, +, +, −, what provided us the possibility to compare amount of suppression in positive and negative trials within consecutive four „pair" of trials. Such a comparison must be done with caution, because order of positive and negative stimuli was different within pairs, as well as time intervals between consecutive trials. However, this analysis has shown significant differences in suppression ratios between positive and negative trials within each „pair" of stimuli (Wilcoxon matched-pairs test, two tailed, compare Table III).

There is one more fact worth mentioning. During the first day of differentiation training the 50 db CS(−) had more disruptive effect in the beginning of each presentation than toward the end, and this difference was significant ($p < .01$, Wilcoxon matched-pairs test, two-tailed, compare Table II). This behavior was maintained only during the first negative trial of the next day (and for this trial alone the difference was significant at $p < .05$), but in the following trials the opposite was true and the difference for the whole second day did not reach significance.

Inspection of Fig. 1 suggests that the introduction of the 50 db CS had some effect on positive trials, however, this effect was not significant neither in amount of suppression in comparison with previous session, nor in variability within session.

Group 2. Differentiation training in this experimental group, with 50 db as the positive CS and 80 db the negative one, was extremely slow, as compare with Group 1. The first S reached criterion after 8 days and next Ss — after 10, 11, 13, 16 and 17 days of training. Four Ss did not reached the required criterion during 20 sessions of the differentiation training.

In two Ss of this group dramatic changes of the ongoing bar-pressing behavior occured: after the first application of 80 db CS they stopped responding for the whole session, and only occasionally they gave a „burst" of responses separated by 15—30 minutes of „silence". Such behavior was caused neither by changes in motivation for food, nor by illness, and after several days rapidly disappeared. A similar, although less pronounced, depressing effect was shown in two other Ss in the beginning of CER training (one from Group 1 and the second from Group 2).

As seen in Table III, during the first two days of differentiation training, the 80 db CS(−) consistently resulted in significant suppression of bar presses. This effect disappeared slowly and only after five days of differentiation training was there no significant suppression to 80 db CS(−) any more. Comparison within „pairs" of stimuli shows that as a rule there were no significant differences in suppression ratios between positive and negative trials. Actually, in the 3rd „pair" of the second day of the differentiation training there was significantly greater suppression to 80 db than to 50 db CS (Table III) and the significant opposite relation occured only in four cases during the 4th, 7th, and 8th days of differentiation training.

Daily suppression ratios to 80 db CS(−) showed regular decrease of the amount of suppression, and Friedman two-way analysis by ranks (Siegel, 1956) applied to this index from the 1st to the 8th day of differentiation training showed that differences between days were far beyond $p < .001$ level. However, this was accompanied by a decrease in the amount of suppression to the 50 db positive CS and analogous analysis showed that these differences were significant at $p < .01$ level.

Throughout the whole differentiation training there was considerable variability in the amount of suppression in positive trials within each session, with greater suppression occuring in the first trials (Table I).

In this experimental group during CER acquisition period there was more suppression in the first than in the second half of the CS-US period. This was also true for the beginning of differentiation training (Table II), but this pattern disapeared later on, concurently with smaller suppression of bar pressing in positive trials. There was no difference in number of bar presses during the first and second half of the CS period on negative trials.

Comparison of the groups. Direct comparison of performance in both experimental groups was done in terms of daily suppression ratios. Corresponding data are given in Table IV for the beginning of differentiation training and in Table V for criterion sessions. As seen from Table IV in the beginning of differentiation training there were significant differences in ratios in positive trials, which conform to differences in the end of CER acquisition period. In negative trials there was more suppression in Group 2 and for the first day of differentiation training this difference was significant ($p < .05$ Mann-Whitney U test, two-tailed).

For the next comparison Group 2 was split into two subgroups: the Ss which reached criterion, and those Ss which did not. For the latter subgroup in the body of Table V are given data from the 19th and the

Table IV

Median (and range) daily suppression ratios in positive and negative trials during the last day of the CER acquisition and the beginning of the differentiation training

	N	CER 5th	Diff. 1st		Diff. 2nd	
		CS(+)	CS(+)	CS(−)	CS(+)	CS(−)
Group 1: 80 db CS(+) 50 db CS(−)	10	.04 (0−.11)	.06 (0−.19)	.43 (.19−.49)	.05 (.01−.64)	.42 (.24−.53)
Group 2: 50 db CS(+) 80 db CS(−)	10	.23 (0−.39)	.21 (0−.36)	.21 (.01−.67)	.27 (.03−.50)	.32 (0−.62)
Comparison between experimental groups:		p<.02	p<.02	p<.05	p<.05	n. s.

Table V

Median (and range) daily suppression ratios in positive and negative trials during criterion sessions

	N	Ist day		2nd day	
		CS(+)	CS(−)	CS(+)	CS(−)
Group 1: 80 db CS(+) 50 db CS(−)	10	.08 (0−.33)	.46 (.19−.52)	.06 (.01−.26)	.46 (.24−.58)
Group 2: 50 db CS(+) 80 db CS(−)					
2a: Ss which reached criterion	6	.24 (.13−.34)	.54 (.49−.56)	.22 (.12−.33)	.56 (.48−.60)
2b: Ss which did not reached criterion	4	.40 (.25−.51)	.51 (.42−.55)	.48 (.12−.58)	.55 (.52−.56)
Comparisons:					
Group 1 vs. Group 2a		p = .0226*	p = .0020*	p = .0164*	p = .0226
Group 1 vs. Group 2b		p = .0110*	p = .0658	p = .0074*	p = .0466
Group 2a vs. Group 2b		p = .144	p = .258	p = .172	p = .352

Adjusted significance levels (two-tailed), for the 1st comparaison: p=.017, for the 2nd comparison: p=.033, for the 3rd comparison: p=.033.

Sign "*" denotes signifficant difference with p=.05 for the set of comparisons.

20th sessions of differentiation training. For comparison of these three samples a multiple comparison nonparametric test suggested by Ryan (1960) was used. In each case the first comparison was done between samples with two most extreme medians, the second — between samples which medians differ less, and the third — between samples which medians were close to each other. Significance levels required for consecutive comparisons given at the bottom of the table were adjusted in such a manner that „the rate of error per experiment" (in our case — „per set of comparisons") equals .05. This analysis has shown that the Group 1 significantly differed from both Group 2a and Group 2b in positive trials. In negative trials differences were small and in the opposite direction than in the beginning of differentiation training. It is necessary to keep in mind, however, that for Group 1 median number of sessions to criterion is two (so data for this group are nearly the same in Tables IV and V, whereas in Group 2a this index equals 12 days.

Table VI

Trend analysis of the number of bar presses emitted during the 3-min. periods preceding consecutive trials

Days of training	Group 1	Group 2
D-day	+ p = .0238	+ p = .1868
P-day	+ .9124	+ .0316
CER 1st	— .8258	+ .2302
2nd	0 1.0000	0 1.0000
3rd	+ .1738	— .2802
4th	+ .9124	— .0001
5th	— .3788	— .4412
Diff. 1st	+ .3898	— .0930
2nd	— .2380	— .1188
3rd	.	— .3222
4th	.	— .0278
5th	.	— .0020
6th	.	— .3734
7th	.	— .0500
8th	.	— .5156

In the body of the table there are given signs of the S statistic and two-tailed probabilities associated to them. The sign "+" denotes increasing trend of the numbers of bar presses emitted in consecutive pre-periods, and the sign „—" indicates decrease of this index toward the end of the session.

The D-day („Dummy Day") means the last session of the bar-pressing training before the Pretest Day. No stimuli were presented during this session, but numbers of responses were calculated in appropriate time intervals, as in following sessions.

Rate of responding during intertrial intervals. The experimental groups differed slightly in number of responses emitted during periods when no stimuli were presented, with higher numbers of responses in the Group 1. However, differences in the numbers of bar presses in pre-periods did not reached significance when groups were compared for each session independently (Mann-Whitney test, two-tailed). One reason for this nonsignificant difference was random factor, as Ss were divided into groups before any training, but the second was related to different patterns of within-sessions variability of this index. During preliminary training there was a tendency for rates of bar presses to increase during session. When the CER training started, in Group 1 changes of this index became unsystematic. In Group 2, however, quite common were high rates before the first trial followed by a more or less regular decrease in bar-pressing rate in periods of time preceding consecutive trials. In some sessions this trend of the numbers of responses in consecutive pre-CS(+) periods reached a significant level (Fergusson's nonparametric method of trend analysis, two-tailed). This information is given in Table VI.

DISCUSSION

We will discuss some of the theories of differentiation conditioning and compare the results obtained in our experiment with predictions emerging from these theories.

Pavlovian theory. Right from the beginning of the investigation of CRs it was discovered that strong CSi evoke a greater outflow of saliva than weak CSi. The direct correspondence between the strength of the CS and the strength of the process of excitation in cortical cells was postulated as a consequence of the notion that an external stimulus is transformed into a neural process, which achieves an effector and brings it into action (Pavlov 1949, p. 57)[5]. This „*basic quantitative law of the higher nervous activity*" was used in Pavlov's laboratories to compare the strength of CSi, which differed not only in intensities, but also in sensory modalities (Pavlov 1927, p. 383). Similarly, it was found that with regard to inhibitory CRs the amount of inhibition evoked by the non-reinforced stimulus during differentiation training or by a conditioned inhibitor was depended in a similar way to the CS(—) strength (Maiorov 1938).

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[5] We do not discuss the problem of the very strong stimuli, as in this case Pavlov postulates some additional mechanisms to explain facts contradictory to this statement.

It was postulated that the strong CS produces activation of a larger „pool of cortical neurons" than the weak one (Konorski 1948). If so, in the case of two conditioned stimuli which differ only in intensity, the area of the projective cortex aroused by the strong CS covers not only a small field aroused by the weak CS, but also the surrounding area. Differentiation of the two stimuli intensities means in these terms that one part of the field of the projective cortex, corresponding to a given sensory modality, is involved in the excitatory process and another one — in the inhibitory process. When a strong stimulus from the pair is used as the CS(+) and a weak one as the CS(−) training would result in the central part of the field becoming inhibitory and the surrounding area excitatory. When the weak stimulus serves as the CS(+), the central part of the area is excitatory and the surrounding area — inhibitory.

This theoretical consideration is not precise enough to predict in which case the differentiation training will be more difficult. However, it seems likely that there should be a complete generalization from the strong CS to the weak CS (probably partially masked by an orienting reflex to a novel stimulus intensity) and an uncomplete generalization from the weak to the strong stimulus when both CSi differ only in intensity dimension. Such a prediction agrees not only with the Pavlovian theory on the „irradiation and concentration" of the nervous processes, but also with Konorski's suggestion of the formation of the CR as a synaptic process (Konorski 1948).

The data of this experiment force us to agree with Hovland (1937) that „*the theory of generalization advanced by Pavlov is completely indequate to cover intensity generalization*". In our experiment, there was much greater generalization from the weaker to the stronger stimulus than there was from the stronger to the weaker.

During differentiation training, when the CS (−) underwent experimental extinction, from the point of view of the Pavlovian theory there should be a greater generalization of extinction from the strong CS (−) to the weak CS (+) than from the weak CS (−) to the strong CS (+). This was in fact observed in our experiment, as in Group 2 there was a marked decrement of the amount of suppression to the 50 db CS (+) in the course of the differentiation training, an effect not observed in Group 1.

Stimulus intensity dynamism (V) theory by Hull. Similarly to Pavlov, Hull (1949) postulates that response strength is a simple function of the stimulus energy. Hull took into account Hovland's data and explained the greater effect of stronger novel stimuli in a generalization test on the basis of the differences in V (Hull 1952). Likewise, the results obtained by Antoinetti (1950) showing that the course of differentiation training was easier if the more intense stimulus from the pair has been used as the CS (+), was explained directly from the greater V of the more intense stimulus. Furthemore, it was not a „post mortem" explanation, because Moore (1964) has shown that such a prediction results from the basic equations of the conditioning paradigm given by Hull.

Basically, the results of this study are in agreement with Hull's stimulus intensity dynamism theory. When a stronger stimulus from the pair served as CS (+) (Group 1), the on-going bar-pressing behavior was suppressed more considerably than in the situation when a weaker stimulus was used (Group 2). Nevertheless, the generalization of the suppression from the strong CS (+) to the weak CS (−) (Group 1) was markedly less evident than the generalization of the suppression from the weak CS (+) to the strong CS (−) (Group 2). In consequence, the differentiation training was much easier in the Group 1 than in the Group 2.

Using Hull's equations Moore (1964) expected that a rapid course of differentiation with a strong CS (+) and a weak CS (−) would be associated with an increased response strength related to the CS (+) rather than with a decreased response strength to the CS (−) as compared with the differentiation training with a weak CS (+) and a strong CS (−). As far as the end of the differentiation training is concerned, this prediction is true (Table V). However, during the first day of introduction of the negative stimulus there were clear differences between experimental groups not only in positive but also in the negative trials (Table IV).

In spite of a good agreement with Hull's predictions, it is difficult to consider the results of our experiment as confirmation of stimulus intensity dynamism theory because they may also be explained from other positions.

„Discrimination" interpretation of the stimulus intensity effect. Several authors (Perkins 1953, Logan 1954, Champion 1962) criticized Hull's theory. They assume that in classical conditioning the S is confronted with two situations: the CS and the ITS (= background = = contextual environment), the responses to the CS being reinforced and those to the ITS — not. As a result of such a procedure the CS acquires the same degree of gross excitatory potential in separate groups of Ss regardless of the actual CS intensity, and this excitatory potential generalizes along the stimulus-intensity continuum. As the responses to the ITS are not reinforced, the ITS acquires the inhibitory potential which also generalizes. If the CS means a great change from the ITS,

then the inhibitory potential acquired by the ITS and generalized from it will be small, whereas if the CS means a small change from the ITS the inhibitory potential of the ITS will be greater. Assuming that excitatory and inhibitory potentials are additive, it is easy to predict from the two generalization gradients greater net excitatory potential and response strength to the stronger CS than to the weaker one.

When a new stimulus is introduced, the response strength related to it will depend not only on generalization from the positive stimulus but also on generalization from the ITS. The amount of inhibition from the ITS will be greater to the weak novel stimulus, which is more similar to the ITS, than to the strong novel stimulus, more apart from the ITS. If in both situations novel stimuli are equal j.n.d. steps from the CS (+), they will receive equal generalized excitatory potentials from it, but the net excitatory potential will be greater at strong novel stimulus than at weak one. Accordingly, we may expect greater „generalization" from weaker to stronger stimulus than vice versa.

If during differentiation training a weaker stimulus from the pair serves as the CS (+), then it will be accruing inhibition which will generalize upon it from both sides: from the ITS and from the stronger CS (−). If the stronger stimulus is the CS (+), then it will receive the same amount of inhibition generalized from the CS (−) as in previous case, but the generalized inhibition from the ITS will be less pronounced because the CS (+) is more remote from it (Logan 1954).

Thus, the predictions of the Perkins-Logan-Champion theory are similar to the Hull's stimulus intensity dynamism theory. However, the „discrimination" interpretation of the stimulus intensity effect predicts that during differentiation of a weak CS (+) and a strong CS (−), response strength related to the CS (+) will be diminished concurrently with the acquisition of the inhibitory potential by the CS (−). This prediction was confirmed in our experiment. Moreover, we are in favor of the Perkins-Logan-Champion theory because it takes also into account the interrelations between the ITS and the CS. This seems to be especially important in CER studies.

In the CER situation, in which one response (bar-pressing for food) is conditioned to the ITS, and another (freezing with remaining components of fear) is conditioned to the CS (+), it is possible to retrace generalization of these reactions to inappropriate stimuli components. Generalization of fear from the CS to the ITS would result in a decrease in the rate of bar presses during the ITS, whereas generalization of alimentary reaction and pressing response to the CS will reduce the suppressing effect of the CS. We think that the within-session decrement of suppression in positive trials (Table I) observed in both experimental groups after the suppression reached asymptote and the decrement of number of bar presses in consecutive pre-periods (Table VI) marked in Group 2 only, reflect such a generalization of inappropriate responses. Similarly, a greater suppression in the first than in the second half of the CS (+) period in Group 2 (Table II) demonstrate the same phenomenon. It is interesting to note that when the 50 db CS (−) was introduced in Group 1, this stimulus also caused greater suppression in the first half of the CS periods throughout the first day of differentiation training. In this case, generalization of the bar-pressing response to the period of the CS (−), more similar to the ITS than the CS (+), facilitates the differentiation of the CS (+) and CS (−), whereas in Group 2 the same phenomenon hinders the differentiation.

„Dynamogenic" theory. Recently, the „discrimination theory" was criticized by Grice and Hunter (1964). They found that the response strength (measured as the percent of CR in eyelid conditioning) to the loud tone was significantly increased, if the same Ss were conditioned also to the soft tone, both CS intensities being presented in separate trials in an unpredictable order. The „discrimination theory" would predict that the addition of a weak stimulus should result in a weaker (in comparison with between-Ss experiment[6]) net excitatory potential of the stronger stimulus because the inhibitory gradient from the ITS should start at a higher level. As their data were not consonant with the Perkins-Logan-Champion theory, Grice and Hunter postulated a „dynamogenic theory", in which departure from adaptation level rather than absolute intensity of the CS is an important variable. When the S is conditioned to one CS, the adaptation level should be near the stimulus value. Thus, the stimulus intensity effect would be small, because in the case of the strong CS the adaptation level will be high, and in the case of the weak CS the adaptation level will be low. In the two-stimuli situation (within-Ss design[6]) the adaptation level lies somewhere between the two CS values and the stimulus intensity effect will be exaggerated.

However, in terms of the „dynamogenic theory" results of the generalization and differentiation along intensity dimension cannot be explained. This was shown in our experiment. In both our experimental

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[6] Two experimental designs are commonly used in studying intensity functions: a between-Ss experiment, in which different groups of Ss are conditioned to each of the intensity studied, and a within-Ss experiment, in which each S is conditioned to two or more CS intensities.

groups the 50 db and 80 db stimuli were applied according to within-Ss design and this theory would expect a marked intensity effect during the first application of the CS (−) in both groups. Such an intensity effect was in fact observed in the Group 1 (the 50 db CS (−) evoked significantly smaller suppression than that caused by 80 db CS (+), whereas in the Group 2 these differences were not significant statistically and the stimulus intensity effect was negligible (Table III).

The presentation and the discussion of the experimental data are given in this paper in terms of a differentiation paradigm with regard to the fear response conditioned to the CS as a determining factor. However, the „conditioned emotional response" is a reflex based on the alimentary-defensive antagonism. We think that it is necessary to investigate the interrelations between the two drives and two responses involved in the CER paradigm more carefully than in this study. Such an investigation may yield another approach to the problem of differentiation training in the CER situation.

SUMMARY

The ability of rats to differentiate between two white noise intensities was investigated emploing the CER technique. Performance in two experimental groups, 10 rats each, was compared. In one group the strong stimulus from the pair served as a positive conditioned stimulus and the weak one as a negative; in the second group the relations between conditioned stimuli were reverse.

During the original training in which only the positive CS was presented, the conditioned suppression to the stronger stimulus was greater than that to the weak stimulus. During differentiation training, the generalization of the suppression of the on-going bar-pressing behavior from the strong CS to the weak CS was markedly less evident than the generalization of the suppression from the weak CS to the strong CS. In consequence, if the strong stimulus from the pair served as the positive CS, the differentiation was much more rapid than if the weak stimulus served as the positive CS. Extinction of the suppression to the strong stimulus significantly generalized to the weak stimulus, but not vice versa.

The results of the experiment are confronted with predictions emerging from same theories of differentiation training.

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THE DIRECTION OF CHANGE VERSUS THE ABSOLUTE LEVEL OF NOISE INTENSITY AS A CUE IN THE CER SITUATION[1]

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It is generally accepted that after acquisition of a stable CR, there is a generalization of the CR from the original conditioned stimulus (CS) to new test stimuli (TSi) presented in the same experimental situation. The generalization of the CR is greater to the TSi similar to the CS than to those more remote from it. However, usually both the CS and the TSi employed in generalization studies change the stimulation level in the same direction with regard to the ambient background stimulation level (intertrial stimulus, ITS). The question arises whether or not there will be observed any generalization from the CS to the TS, when the CS is an increase of the ITS intensity level, and the TS is an decrease of the ITS intensity, or vice versa.

Some information concerning this problem was given by Champion (1962), who investigated the effect of onset and offset of an acoustic stimulus on the latency of a key-pressing response (reaction time) in human Ss using a within-Ss design[3]. „Onset" consisted in the change from

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[3] Two experimental designs are commonly used in studying intensity functions: a between-Ss experiment, in which different groups of Ss are conditioned

silence to a 2000 cps sine-wave tone of 60 or 80 db intensity, „offset" consisted in the change of the same tone of 60 or 80 db intensity to silence. When only intensity of the CS was changed, a positive transfer was observed as indicated by mean reaction time. However, when between consecutive blocks of trials there was a shift not only in CS intensity, but also a shift from onset to offset or vice versa, a highly significant negative transfer was observed. These data clearly suggest that the relations of the CSi to the ITS intensities have cueing functions.

Similar considerations help to explain certain aspects of the transposition phenomenon. Spence's theory (1937) predicted that transposition would decrease as the test stimuli became less and less similar to the training stimuli. However, it was shown that at least in the case of brightness differentiation the animal responds to the relationship between the test stimuli and the background. It is a change in this relationship rather than a change in the absolute values of the stimuli that causes the breakdown in transposition (Riley 1958).

It seems that relations between the CS and the ITS can be fruitfully investigated by techniques in which two different drives along with their corresponding responses are conditioned to these two stimulus situations. For example one can use the conditioned emotional response (CER) technique which consists in „the suppression of some stable aspects of an animal's on-going behavior under conditions of emotional disturbance" (Brady and Hunt 1955, p. 313). Typically, the on-going behavior is a bar-pressing response reinforced by food. The emotional disturbance is acquired as a result of pairing some change in the experimental situation — a CS with an unavoidable shock. Thus, the CER is based on alimentary-defensive antagonism.

The present experiment was designed to investigate the role of the relational cues such as direction and amount of change from the background noise intensity level in the CER situation. As CER acquisition depends on the discrimination training of two antagonistic modes of behavior, it may be expected that when white noise intensity is used as the CS, an increase of the noise intensity evokes one mode of behavior and a decrease of the noise intensity evokes the antagonistic behavior.

This hypothesis was tested in our experiment by two different methods. Fear was conditioned to a CS. The first test consisted in presenting

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to each of the intensity studied, and a within-Ss experiment, in which each S is conditioned to two or more CS intensities.

a test stimulus (TS) which was a change of the background white noise intensity level in the opposite direction from the CS. This test constitutes stage 2 of the experiment. The second test consisted in changing the background noise intensity level, whereas the intensities of the CSi and TSi were without change. This test constitutes stage 3 of the experiment.

MATERIAL AND METHOD

The Ss were 20 experimentally naive male hooded rats, supplied by Canadian Research Animal Farms, 300 to 350 grams. Four standard Grason-Stadler operant-conditioning units were used in the experiment. The apparatus and method of shaping of the bar-pressing response for food were similar to those previously described (Zieliński 1965). Prior to any training the Ss were randomly distributed into two experimental groups, 10 Ss each; however, in the course of training two (one from each group) Ss were discarded due to illness or because it stoped bar-pressing for several days. The experiments were run in five squads counter-balanced between experimental groups. The experimental units were not completely counter-balanced between groups. Both experimental groups had exactly the same treatment in all stages of the experiment except for white noise intensities used as conditioned and test stimuli.

Starting from the second day of bar-pressing training under the 2.5 min. variable interval (VI) schedule of food reinforcement, a white noise of 60 db intensity was present all the time in the experimental space. For Group 1 the CS (terminated with shock application) consisted in an increase of the 60 db background white noise intensity to 70 db, and the TS — in a decrease from 60 db to 50 db. For Group 2 the decrease from 60 db to 50 db was the CS, and the increase from 60 db to 70 db was the TS. Each stimulus was presented four times during each two hours daily experimental session. Onsets of the CSi were at 18.5, 53.5, 74.5, and 92.0 min., and onsets of the TSi at 29.0, 43.0, 61.0, and 106.0 min. after the beginning of the session. The CS and TS durations were 3 min. troughout the whole experiment. The offset of the CSi coincided with .85 ma. shock of .5 sec. duration.

Bar-pressing training under the 2.5 min VI schedule of food reinforcement lasted for five days. The fifth day of this training was so called „Pretest day". During this session conditioned and test stimuli were presented in the appropriate order, both without shock application. The food-reinforcement schedule and the presentation of the CSi and TSi were programmed independently throughout the whole experiment.

The experiment was run in three stages. Stage 1 started the day after the Pretest day and constituted the CER acquisition period, which continued for six days. Only CSi together with shock were presented during this stage of the experiment. Stage 2 consisted in three identical testing sessions in which the TSi, which were never followed by shock, were introduced. The CSi, terminated with shock, were presented as before. The first application of the TSi constituted a generalization test, whereas the whole of Stage 2 was essentially a differentiation training. Then the Ss within each group were split into two subgroups to fit the following 2 × 2 table:

Intensites of the CS and TS	Background noise intensity during test sessions	
	40 db	80 db
70 db CS 50 db TS	Subgroup 1A (n = 4)	Subgroup 1B (n = 5)
50 db CS 70 db TS	Subgroup 2B (n = 5)	Subgroup 2A (n = 4)

The test, which constitutes Stage 3 of the experiment consisted in a change of the background noise intensity level. For subgroups 1A and 2B the 60 db background white noise was changed to a white noise of 40 db intensity, and for subgroups 1B and 2A the background noise was changed to 80 db intensity. The intensities of the CSi and TSi were without change, however, both of them were presented without shock. There were two test sessions during this stage of experiment separated by one retraining session identical to those of Stage 2. During the second test session the order of the CSi and TSi was reversed; thus onsets of the TSi were at 18.5, 53.5, 74.5, and 92.0 min., and onsets of the CSi — at 29.0, 43.0, 62.0, and 106.0 min. after the beginning of the session. The scheme of the experiment is presented in Fig. 1.

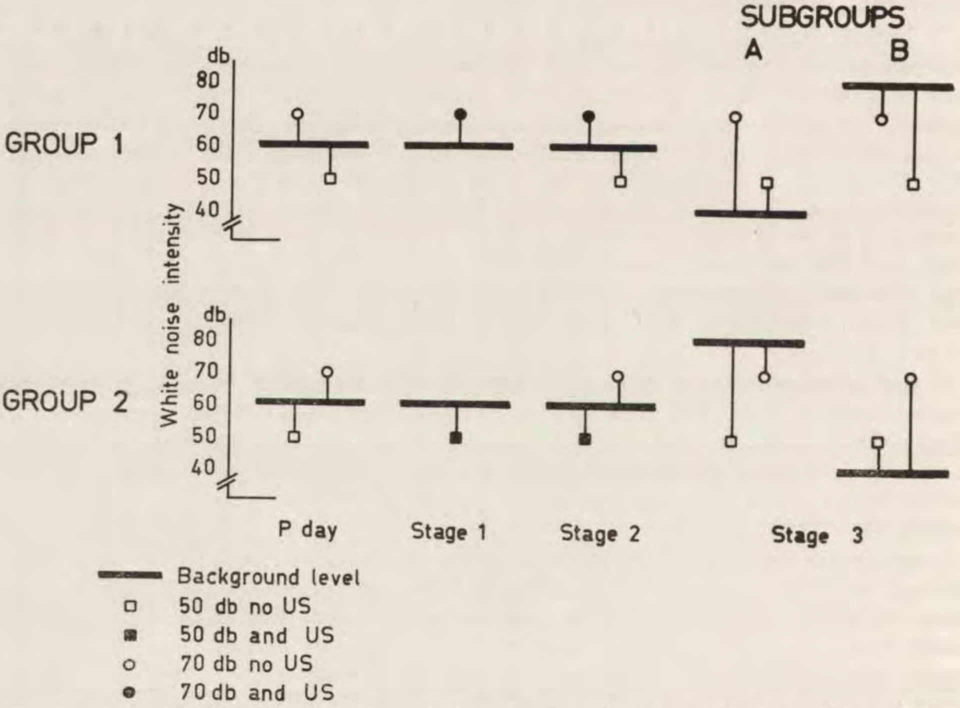

Fig. 1. The schematic presentation of the relations between the intensities of the conditioned and test stimuli and the background noise intensity during consecutive stages of the experiment

Measures. For each trial numbers of bar presses were counted independently for the three minutes before the onset of the CS or the TS (pre-period), for the three minutes during the action of the stimulus (CS-period or TS-period), and for the three minutes after the stimulus offset (post-period). The number of bar presses emitted during the 3-min. pre-period will be denoted as A, number of bar presses emitted during the 3-min. CS-period (or TS-period) — as B, and number of bar presses emited during the 3-min. post-period — as C. The magnitude of the CER was measured by computing the „suppression ratio" according to formula $\frac{B}{A+B}$, described by Annau and Kamin (1961). The effect of stimulus offset (or, in other words, the effect of background noise intensity after stimulus termination) was also investigated by comparison of the number of responses emitted during the post-period and stimulus (either CS or TS) period, using the formula $\frac{C}{B+C}$. In both cases, a ratio of .50 indicates no change in number of responses emitted in consecutive time intervals, ratios less than .50 indicate a decrease of response rate in a given time interval with regard to the preceding one, and ratios more than .50 indicate an increase of response rate in a given time interval with regard to the preceding time interval. If not indicated otherwise, „daily" ratios were computed for each S, summing numbers of responses emitted in appropriate time intervals of four CS (or four TS) presentations during a given day, and using as A, B, and C in formulas mentioned above.

RESULTS

Pretest day. The first change of the background white noise intensity interfered with bar-pressing, however, this effect was very shortlasting one. In Group 1 the first presentation of the 70 db stimulus evoked marked suppression of the on-going bar-pressing behavior, as shown by a comparison of the number of bar-presses in the last minute before and first minute after the change of the white noise intensity ($p < .01$, Wilcoxon matched-pairs test[4], Siegel 1956). During the next minute of the 70 db stimulus there was a partial recovery, significant at $p < .05$ level. The disturbing effect of the 50 db stimulus was hardly visible in both groups.

Daily supression ratios computed for each stimulus intensity and individual Ss independently ranged from .44 to .61. Comparison of these ratios for different white noise intensities within each group (Wilcoxon matched-pairs test), as well as for the same intensity in different groups (Mann-Whitney test, Siegel 1956) showed no significant differences.

Stage 1: CER acquisition. The median daily suppression ratios in consecutive sessions are given in Fig. 2 for Group 1 and in Fig. 3 for Group 2. As seen from the Figures, the acquisition of the CER was slow, and amount of suppression not great. However, in both experimental groups

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[4] In all cases the two-tailed tests were used.

the suppressing effect of the CSi on the bar-pressing rate reached significance on the 4th day of CER acquisition and remained significant during the next days of this stage. This effect was tested by comparison of the number of responses during the pre-periods and the CS-periods (pooled

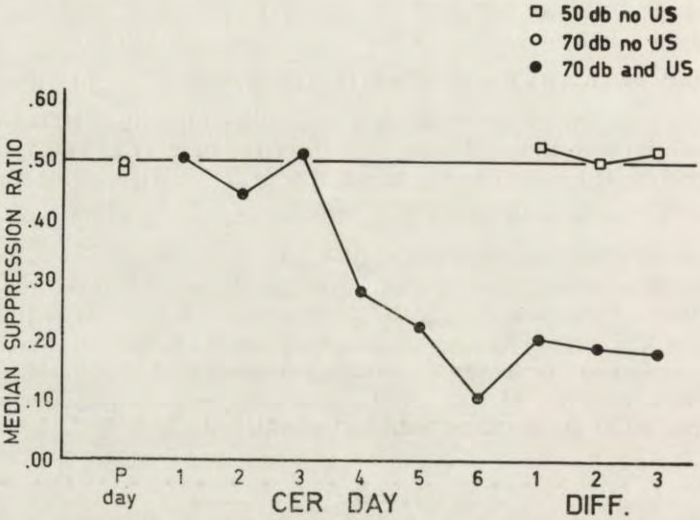

Fig. 2. Median daily suppression ratios during the P-day, CER acquisition (Stage 1 of the experiment), and differentiation training (Stage 2 of the experiment) in Group 1

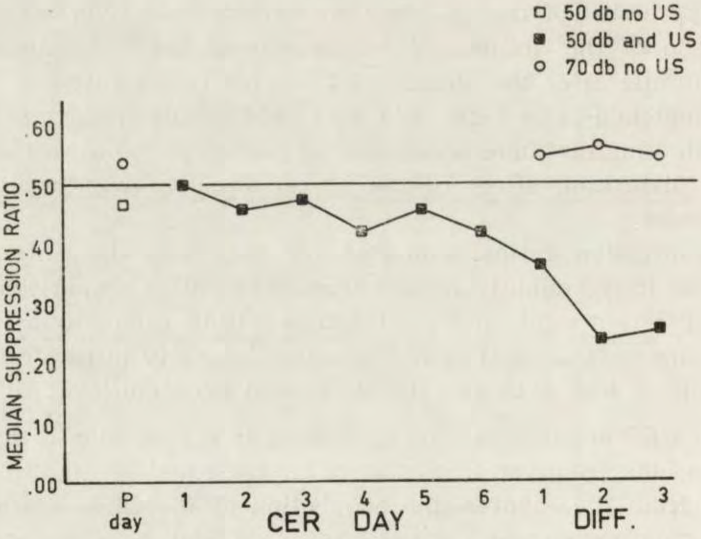

Fig. 3. Median daily suppression ratios during the P-day, CER acquisition (Stage 1 of the experiment), and differentiation training (Stage 2 of the experiment) in Group 2

for a given day) using the Wilcoxon matched-pairs test for each experimental group independently.

Comparison of the two experimental groups shows that the 70 db CS (Group 1) evoked greater suppression than the 50 db CS (Group 2). This difference reached significance on the 5th CER acquisition day ($p < .05$), and was very pronounced on the 6th day ($p < .002$, Mann--Whitney test).

As an index of responding during the intertrial intervals the number of bar-presses in four 3-min. pre-periods were summed together and the mean rate of responding per minute was calculuted. As seen from Figure 4, the introduction of the CSi and shock depressed the responding rate in intertrial intervals. The recovery was slow and not complete.

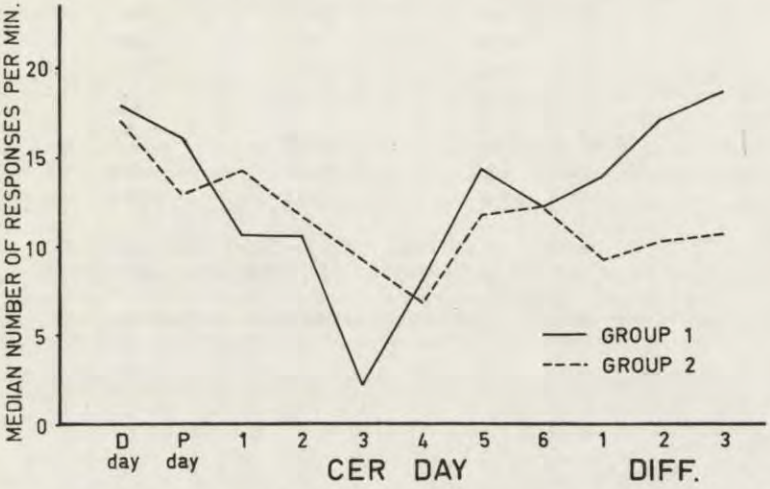

Fig. 4. Median number of bar-pressing responses per minute emitted in pre-CS periods during the D-day, P-day, CER acquisition (Stage 1 of the experiment), and differentiation training (Stage 2 of the experiment) in both experimental groups

In both groups there was also a marked decrease of the bar-pressing rate within each session. A comparison of the number of bar-presses in consecutive pre-periods was done using the method of non-parametric trend analysis suggested by Fergusson (unpubl.)[5], and the results are given in Table I. As seen from this data, in both groups the rate of

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[5] The method developed by Fergusson (unpubl.) employs the S statistic as used by Kendall in the definition of a coefficient of rank correlation, tau. The null hypothesis was tested against the two-tailed research hypothesis that a monotonic (increasing or decreasing) trend in amount of suppression over consecutive trials within a given experimental session exists.

responses decrease in consecutive pre-periods. This trend was statistically significant in most of the sessions of Stages 1 and 2 in Group 1, and only occasionally reached significance in Group 2.

Table I

Trend analysis of the number of bar presses emitted during the 3-min. periods preceding consecutive CS presentations

Days of training		Group 1	Group 2
D-day		+ .9124	+ .5754
P-day		— .6242	— .4654
Stage 1:	1st	— .0292	— .2542
	2nd	— .0005	— .0064
	3rd	— .0110	— .0001
	4th	— .7264	— .4552
	5th	— .0910	— .4902
	6th	— .0042	— .1118
Stage 2:	1st	— .0022	— .2076
	2nd	— .0384	— .0404
	3rd	— .0384	— .0910

In the body of the table there are given signs of the S statistic and two-tailed propabilities associated to them. The sign "+" denotes increasing trend of the numbers of bar presses emitted in consecutive pre-periods, and the sign "—" indicates decrease of this index toward the end of the session.

The D-day ("Dummy Day") means the last session of the bar-pressing training before the Pretest Day. No stimuli were presented during this session, but numbers of responses were calculated in appropriate time intervals, as in following sessions.

Similar trend analysis was done with regard to suppression ratios in consecutive trials. Generally, the suppression was better in the beginning than toward the end of a given session. However, in Group 2 this trend never reached $p < .05$ level. In Group 1 this trend was significant for the 6th day of Stage 1 and for the 1st and 2nd days of Stage 2.

Stage 2. Introduction of the TSi did not change considerably the process of acquisition of the CER evoked by the CSi. As seen from Fig. 2, in Group 1 the asymtote was reached on the 6th Day of Stage 1, and during Stage 2 the CS evoked slightly less suppression. However, in this group there was no significant difference in the suppressing effect of the CS between Day 6 of Stage 1 and Day 1 of Stage 2 (Wilcoxon matched-pairs test). In accordance with the slow acquisition of the CER in Group 2, the asymptote was reached only on Day 2 of Stage 2 (Fig. 3). Comparison of the daily suppression ratios for Day 6 of Stage 1 and

Day 1 of Stage 2 shows in this group a significant difference ($p < 01$, Wilcoxon matched-pairs test). In each session of Stage 2 the CS evoked significant suppression of the ongoing bar-pressing behavior in both groups.

No generalization of the suppression from the CS to the TS was observed in either group. Even the first application of the TS did not change considerably the bar-pressing response rate. The median $\frac{B}{A+B}$ rations for the first TS application were .53 for the 50 db TS (Group 1) and .57 for the 70 db TS (Group 2); both were not significant as estimated by comparison of the number of bar-presses emitted during the 3 min. pre-period and 3 min. TS period (Wilcoxon matched-pairs test). When this comparison was done between the numbers of bar presses during pre-periods and TS-periods each pooled for a given session, as a rule a facilitatory effect of the TS on the bar-pressing rate was observed. If this data were put in the formula $\frac{B}{A+B}$, the daily ratios for most Ss were above .50. During each day of Stage 2, „suppression ratios" computed for CS and TS differed at the $p < .01$ level within each group, whereas during P-day these differences were not significant (Wilcoxon matched-pairs test). Daily $\frac{B}{A+B}$ ratios for the CS and TS during Stage 2 of the experiment are given in Table II.

Table II

The effect of the CS and TS presentations on the bar-pressing rate in terms of median daily $\frac{B}{A+B}$ ratios during the P-day, the 6th Day of Stage 1, and the 1st — 3rd Days of Stage 2

	P-day	Stage 1	Stage 2		
		6th Day	1st Day	2nd Day	3rd Day
Group 1					
70 db CS	.50	$\underline{\underline{\underline{.11}}}$	$\underline{\underline{\underline{.21}}}$	$\underline{\underline{\underline{.19}}}$	$\underline{\underline{\underline{.18}}}$
50 db TS*	.48	.50	$\underline{.53}$	.50	$\underline{.52}$
Group 2					
50 db CS	.46	$\underline{\underline{\underline{.42}}}$	$\underline{\underline{\underline{.36}}}$	$\underline{.24}$	$\underline{\underline{\underline{.25}}}$
70 db TS*	54	$\underline{.48}$	$\underline{.55}$	$\underline{\underline{\underline{.56}}}$	.54

Scores underlined with a single line denote suppression or facilitation significant at $p < .05$ level, with a double line — at $p < .02$, and with a triple line — at $p < .01$ level (two-tailed).

* Scores given in these rows for the 6th Day of Stage 1 are for so called "dummy trials" (see explanation in the text).

The lack of generalization of the suppression from the CS to the TS suggests that direction of change from the background noise intensity level served as the cue for the fear response and indicates that rats perfectly discriminate directions of change of the noise intensity from the background stimulation level. Additional support of this hypothesis may be given by the $\frac{C}{B+C}$ ratios computed for the TS trials, as the TS offset means shift in the noise intensity in the same direction as that evoked by the CS onset. As seen from Table III, the TS offset evoked suppression of bar pressing rates in both experimental groups. This effect was significant at $p < .01$ level for each but Day 3 of Stage 2 in Group 1 (Wilcoxon metched-pairs test). The termination of the CS caused recovery of the bar pressing response rate to the same as that before the onset of the CS.

Table III

The effect of the CS and the TS terminations on the bar pressing rate in terms of median daily $\frac{C}{B+C}$ ratios during the P-Day, the 6th Day of Stage 1, and the 1st — 3rd Days of Stage 2

	P-day	Stage 1	Stage 2		
		6th Day	1st Day	2nd Day	3rd Day
Group 1					
After 70 db CS	.47	.88	.77	.84	.82
After 50 db TS*	.51	.52	.47	.45	.45
Group 2					
After 50 db CS	.54	.61	65	.72	.76
After 70 db TS*	.44	.50	.40	.44	.44

An especially pronounced suppressing effect of the TS offset was observed during the first TS application. The median $\frac{C}{B+C}$ ratios for the first TS application in Day 1 Stage 2 were .33 for the 50 db TS (Group 1) and .41 for the 70 db TS (Group 2); both were significant at $p < .01$ level. The $\frac{C}{B+C}$ ratios for the first TS application and the $\frac{B}{A+B}$ ratios for the first CS trial on Day 1 of Stage 2 showed positive correlation. In Group 1 this correlation was significant at $p < .02$ level, however, for Group 2 it failed to reach significance (Spearman rank correlation, Siegel 1956). Similar analysis for daily ratios showed no significant correlation in either experimental group.

Stage 3. It was expected that as a result of changes of the background noise intensity, the amount of suppression evoked by the CS presentations will be different in subgroups A and B. If the direction of change serves as a cue for the fear response, then in subgroups 1A and 2A the suppressing effect of the CS would be enchanced, whereas in subgroups 1B and 2B the suppressing effect of the CS should disappear. In other words, during the test sessions a significant interaction effect was expected.

The statistical analysis of the $\frac{B}{A+B}$ suppression ratios confirmed our prediction. As far as the CS presentations were concerned, the interaction terms were significant far beyond the $p < .01$ level during both Test Sessions. For the TS the interaction was significant during the first Test Session only. In no case were main effects significant. Neither for Day 3 of Stage 2, nor for the retraining session did the interaction and main effects reach significance. The corresponding values of the F statistic are given in Table IV.

Table IV

The values of the F statistic obtained in the analysis of variance of the $\frac{A}{A+B}$ ratios of the CS and TS presentations during the Day 3 of Stage 2, two Testing Sessions, and the Retraining Day

Effect of:	Day 3 Stage 2		Test 1		Retraining		Test 2	
	CS	TS	CS	TS	CS	TS	CS	TS
Intensity of stimuli	<1	1.1	<1	<1	2.3	2.1	<1	<1
Intensity of background	<1	<1	<1	2.8	<1	1.2	<1	2.5
Interaction	<1	<1	60.3**	9.8*	<1	1.3	34.5**	3.9

Each of the main effects and the interaction involve 1 df, the error term involves 14 df. The sign "*" denotes an effect significant at $p < .01$ level, and the sign "**" denotes an effect significant at $p < .005$ level.

One may criticize the method of statistical analysis employed, because the distribution of the „suppression ratios" does not fulfil the condition of normality and they are on a weaker than the interval scale of measurement. However, the nonparametrical Mann-Whitney test gives similar results as those obtained by the analysis of variance. The median values of the $\frac{B}{A+B}$ ratios and the result of comparison between the 1A and 2A (combined) versus the 1B and 2B (combined) subgroups are given in Table V.

As seen from the data presented, the changes of the background

Table V

The effect of the CS and TS presentations on the bar-pressing rate in terms of median daily $\frac{B}{A+B}$ rations during the Day 3 of Stage 2, two Testing Sessions, and the Retraining Day

Subgroups	Day 3 Stage 2	Test 1	Retraining	Test 2
CS				
1A (70 db)	.20	.17	.28	.18
2A (50 db)	.25	.15	.44	.13
1B (70 db)	.18	.51	.30	.49
2B (50 db)	.25	.48	.38	.53
Comparison between A and B, $p <$	n.s.	.002	n.s.	.002
TS				
1A (50 db)	.51	.46	.48	.50
2A (70 db)	.55	.44	.55	.43
1B (50 db)	.52	.48	.50	.51
2B (70 db)	.51	.54	.50	.52
Comparison between A and B, $p <$	n.s.	.02	n.s.	n.s.

For the comparison the subgroups 1A and 2A constitute one sample ($n = 8$), and the subgroups 1B and 2B constitute another sample ($n = 10$). Mann—Whitney test.

noise intensity had very pronounced effect on the responding rate during the CS presentations, whereach the effect on the responding rate during the TS presentations was much smaller.

Similarly as during Stage 2 of the experiment, analysis of the effect of the CS offset and the TS offset may provide additional support for the hypothesis tested in this study. In subgroups 1A and 2A, in which during the Test Sessions the suppressing effect of the CS onset was enchanced, the offset of the CS should result in greater increase of the bar pressing rate. In the same subgroups we may expect that during the Test Sessions the TS offset will also increase instead of decrease the bar pressing rate, because the change of the background intensity reverses (in comparison to the 60 db background situation) the direction of change in the noise intensity evoked by the TS termination. On the other hand, in subgroups 1B and 2B during the Test Sessions both the CS and the TS offsets should have a depressing effect on bar pressing rate. Thus, clear differences in the $\frac{C}{B+C}$ ratios between subgroups

1A and 2A (combined) and subgroups 1B and 2B (combined) should be observed during the Test Sessions. The data presented in Table VI are in agreement with this prediction.

Table VI

The effect of the CS and the TS terminations on the bar pressing rate in terms of median daily $\frac{C}{B+C}$ ratios during the Day 3 of Stage 2, two Testing Sessions, and the Retraining Day

Subgroups	Day 3 Stage 2	Test 1	Retraining	Test 2
CS				
1A (70 db)	.79	.80	.73	.80
2A (50 db)	.78	.83	.66	.83
1B (70 db)	.83	.49	.67	.49
2B (50 db)	.74	.50	.62	.51
Comparison between A and B, $p <$	n.s.	.002	n.s.	.002
TS				
1A (50 db)	.46	.54	.51	.49
2A (70 db)	.42	.57	.45	.57
1B (50 db)	.45	.50	.47	.51
2B (70 db)	.46	.39	.45	.48
Comparison between A and B, $p <$	n.s.	.002	n.s.	n.s.

The comparison was done similarly as for the data presented in Table V.

DISCUSSION

In most experimental set-ups it is difficult or impossible to know which of the number of cues provided by the sporadic stimulus is utilized by the S during the shaping of the CR. Even in the case in which white noise is used as the CS and the same noise of different intensity is acting during the intertrial intervals, the question arises whether the absolute level of the CS intensity plays a signalling role, or the change in stimulation level due to the CS onset, or both.

In this study the importance of absolute versus relational properties of the CS were investigated. Usually this problem was investigated using experimental designs involving changes of the background and/or absolute intensities of the CSi. Such a design was also used in this study and constitutes Stage 3 of the experiment. However, there is a posibility of another approach to the problem.

Let us analyse the test which constitutes Stage 2 of the experiment. We will consider the situation with a controlled background noise intensity level, which constitutes the ITS. A conditioned stimulus, which is of a higher intensity than the ITS will be denoted as CS$^{\uparrow}$, and of lower intensity than the ITS as CS$^{\downarrow}$. Similarly, the test stimulus of a higher intensity than the ITS will be denoted as TS$^{\uparrow}$, and of a lower intensity than the ITS as TS$^{\downarrow}$. We will narrow our discussion to the CER situation, in which two drives and two responses, fear and bar-pressing for food, are involved.

Generalization has usually been studied in the CS$^{\uparrow}$, TS$^{\uparrow}$ situation („increase procedure"), and occassionally in the CS$^{\downarrow}$, TS$^{\downarrow}$ situation („decrease procedure"). Predictions emerging from several theories concerning generalization in the „increase procedure" were discussed in the previous paper (Zieliński 1965). We will discusse now predictions concerning „reverse procedures", namely the CS$^{\uparrow}$, TS$^{\downarrow}$, and CS$^{\downarrow}$, TS$^{\uparrow}$ situations. Similarly as for the „increase procedure", different theories are not consonant in predictions of the outcome of the generalization test in the „reverse procedures". We will list several of them.

1. One may think that in the CER situation any change in experimental situation evokes the fear response. It is in agreement with the postulate that stimulus generalization indicates nothing more than a „failure of association" (Lashley and Wade 1946). Thus, any TS should have suppressing effect on the on-going bar-pressing response. On the basis of such an amorphous hypothesis it is difficult to predict whether greater generalization will be observed from the CS$^{\uparrow}$ to the TS$^{\downarrow}$, or from the CS$^{\downarrow}$ to the TS$^{\uparrow}$.

2. Hull's (1949, 1952) stimulus intensity dynamism theory takes into account only the absolute properties of the stimuli and neglects their relations to the ITS. Thus, the CS$^{\uparrow}$, TS$^{\downarrow}$ situation is similar to the case with strong CS$^{\uparrow}$ and weaker TS$^{\uparrow}$ and should result in smaller generalization to the TS than in the CS$^{\downarrow}$,TS$^{\uparrow}$ situation, which is similar to the case with weak CS$^{\uparrow}$ and stronger TS$^{\uparrow}$. In any case generalization of suppression from the CS to the TS should be observed.

3. The Perkins-Logan-Champion interpretation of the stimulus intensity effect takes into account the role of the ITS and assumes that the ITS acquires inhibitory properties due to nonreinforcement of the CR which generalizes to the ITS from the CS (Logan 1954, Perkins 1953, Champion 1962). Thus, the TS is under influence of the excitatory potential generalized from the CS, and the inhibitory potential generalized from the ITS. The „net" effect related to the TS depends how much it differs from both the CS and the ITS. In the „increase procedure" with stronger CS and weaker TS, the generalization to the TS

will be smaller than from the weaker CS to the stronger TS. It is because the amount of inhibition from the ITS will be greater to the weak TS, more similar to the ITS, than to the stronger TS, more apart from the ITS. This theory assumes a regular slope of both generalization gradients, and diagramically these relations are presented in Fig. 5A.

On the basis of this theory it is easy to predict no „generalization" to the TS in both the $CS^{\uparrow}$. $TS^{\downarrow}$ and the $CS^{\downarrow}$, $TS^{\uparrow}$ situations. This is because the amount of excitation generalized to the TS from the CS, and the amount of inhibition acqured by the ITS and generalized to the TS are the same. These relations are presented in Fig. 5B.

So, the test which constitutes Stage 2 of the experiment presented here, puts in contradiction Perkins-Logan-Champion's and Hull's theories. However, during the action of the TS a slight but significant increase of the bar-pressing response rate was observed in both groups, and predictions of theories listed above were not confirmed in our experiment.

4. If we agree that the CER acquisition (Stage 1) is a discrimination training of two drives and corresponding overt responses, one conditioned to the CS, and the second to the ITS intensities, then the effect of the TS in „reverse procedures" can be easily explained in terms of transposition of discrimination. It is known that after differentiation training there is observed a shift both in the mean and the mode of the generalization gradient away from the value of the stimulus which underwent experimental extinction, i.e. the CS (−) (Spence 1937, Honig, Thomas and Gutman 1959). If the pair of stimuli is presented consisting of the original positive conditioned stimulus CS(+), and a TS more remote than the CS (+) from the CS (−), then the CR is more strongly evoked by such a TS than by the original CS (+) (Honig 1962). In the CER situation the TS in the „reverse procedures" is more remote from the fear-evoking CS than the ITS. Thus, the facilitatory effect of the TS presented against the ITS on bar-pressing response rate, which was observed during Stage 2 of the experiment, may be explained by this theory.

5. The last hypothesis to be discussed assumes that the direction of change between the CS and ITS is the major cue for CER learning and performance. Thus the change from the ITS to the CS, which signals shock, elicits the fear response, while the change from the CS to the ITS, which signals a safe period, elicits increased bar-pressing. In the $CS^{\uparrow}$, $TS^{\downarrow}$ and the $CS^{\downarrow}$, $TS^{\uparrow}$ situations the TS onset should have similar effect as the CS offset and result in an increase of bar-pressing response rate. On the other hand, the TS offset hould have, according to this hypothesis, a suppressing effect on the bar-pressing response rate.

Results of Stage 2 of the experiment are in full agreement with this hypothesis. During the first application of the TS in both experimental groups there was no generalization of the suppression from the CS to the TS measured by the $\frac{B}{A+B}$ ratios, and the TS onset had rather a facilitatory than suppressing effect on the bar-pressing response rate. The TS offset suppressed the bar-pressing response and the $\frac{C}{B+C}$ ratios were below .50 in both groups. This suppressing effect was at the first TS application significant at $p < .01$ level for both groups. The CS onset and the TS offset effects were positively correlated and this correlation was significant in Group 1 (70 db CS$^{\uparrow}$ and 50 db TS$^{\downarrow}$).

The 4th and 5th theories listed above have many points in common and predictions emerging from them are similar. We have no experimental control for choosing the more appropriate one; however, a statistical control is possible. The last hypothesis emphasize the TS offset effect and assume that in „reverse procedures" correspondence between

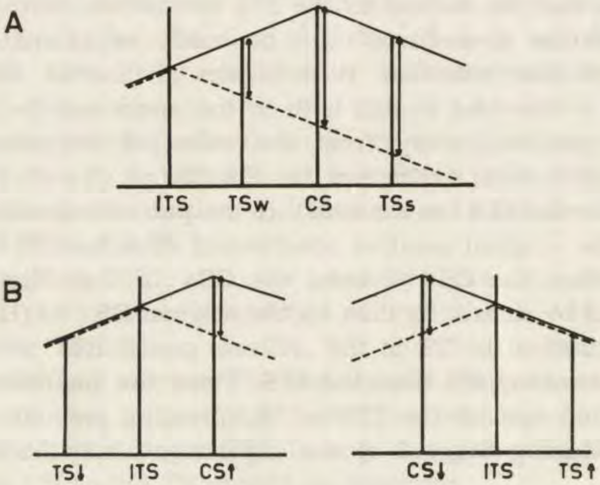

Fig. 5. Perkins-Logan-Champion hypothesis. The hypothetical gradients of excitation (continuous line), inhibition (broken line), and „net" excitation (double arrows) after reinforcement of responses to the CS with nonreinforcement of responses to the intertrial stimulus (ITS). A. The „increase procedure", i.e., the CS↑, TS↑ situation. The „net" excitation related to the TSw, which is weaker than the CS is less than the „net" excitation related to the TSs, which is stronger than the CS. B. The „reverse procedures", i.e.„ the CS↑, TS↓ situation (left), and the CS↓, TS↑ situation (right). In both „reverse procedures" the „net" excitation related to the TS equals nil, because the amount of excitation generalized to them from the CS is the same as the amount of inhibition generalized from the ITS

the CS onset and the TS offset effects is due to the identity in direction of change from the ITS to the CS and from the TS to the ITS. On the contrary, the transposition hypothesis would consider the TS offset effect as a by-effect of the facilitatory role of the TS onset on the bar-pressing response. Obviously, when the stimulus evoking an increase of the bar-pressing rate is terminated, slowing down of responding should be observed. Thus, the method of partial correlation may help us to choose the more appropriate explanation of the data. The positive correlation between the $\frac{B}{A+B}$ ratios for the CS and the $\frac{C}{C+B}$ ratios for the TS is in agreement with both theories. However, according to transposition hypothesis, it is because both these variables are correlated with the $\frac{B}{A+B}$ ratios for the TS, and the elimination of the effects of this third variable should markedly reduce the correlation between the CS onset and the TS offset effects on bar-pressing response rate. According to the „directional" hypothesis the correlation between the CS onset and the TS offset effects should not be affected, when the effect of the TS onset is kept constant.

The method of the Kendall partial rank correlation coefficient was used (Siegel 1956), and the results of the analysis are given in Table VII. This analysis shows that there is a negligible difference between τ_{xy} and $\tau_{xy.z}$ correlation coefficients. If anything, the elimination of the TS onset effect increases the correlation coefficient between the CS onset and the TS offset effects. Thus, the „directional" hypothesis is more appropriate as an account of the data of our experiment than Spence's „transposition" hypothesis.

It does not mean that the „directional" hypothesis does not accept the importance of the transposition phenomenon. The question in which the two theories differ is: whether direction of change from the ITS intensity provided by the CS onset or the absolute value of the CS intensity have cueing functions.

The test, which constitutes Stage 3 of the experiment, directly compare the importance of the absolute and relational properties of the CS for the evocation of the suppression of the bar-pressing response. The method of change of the ITS intensity reminds one of the Lashley and Wade procedure (1946) used a number of times for studying transposition along the brightness dimension (Thompson 1955, Campbell and Kral 1958, Riley, Ring and Thomas 1960, Liss 1962). The Test Sessions during Stage 3 of the experiment were designed in such a manner that both „reverse procedures" investigated in Groups 1 and 2 were changed into „non-reverse", either increase or decrease, proce-

Table VII

Correlations between the effects of the CS onset, the TS onet, and the TS offset on bar-pressing response rate

	τ_{xz}	τ_{xy}	τ_{yz}	$\tau_{xy.z}$
A				
Group 1	+ .583	+ .194	+ .028	+ .590
Group 2	+ .222	+ .111	− .222	+ .255
B				
Group 1	+ .583	+ .083	+ .028	+ .584
Group 2	+ .222	+ .111	− .167	+ .246

X variable: $\frac{C}{B+C}$ ratios of the TS; Y variable: $\frac{B}{A+B}$ ratios of the CS; Z variable: $\frac{B}{A+B}$ ratios of the TS. A, the correlations between ratios estimated for the first application of the CS and the first application of the TS during Day 1 of Stage 2. B, the correlations between daily ratios of the CS and the TS estimated for Day 1 of Stage 2.

dures. The absolute values of the CSi and the TSi intensities were the same as during previous stages of the experiment and only the ITS values were different. In subgroups A the direction of change provieded by the CS onset was the same and the amount of change was increased in comparison with previous sessions. In subgroups B the direction of change in the noise intensity provided by the CS onset was reversed and the amount of change was the same as during previous sessions. As a result of this procedure marked differences between subgroups A and B in the suppressing effect of the CS onset appeared. The CS onset lost all suppressing effect when the direction of change provided by it was reversed. This indicates that the direction of change and not the absolute volues of the CSi have cueing functions for the CER evocation. Changes in the TS onset and offset effects provide additional support for this hypothesis.

This does not mean that only direction of change can be used by Ss as a cue. Results of the experiment illustrate only that „in discrimination the direction of difference is far more readily detected than are any absolute properties of the stimuli compared" (Lashley and Wade 1946, p. 85). The importance of the absolute values of the CSi presumably increase with the prolongation of training. If only the direction of change has cueing function, the TS onset in Subgroups A should have during Test Sessions of Stage 3 as much of a suppressing effect on rate of responding as did the CS onset during previous sessions. This was not the case, although it might have occured if Stage 2 had not intervened, since during Stage 2 the Ss had the opportunity to differentiate between changes in noise intensity evoked by the CS onset and the TS offset based on absolute intensity levels. It should be noted that the suppressing effect of the TS offset on bar-pressing response rate was more marked at the first than during next TS applications.

Regardless of the relation of the experiment presented in the paper to the theory of generalization along intensity dimension, these results support the notion that analysis of the CER technique has to be done in terms of antagonism between fear and alimentary CRs. The facilitatory effect of the TS in „reverse procedures" on bar-pressing response cannot be expected and explained from the position that only fear response is a determining factor in the CER paradigm.

It seems that the theory of conditioning, generalization, and differentiation learning along the intensity dimension is far from complete. The cueing function of the direction and amount of change from the background must be covered by such a theory. The theory may also have to assimilate the notion that *„perhaps the absolute intensity of a stimulus rather than acting to V theory, instead acts on an arousal or generalized drive mechanism..."* (Mattson and Moore 1964, p. 400). For example, it was noticed during Stage 2 of the present experiment that the CS$^{\uparrow}$ had a greater suppressing effect than the CS$^{\downarrow}$ stimulus, whereas the TS$^{\uparrow}$ stimulus had a greater facilitating effect than the TS$^{\downarrow}$. It is interesting to note that the greater arousal effects of the CS$^{\uparrow}$ and TS$^{\uparrow}$ were specific: the CS$^{\uparrow}$ for the fear response, and the TS$^{\uparrow}$ for the bar-pressing response. This seems to indicate that the cueing function of the stimulus determine which response is appropriate, while its arousal properties helps determine the strength of the response. These problems call for further investigation.

SUMMARY

This study is concerned with the following problem: does the absolute intensity of the stimulus or the direction of the change from the background stimulation level provided by its onset have cueing functions? White noise of different intensities and the CER technique were used. Two methods of testing were employed. The first test consisted in the presentation of a test stimulus (TS), which was a change of the background noise intensity in the opposite direction as provided by the conditioned stimulus (CS) to which the fear response was previously conditioned. It was found that in such conditions there was no generalization of the CER from the CS to the TS. On fact, the TS onset increased bar-pressing response rate, whereas the TS offset decreased response rate. A partial correlation coefficient analysis suggests that the correspondence between the CS onset and the TS offset effects is due to a transfer of the fear

response caused by an identity in the direction of change of the noise intensity in the two conditions.

The second test consisted in changing the background noise intensity level, whereas the absolute values of the conditioned and test stimuli were the same as during previous stages of the experiment. It was found that the CS lost any suppressing effect when the direction of change in the noise intensity provided by its onset was reversed.

It is postulated that CER acquisition is a discrimination training of two antagonistic modes of behavior. When the intensity dimension is used, an increase of the stimulation evokes one mode of behavior and a decrease of the stimulation evokes the antagonistic behavior. The relational cues: direction and amount of change of the stimulation level are of primary importance in the CER situation.

The author is indepted to Dr. P. Liss for interesting discussions during preparation of this paper and for correction of the English text.

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TEMPORAL FACTORS IN DIFFERENTIATION OF INSTRUMENTAL CONDITIONING VARIETY[1]

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The differentiation (successive discrimination or „go no-go") procedure involves a successive presentation of positive and inhibitory conditioned stimuli (CSi). Conditioned responses (CRs) in the presence of a positive CS are reinforced, and CRs in the presence of an inhibitory CS are not reinforced. During pretraining, the positive CS alone is presented until the CR is well established. Then the proper differentiation begins in which the positive CS is continued to be reinforced but on randomly alternated trials an inhibitory CS is presented and this CS is not reinforced. As a result of this training the CR on inhibitory trials becomes suppressed.

The present experiment is designed to compare differentiation learning of instrumental conditioning variety in two groups of dogs in which either a short or a long intertrial interval is used. There are no reports of such comparison.

MATERIAL AND METHOD

Animals. Sixteen experimentally naive male mongrel dogs, divided in two groups of eight animals each, were used. The dogs ranged in age from 2 to 4 years and in weight from 8 to 12 kg. They were individually housed in the animal building.

Experimental conditions. The animals were trained in a Pavlovian frame mounted within a soundinsulated room. In the anterior part of the frame a food box was situated which enclosed a rotating disc with 16 food cups. An opening

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in the top lid of the box provided access to one food cup at a time. All cups, except that visible through the opening were baited with experimental food and could be moved within the reach of the animal's mouth by a partial rotation of the disc. The experimenter was seated in the pretesting room. He could activate remotely the rotation of the disc and the CSi which were delivered through a loudspeaker from the top of the Pavlovian frame. The CS presentations were monitored by a loudspeaker situated in the pretesting room.

Procedure. The experiment consisted of (a) adaptation, (b) preliminary training and (c) differentiation training. During adaptation and preliminary training an assistant was present in the testing room. The door of the testing room was then open.

The time required for the animals to adapt ranged from 4 to 6 days. On the first and second days of adaptation, the animals were allowed to explore the pretesting and testing rooms, respectively, and were given food in a cup placed on the floor. From the third day onward, the animals were leashed in the Pavlovian frame so as to face the food box. Crouching and gross bodily movements were prevented by attaching thongs to the hindlegs and anchoring them to a binding post in the rear. First food was offered from a cup situated on the top lid of the food box. Subsequently, the animals were taught to eat bread cubes soaked in bouillon (weighing approximately 3 g.) which were delivered successively from food box cups. Initially the animals showed agitation since they were clearly surprised with the click produced by the delivery of experimental food and refused to eat but, after a few trials, they decreased their agitation and started eating. The adaptation procedure was continued until each animal took 30 bread cubes offered in successive trials.

Following adaptation the preliminary training was begun which was basic to the method described by Konorski and Miller (1933). In the presence of a positive CS (CS+), which was a 1000 cy/sec. tone, the assistant placed the dog's right forelimb on the food box and this was followed by the delivery of a bread cube. Occasionally, the animals were induced to perform the CR verbally, by light stroking the trained limb, by pointing to it, by raising it for a few times, etc. In addition to food reinforcements, the animals received strokings on the head and other kinds of emotional incentives for performing the correct CR which was an active placing the right forelimb on the food box. Adventitious forelimb movements between the CS presentations were also reinforced. After the instrumental response was established, only were those responses reinforced which occurred in the presence of the CS+. Each animal then was given 30 presentations of the CS+ at short intervals per day. The assistant, who had originally stood nearby the animal, moved away gradually until he eventually left the testing room. Then the door was locked. The preliminary training was continued until an animal responded actively to 30 successive presentations of the CS+.

On the next day, the differentiation training sessions began in which on half the trials (15 trials) the inhibitory CS (CS−), which was a 700 cy/sec. tone, was substituted. From then on, 15 positive (reinforced) and 15 inhibitory (unreinforced) trials were presented daily. Both trials were alternated irregularly. They were separated by 15 sec. intervals in one group of dogs, and by 60 sec. intervals in the second group. There were given 1, 2 or 3 trials of the same type (positive or inhibitory) in succession. The positive CS always overlapped from 1 to 2 seconds with the presentation of food. An error was defined as failing to respond on positive trials or responding on inhibitory trials within the 5 seconds during which the CSi were presented. The presentation of the positive CS was followed by a food reinforcement even if the CR failed to occur. A noncorrection technique was used, that is, whether or not the dog committed an error it was given the next scheduled trial. Out of the experimental situation the animals were fed twice a day a diet of cereal, beef bouillon, horse meat and vegetables. Half of the daily diet was offered before testing. The differentiation training continued until the animals attained the criterion of 45 correct inhibitory CRs in 50 consecutive trials which equaled the criterion of 95 correct CRs in 100 (considering both positive and inhibitory) trials since errors in the positive trials occurred occasionally, if at all. (Brutkowski and Mempel 1961, Brutkowski and Dąbrowska 1963).

RESULTS

In Table I data are given for the individual animals in the two groups. It is seen that the number of inhibitory trials to complete criterion in the 60-sec. intertrial interval group is significantly lower than that in the 15-sec. interval group ($p < .001$, Mann-Whitney two-tailed test, Siegel 1956). This indicates that the intertrial interval of 60 seconds is obviously superior to that of 15 seconds for learning the 1000 cy/sec. (as CS+) vs. 700 cy/sec. (as CS−) tone differentiation in dogs. In behavioral terms, these data suggest a greater difficulty with differentiations trained on a short intertrial interval schedule.

Table I

Number of inhibitory trials to criterion (A) and intertrial CRs (B) during differentiation training with 15-sec. and 60-sec. intertrial intervals

15-sec.intertrial interval group			60-sec. intertrial interval group		
Dogs	A	B	Dogs	A	B
Kondor	270	12	Fucek	135	18
Mały	345	136	Rudy	150	10
Bąk	420	325	Czarek	165	0
Kaprys	435	114	Diablik	180	14
Poker	525	319	Reks	180	72
Druh	555	52	Filutek	180	17
Beza	555	670	Mops	195	22
Kibic	675	105	Kudłacz	270	40

The CRs during intertrial intervals, which occur upon acquisition of an active CR, gradually drop out and eventually the occurrence of the CR is confined to the CS presentations. A point of interest is the fact that the 60-sec. interval group shows a significantly lower rate of responding ($p. < .006$, Mann-Whitney two-tailed test) and faster extinction during intervals than the 15-sec. interval group.

CONCLUSIONS AND SUMMARY

The general conclusion to be drawn from the results of this experiment is that the development of a differentiation, defined in terms of suppression rate of the CR on inhibitory trials and during intertrial intervals, is more rapid under circumstances of CSi presented at long intervals. This can be explained by an increased inhibition with long intervals. After a long interval, an inhibitory trial is associated with a phase of reduced facilitatory effect following the preceding positive trials — a condition which is beneficial for inhibition.

A slow development of a differentiation trained at short intertrial intervals, which is reflected in a low suppression rate of the CR on inhibitory trials and an excess of responding during intervals, may be attributed to the fact that after a short interval an inhibitory trial is associated with a high level of facilitatory effect resulting from the preceding positive trials — a factor which clearly interferes with inhibition.

The intertrial interval responding may be looked at in still another way. With short intervals, the chance of presenting the food reinforcements is greater. Hence, there is the possibility that a high rate of responding during intertrial intervals in the short interval situation is due to this adventitious secondary reinforcement.

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FURTHER STUDIES ON CONDITIONED BRADYCARDIA IN CATS[1]

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In previous work, cats were found to show a decrease of heart rate during the CS-US interval in a classical defensive conditioning situation (Santibáñez-H. et al. 1963). This response was rather surprising because dogs and rats respond to a CS with tachycardia in a somewhat similar experimental situation (Gantt 1960, Bloch-Rojas et al. 1964). The neurophysiological mechanisms involved in the conditioned cardiac response are unknown.

Gantt (1960) was unable to show changes in the cardiac response of a dog after full excision of the cerebral cortex of one hemisphere and the cingulate cortex of the other hemisphere, although electrical stimulation of the cingulate cortex and the orbitofrontal cortex has been shown to change cardiac and respiratory rates (Smith 1945, Delgado 1960).

In the present experiments two questions were posed: the role of the restriction of movements of the animals during training and the function of the frontal and cingulate cortex in a bradycardic conditioned response.

METHOD

Subjects. The subjects were 34 cats (males and females) whose weights ranged from 2.3 to 4.0 kg. The animals were housed in individual cages, maintained at a constant temperature and fed with meat and milk during the period of work. They were divided, according to the training procedure and the operations per-

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formed, in the following way: a) two control groups: a restrained normal group (RN) harnessed to a hammock, and a freely moving normal group (FN); b) five experimental groups: extensive frontal lesion group (EF), gyrus proreus lesion group (GP), gyrus sygmoideus anterior lesion group (GS), gyrus genualis lesion group (GG) and extensive lesion of the medial wall group (EM). All operated animals were restrained in a hammock during training.

Apparatus and recording. Training was carried out in a wire cage (90 × 90 × 120 cm.), placed in a sound-proof chamber. The animals were observed through a one-way vision screen.

In all harnessed cats, heart rate was recorded through circular steel electrodes 5 mm. in diameter and 0.2 mm. thick, attached by an elastic bandage to the shaved surfaces of the left fore and right hind limbs; similar electrodes attached to the right fore limb, were used for the bipolar electrical stimulation.

In the free-moving cats, the electrodes consisted of silver wires attached around the distal portion of the limbs. The wires were placed beneath the skin and insulated through their whole subcutaneous extension from the distal portion of the limbs to the head, and were there soldered to a socket fixed to the skull. Bipolar electrical stimulation of the radial nerve of the right fore limb was performed with similar subcutaneously implanted electrodes.

A Grass ink-writing poligraph was used to record the EKG.

The CS was a moderately intense tone of 500 cps generated by a Phillips tone generator. The US was delivered through a Grass stimulator and consisted of a single electric shock. The intensity varied from one cat to another; it was considered effective when it produced retraction of the limb.

Operations. Operations were performed aseptically under pentobarbital-sodium anesthesia, with the suction technique. In bilateral ablations, the intention was to remove gyrus proreus plus gyrus sygmoideus anterior in the extensive lesion group (EF); gyrus proreus alone in the GP group; gyrus sygmoideus anterior in the GS group; gyrus genualis in the GG group, and a more extensive area than genualis in the medial wall, in the EM group. The lesions were aimed at cortical areas where stimulation has been shown to induce changes in heart rate.

Anatomical control. At the end of the training period the brains were perfused with saline and 10 per cent formalin and prepared histologically for study of the extent of the lesions.

Training. Ten days after operation, adaptation to the experimental situation was begun. The animals were kept in the cage for 30 minutes each day for one week. At the end of the week, basic cardiac rates were recorded in response to the presentation of a 500 cps tone and to an electric shock, given separately. Then all subjects were trained in a classical defensive conditioned reflex situation during 15 daily sessions of 10 trials each. The CS, which lasted 5 sec., was followed by a 5 sec. interval, at the end of which the US, an electric shock applied to the right fore limb, was given. The interval between the onset of the CS and the shock was 10 seconds.

Heart rate was recorded at every trial, and heart beats were counted for 10 seconds before the onset of the CS, as a control for the basic cardiac frequency. Heart beats were counted again after the onset of the tone, and during the interval, until the US was delivered.

RESULTS

I. Comparison between restrained and unrestrained normal cats. This experiment was performed in order to control the possible importance of the position of the animal during the experiment in the production of the conditioned bradycardia.

Comparing the heart rate between free and restrained cats prior to training, statistically significant differences were obtained (significant at the level $p < .001$). While the restrained animals had a mean heart rate of 32.1 beats per 10 sec., the free-moving cats had only 20.9 beats per 10 sec, i.e., cats which were allowed to move around freely were significantly more bradycardic, showing a lower basal rate than the harnessed cats. However, on comparing the means of the heart rate change (difference in cardiac rate during the CS-US interval and during the 10 sec. prior to the onset of the CS) in the CS-US interval, it was found that both groups showed bradycardia.

The mean was -2.3 beats per 10 sec. for the RN group and -1.6 beats per 10 sec. for the FN group. The difference was not statistically significant.

II. Effects of cortical lesions on the conditioned bradycardia. Effects of extensive lesions of the frontal pole (EF group): The lesions involved gyrus sigmoideus anterior, gyrus sigmoideus posterior (partially), and gyrus proreus. In Fig. 1 (6 to 10), the reconstructed lesions are shown. During conditioning, the CS elicited an increase in the cardiac rate in these animals, as one can see in Table I, and more clearly in Fig. 2 (6 to 10). The general behavior of these animals was very similar to that of the normal cats; however when they were harnessed, they showed an increased motor activity, especially during intertrial intervals. Such behavior was rarely seen in the normal cats.

Effects of restricted lesions of the frontal pole (GP and GS groups): Two types of lesions were attempled: extirpation of gyrus proreus alone and extirpation of gyrus sigmoideus anterior alone. The results of these animals (Fig. 1, 11 to 15 and 16 to 20) were rather equivocal. Only 3 cats of the GP group presented conditioned bradycardia (11, 12 and 13), while in the other two (14 and 15) there was practically no change of heart rate during conditioning (Table I and Fig. 2, 11 to 15).

The animals of the GS group (Fig. 1, 16 to 20) reacted very irregulary to the CS after conditioning; in two of them (19 and 20) the heart rate was lowered; in one (18) was increased and in the other two (16 and 17) it did not change during the presentation of the CS (Table I and Fig. 2, 16 to 20).

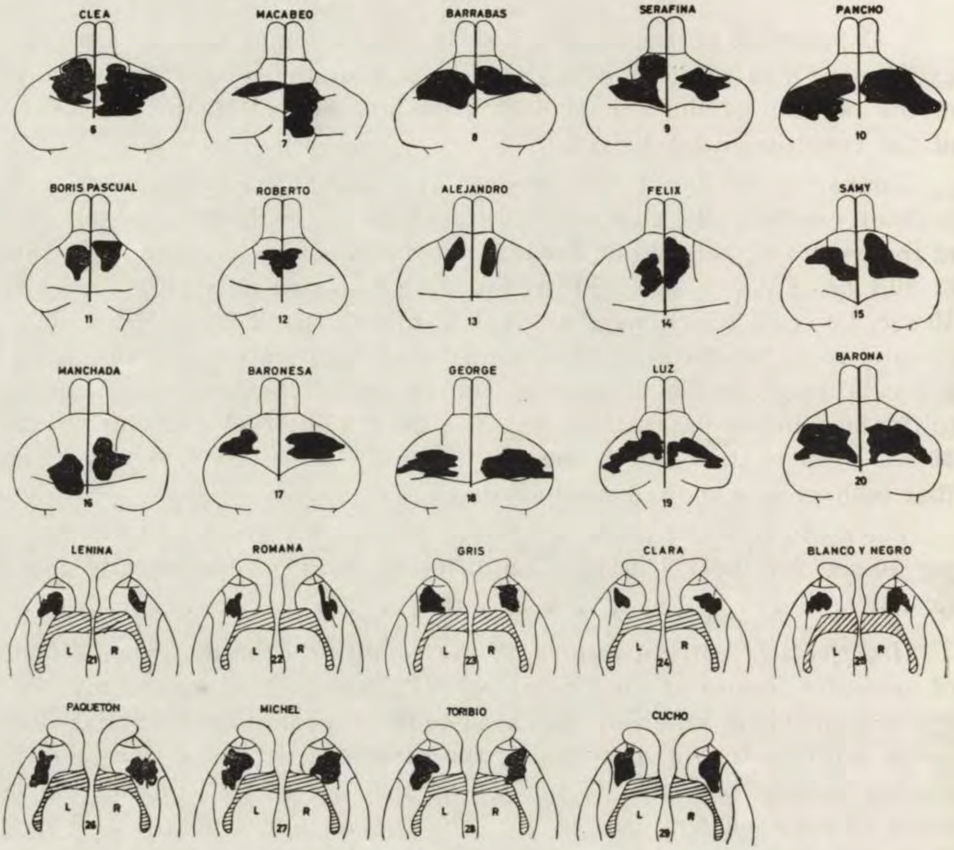

Fig. 1. Extent of the lesions: frontal pole 6—20, and medial surface, 21—29

Effects of lesions of the medial surface of the hemisphere (GG and EM groups): Two types of lesions were performed. One, partially destroying gyrus genualis (Fig. 1, 21 to 25), which produced no effect on the conditioned heart rate. The animals showed bradycardia during the CS-US interval (Table I, and Fig. 2, 21 to 25) just as normals. The second operation involved a larger area of the cingulate cortex; in these animals conditioned bradycardia was more intense than in normals (Fig. 2, 26 to 29).

Comparison among normal, genualis and extensive medial wall groups: Analysis of variance (one way classification) was used to compare the groups. Table II shows that the three groups do not belong to the same population in A and that the normal and genualis groups are statistically different from the medial wall extensive group, in B.

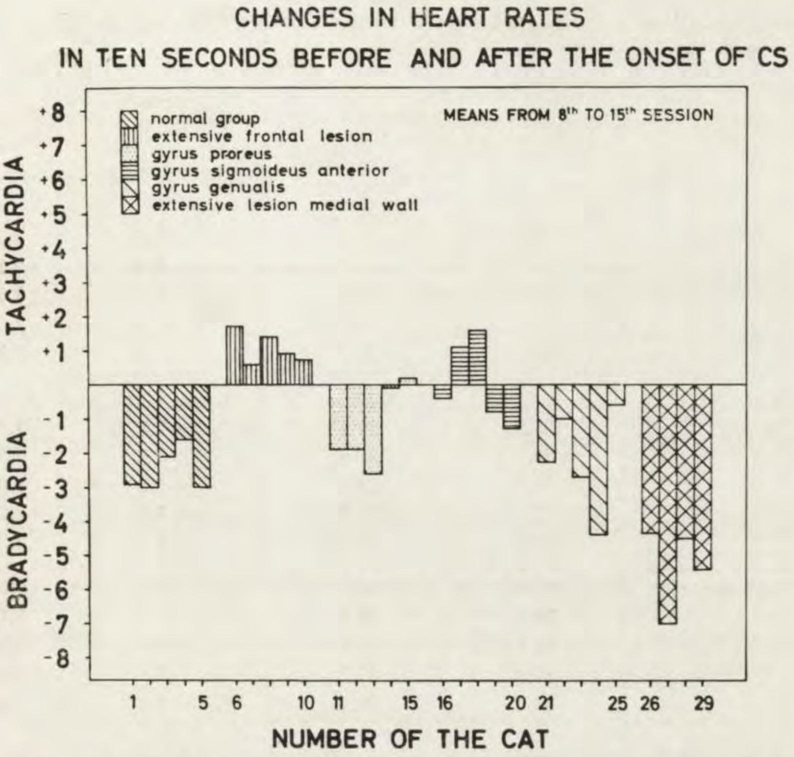

Fig. 2. Effect of lesions on the conditioned cardiac response. Mean heart rate differences (10 sec. before CS and 10 sec. interval CS-US) in the last 8th sessions

Comparison among normal, extensive frontal and extensive medial wall groups: Fig. 3 shows the curves of heart conditioned response of the three groups. The extensive frontal group shows tachycardia during the CS-US interval, while the normal and extensive medial wall groups, exhibit bradycardia. Normal and extensive medial wall groups are statistically different at the level $p < 0.01$.

DISCUSSION

A comparison of the performance of the restrained and unrestrained groups clearly reveals that posture influences basic heart rate but does not influence the cardiac conditioned response. Therefore, the idea that conditioned bradycardia is a postural artefact during training must be discarded.

The effect of extirpation of the frontal cortex and that of extirpation of the cingulate cortex on conditioned bradycardia, deserves a comment.

Table I
Individual results of heart rate during defensive classical conditioning

Number of cat	Lesion	Mean heart rates in the last 8 sessions, 10 seconds		Difference between CS-US interval and control Mean	"t" test
		Before CS	After CS		
1	Normal, EF	32.9	30.0	−2.9	3.79*
2		34.3	31.3	−3.0	7.10*
3		26.6	24.5	−2.1	8.02*
4		31.7	30.1	−1.6	2.56***
5		38.3	32.3	−3.0	3.31**
6	Extensive frontal, EF	35.9	37.6	+1.7	1.89
7		30.0	30.6	+0.6	1.80
8		27.2	28.6	+1.4	3.04**
9		30.1	31.0	+0.9	2.25
10		27.3	28.0	+0.7	2.38***
11	Proreus, GP	34.2	32.3	−1.9	6.50*
12		36.5	34.6	−1.9	5.12*
13		34.1	31.5	−2.6	3.50*
14		37.8	37.7	−0.1	0.24
15		36.2	36.4	+0.2	0.49
16	Sygmoideus anterior, GS	30.7	30.3	−0.4	0.72
17		38.6	39.7	+1.1	1.90
18		24.4	26.0	+1.6	4.76*
19		25.6	24.8	−0.6	1.40
20		25.0	23.7	−1.3	1.99
21	Genualis, GG	21.8	19.6	−2.2	3.92*
22		34.1	33.1	−1.0	11.30*
23		25.2	22.5	−2.7	3.05**
24		23.5	19.1	−4.4	11.21*
25		25.7	25.1	−0.6	8.0 *
26	Extensive lesion of the medial wall, EM	31.1	26.8	−4.3	4.21*
27		25.5	18.5	−7.0	11.90*
28		28.1	23.6	−4.5	12.0 *
29		27.0	21.6	−5.4	12.60*

* Significant at 1% level. ($p < .01$)
** Significant at 2% level. ($p < .02$)
*** Significant at 5% level. ($p < .05$)

Many authors have observed a relation between frontal cortex and autonomic functions. Stimulation of the frontal pole has been shown to induce salivation, respiratory acceleration and pupillary reactions

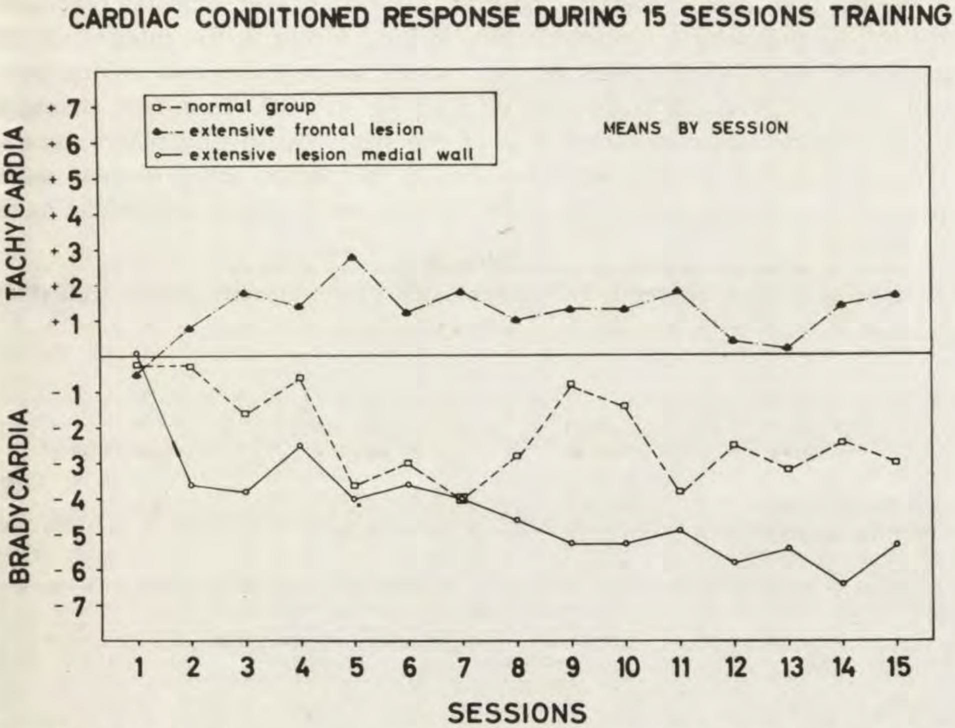

Fig. 3. Cardiac conditioned response during 15 sessions of training. Normal, extensive frontal and extensive medial wall groups

(Akert, Hess and McDonald 1950), vasodilatation of muscular arterioles (Eliasson, Lindgren and Uvnäss 1952—1953), and facilitation of the effect of hypothalamic stimulation on systemic arterial pressure (Bittman and Raiciulescu 1963). On the whole, stimulation experiments seem to produce sympathetic effects. Ablation, involving the zones extirpated in the present work, causes facilitation of the salivary outflow, disinhibition of inhibitory salivary responses and an increase in spontaneous motor activity (Brutkowski 1959a, 1959b, 1964).

On the other hand, evoked potential experiments have shown that the frontal region not only contains somatic sensory motor areas, but it also receives different types of sensory inputs. Potentials elicited by stimulation of the radial nerve of the ipsilateral limbs (Albe-Fessard and Rougeul 1955, 1958) as well as visual and auditory responses have been observed (Buser, Borenstein and Bruner 1959, Thompson, Johnson and Hoopes 1963, Thompson, Smith and Bliss 1963).

Since the frontal cortex mediates autonomic and sensory reactions it is quite understandable that it should play a role in the integration of a cardiac conditioned reflex. In our experiments, extensive lesions prevent the decrease of heart rate elicited by the CS. This fact strongly suggests a frontal cortical control of the heart during defensive conditioning. However, the present results are not quite in agreement with the data mentioned in the literature. A decrease of heart rate might have been expected. Instead, the lesions resulted in an increase in cardiac rate and motor activity. At present, it is rather hard to explain these discrepancies and even harder to explain the reported findings. It is clear that more experimental work is needed before the role of frontal cortical mechanisms in the conditioned cardiac responses can be understood.

Table II

Analysis of Variance. Normal (RN), genualis (GG) and extensive medial wall (EM) groups

A

Sources of variation	Sums of squares	d.f.	Variance estimate	F (variance ratio)
Between groups	23.94	2	11.97	9.8*
Within groups	14.22	11	1.21	
Total	38.16	13		

B

Groups	Difference	S.E. of diff.	"t"
RN and GG	0.34	0.704	0.5
RN and EM	1.72	0.737	2.3**
GG and EM	2.06	0.737	2.7**

* Significant at 1% level ($p < .01$)

** Significant at 3% level ($p < .003$)

Concerning medial wall lesions, unpublished data collected by Woolsey have shown that stimulation of the anterior part of the cingulate cortex has a clear-cut sympathetic effect. Extirpation of the same zone produces a disinhibition of the inhibitory type II CR response (Brutkowski and Mempel 1961). Our results confirm the sympathetic nature of the anterior part of the cingulate cortex since its excision determines a vagal effect.

In conclusion, the frontal pole and the anterior cingulate cortex seem to act antagonistically in the control of heart activity during a classical defensive conditioned reflex.

SUMMARY

The importance of the training, posture and of the frontal and cingulate cortex in the acquisition of a bradycardic conditioned response were studied. Thirty four cats were used, divided in 7 experimental groups. Two groups served as controls: one group received training while placed in a hammock, and the other while moving freely. Five types of lesions were performed: one group with a lesion of the proreal and sygmoid gyri, one group with a lesion of the proreal gyrus, another group with a lesion in the anterior sygmoid gyrus, one group with a lesion involving the gyrus genualis, and finally, one group with a lesion involving a larger area than genualis. All the animals were trained in a classical defensive conditioned reflex performance.

Both control groups showed conditioned bradycardia in spite of the fact that the basic cardiac frequency is higher in the restrained than in the freely moving animals. Lesions involving proreal and sygmoid gyri prevent the bradycardic conditioned response and replace it by an increase in heart rate. Less extensive lesions of the frontal pole do not have a clear-cut effect. Lesion of gyrus genualis fails to produce any effect, but a more extensive lesion of the cingulate cortex intensifies the bradycardic response.

The results suggest that the frontal cortex and the anterior cingulate cortex are involved in the cardiac control in a defensive conditioned reflex.

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THE EFFECT OF SUBPROREAL LESIONS OF THE PREFRONTAL AREA ON ALIMENTARY CONDITIONED REFLEXES IN DOGS[1]

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(Received November 16, 1964)

It has previously been shown that lesions of the prefrontal areas anterior to the presylvian and genual sulci on the lateral and medial aspects, respectively, of the hemisphere in the dog produce an impairment of inhibitory CRs (Brutkowski et al. 1956, Szwejkowska et al. 1963). It has furthermore been shown that this impairment is produced by lesions of some parts of the frontal cortex but not by lesions of other parts of the frontal cortex (Brutkowski 1964, Brutkowski, 1966).

This study aims at further localizing the prefrontal areas focally involved in CR inhibition. Specifically, the present paper is concerned with investigating the effect of lesions of the subproreal area on alimentary conditioned reflexes (CRs) in dogs.

MATERIAL AND METHODS

Five male, adult monogrel dogs were trained to place the right foreleg on the food tray in response to the presentation of a buzzer, used as a positive conditioned stimulus (CS). This movement was reinforced by food. Eight trials were given daily. The intertrial intervals were 1 to 2 min. When the positive CR was firmly established the conditioned inhibition training was started: a compound of the successive presentations of a metronome and a buzzer was used without food reinforcement. Then, both components were separated by a progressively increasing interval up to 6 sec. Each component of the inhibitory compound was presented for 5 sec. Six positive trials and 2 conditioned inhibition trials were

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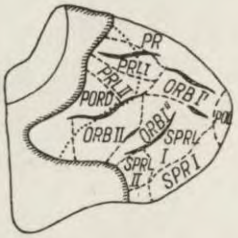
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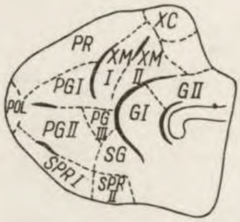
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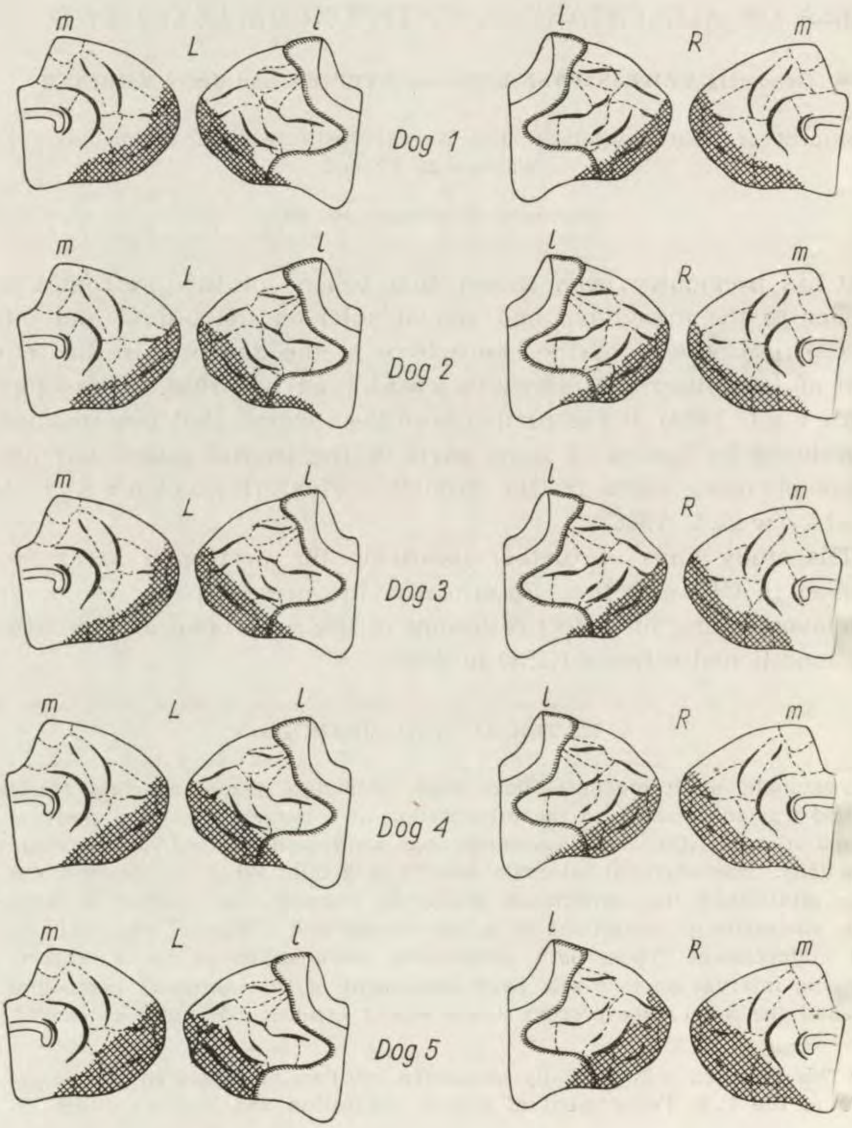
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Fig. 2. Effects of subproreal lesions on inhibitory CRs. Each column denotes 5 session blocks (10 inhibitory trials). Black parts of the columns denote errors in inhibitory trials

used daily in the further training. The animals were trained to a criterion of one error in 10 successive inhibitory trials. Then the cortex of the subproreal areas was removed under aseptic conditions. Testing was resumed one week after the surgery, and the animals were trained to the same criterion as before.

After the completion of the postoperative testing the animals were killed and the rostral parts of the brains were sectioned and stained by Nissl and Klüver methods. The lesions were reconstructed on the basis of the myeloarchitectonic map of the dog prefrontal areas (Kreiner 1961).

RESULTS

Anatomy. The extent of lesions is shown in Fig. 1. It is seen that the entire subproreal area on both the dorsal and medial surface of the hemisphere (SPR I, SPR II, SPRL I and SPRL II) and a part of the pregenual area on the medial aspect of the brain were damaged in all animals. In dogs Nos. 1, 2, 3 and 4 the lesions were identical; in addition to the subproreal area a small protion of the pregenual area, PG II, was damaged. In dog No. 5 the lesion was larger and involed the entire PG II (Table I).

Fig. 1. Extent of subproreal lesions in dogs Nos. 1—5. Top, maps of dorsolateral and medial surfaces of the prefrontal region. Below, schemes of myeloarchitectonical areas of the prefrontal cortex with the indications of the placement of the lesions.

Heavy lines, sulci; broken lines, borders of areas; dotted line, the rostral border of the anterior composite gyrus which corresponds with the presylvian sulcus; the olfactory bulb and tract and the composite gyrus were removed at the indicated place for convenience of reproduction. 1, lateral aspect; m, medial aspect; POL, area polaris; PR, area prorealis; PR LI, area prorealis lateralis I; PRL II, area prorealis lateralis II; SPR I, area subprorealis I; SPR II, area subprorealis II; SPRL I, area subprorealis latealis I; SPRL II, area subprorealis lateralis II; ORB I', area orbitalis I'; ORB I'', area orbitalis II''; ORB II, area orbitalis II; PORD, area paraorbitalis dorsalis; PG I, area praegenualis I; PG II, area praegenualis II; PG III, area praegenualis III; G I, area genualis I; G II, area genualis II; XM I, area praecruciata medialis I; XM II, area praecruciata medialis II; XC, area praecruciata centralis. L, left hemisphere; R, right hemisphere.

Table I

Extent of subproreal lesions

Dogs	POL	PR	SPR I	SPR II	SPRL I	SPRL II	PG I	PG II	SG
1	t	p	t	t	p	—	p	p	p
2	t	p	t	t	p	—	—	p	—
3	t	p	t	t	p	p	—	p	—
4	t	p	t	t	t	p	—	p	—
5	t	p	t	t	t	t	p	t	p

t, total lesion; p, partial lesion.

Behaviour. The positive CR remained unaffected postoperatively. On the other hand, the lesions impaired the performance on the inhibitory trials (Fig. 2). However, the impairment was slight and transient. Within from 5 to 10 days after surgery the animals attained the preoperative criterion.

DISCUSSION

The results point to a slight and transient impairment in conditioned inhibition performance following lesions of the subproreal area with an encroachment on the pregenual area. As compared with previously made lesions of the prefrontal cortex, the impairment of inhibition after lesions of the subproreal area is superior to that after lesions of the dorsolateral prefrontal areas but inferior to that after lesions of the proreal and pregenual ares on the medial aspect of the hemisphere (Szwejkowska et al. 1963). This suggests that the damage to the pregenual areas and not the damage to the subproreal areas alone is responsible for the impairment of inhibitory CRs in the animals of the present investigation. This is supported by the evidence that subproreal lesions do not impair inhibitory performance in a differentiation task (Brutkowski and Dąbrowska, in press).

SUMMARY

Lesions of the subproreal area on both dorsal and medial aspects of the hemisphere with an encroachment on the pregenual area on the medial surface in the dog produce a slight and transient impairment of the conditioned inhibitory performance. It is suggested that the damage to the pregenual area is responsible for this impairment.

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Acta Biol. Exper. (Warsaw), vol. XXV, No. 4, pp. 379—386, 1965

THE EFFECT OF PREFRONTAL LESIONS ON INSTRUMENTAL CONDITIONED ALTERNATION REFLEXES IN DOGS[1]

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(Received February 5, 1965)

In a previous paper (Szwejkowska et al. 1964), it has been shawn that when a conditioned stimulus (CS) is presented at a fixed intertrial interval schedule in the instrumental conditioning situation, being alternately reinforced and not reinforced by food, a pseudoalternation conditioned reflex (CR) is established, in which the time elapsed after the intake of the reinforcement food determines the animal's response. When the intervals between the positive (reinforced) and inhibitory (non-reinforced) trials in the alternating procedure are variable (a true alternation CR) the task appears to be very difficult, but the animal nevertheless is capable to master it (Szwejkowska 1964).

Brutkowski and Dąbrowska (1963), and Szwejkowska et al. (1963) have shown that the inhibitory CRs are markedly impaired after lesions of the medial prefrontal cortex (involving area pregenualis I and area precruciata), whereas after lesions of the dorsolateral prefrontal cortex (involving area prorea and area orbitalis) these reflexes are either slightly impaired or unimpaired.

The purpose of this paper is to investigate the effect of either lesion on the pseudoalternation and true alternation CRs.

MATERIAL AND METHODS

Experiments were performed in a soundproof chamber on 8 dogs. In the preliminary training, the animals were taught under food reinforcement to place the right foreleg on the food tray in response to a buzzer. When this task was

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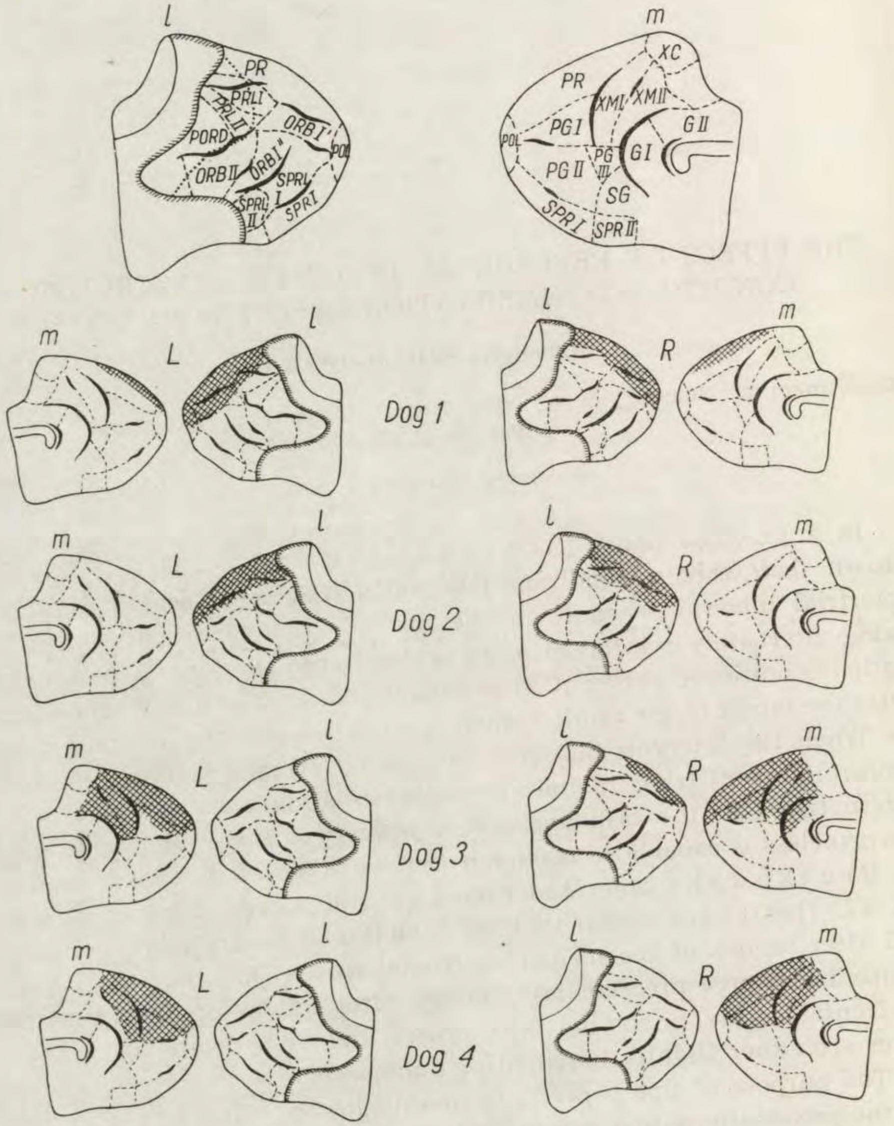
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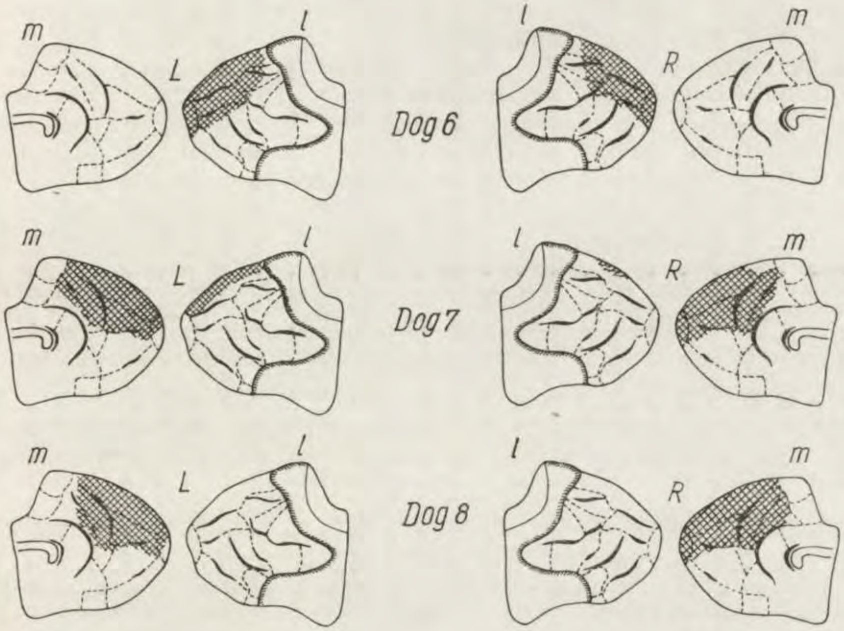

Fig. 1. Extent of prefrontal lesions in dogs Nos. 1 to 8. Top, maps of dorsolateral and medial surfaces of the prefrontal region. Below, schemes of myeloarchitectonical areas of the prefrontal cortex with the indications of the placement of the lesions

Heavy lines, sulci; broken lines, borders of areas; dotted line, the rostral border of the anterior composite gyrus which corresponds with the presylvian sulcus; the olfactory bulb and tract and the composite gyrus were removed at the indicated place for convenience of reproduction; l, lateral aspect, m, medial acpect. POL, area polaris; PR, area prorealis; PRL I, area prorealis lateralis I; PRL II, area prorealis lateralis II; SPR I, area subprorealis I; SPR II, area subproprealis II; SPRL I, area subprorealis lateralis I; SPRL II, area subprorealis lateralis II; ORB I′, area orbitalis I′; ORB″, area orbitalis I″; ORB II, area orbitalis II; PORD, area paraorbitalis dorsalis; PG I, area pregenualis I; PG II, area pregenualis II; PG III, area pregenualis III; G I, area genualis I; G II, area genualis II; XM I, area precruciata medialis I; XM II, area precruciata medialis II; XC, area precruciata centralis. L, left hemisphere; R, right hemisphere.

mastered the buzzer was no more presented, but, instead, a new auditory stimulus, a metronome (the proper CS), was introduced which was alternately reinforced and not reinforced by food. Eight positive and eight inhibitory trials were given in each experimental session. In positive trials, the animal received food immediately after the performance of the trained movement in response to the presentation of the CS. In inhibitory trials, the CS was presented within 5 sec. A few pieces of bread moisted in broth served as reinforcement.

Two series of experiments were carried out. In series I, performed on 4 dogs (Nos. 1 to 4), the CS was presented at a 1 min. intertrial schedule. In series II, performed on 4 other dogs (Nos. 5 to 8), the intertrial intervals were variable (1.0, 1.5 and 2.0 min.).

When the dogs reached criterion of 90 errorless responses in 100 consecutive trials, they were surgically operated upon. Bilateral lesions were made by suction in either the dorsolateral parts (comprising area prorea and area orbitalis) or the medial parts (area pregenualis and area precruciata) of the prefrontal cortex. Each type of lesion was made in 4 dogs, two of them being trained at the fixed (1 min.) intertrial interval schedule and two, trained at the variable intertrial interval schedule. One week after surgery the experiments were reasumed and conducted till the steady state of performance was reached. Thereafter the dogs were sacrificed, the brains removed and lesions reconstructed (Fig. 1).

RESULTS

Series I (fixed intertrial interval schedule). After both medial and dorsolateral lesions the positive CRs were practically unimpaired. Only in 2 dogs (one after medial and another one after dorsolateral lesion) in the first postoperative days were the CRs somewhat irregular.

As far as the inhibitory CRs are concerned, the impairment occurred in the dogs with medial prefrontal lesions. The inhibitory CRs in the first 10 sessions were impaired in about 30 per cent, and the preoperative level of performance was reached in the second or third 10 session block. On the other hand, after the dorsolateral lesions the impairment of the inhibitory CRs was quite negligible (Fig. 2).

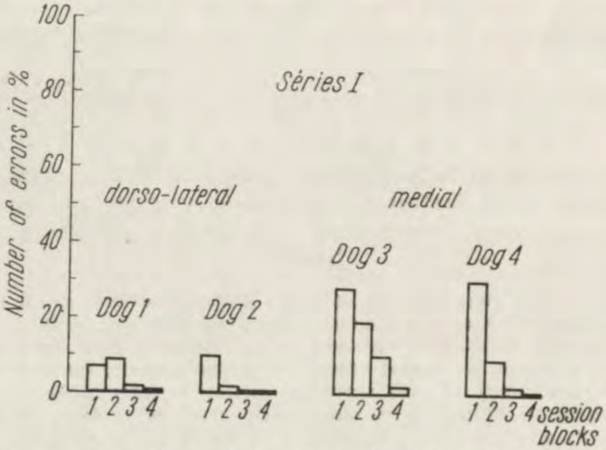

Fig. 2. The effect of dorsolateral and medial lesions on inhibitory alternation CRs (series I, fixed intertrial interval schedule). Each column denotes a successive 10 session block (80 inhibitory trials)

Series II (variable intertrial interval schedule). The performance of all the 4 dogs in response to the positive CS was unaffected. Only in one dog (after medial lesion), were the positive CRs irregular, but an irregular performance to the presentation of the CS was also seen in this dog in the begining of the preoperative training. The ihibitory CRs were, on the contrary, severely affected in all the 4 dogs (Fig. 3). After

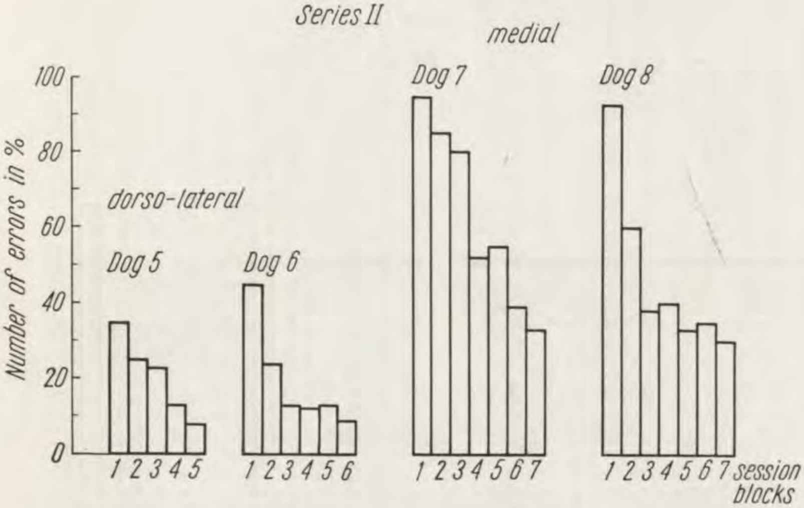

Fig. 3. The effect of dorsolateral and medial lesions on inhibitory alternating CRs (series II, variable intertrial interval schedule). Each column denotes a successive 10 session block (80 inhibitory trials)

dorsolateral lesions the inhibitory CRs were impaired in about 40 per cent and the preoperative level of performance was attained after 50 sessions. Following medial lesions, the impairment was even greater. In the first postoperative period, the inhibitory performance was impaired nearly in 100 per cent. Then, the percentage of errors gradually decreased, attaining after 70 sessions (560 trials) about 30 per cent.

In Fig. 4 the distribution of errors is given. It is seen that most errors are committed when the 2 min. intertrial interval is used; after 1.5 min. interval, the errors are fewer and still fewer after 1 min.

DISCUSSION

The results of this paper indicate that the impairment of the alternation CR depends on the site of the lesion and the type of the inhibitory task. Thus, it has been found that medial prefrontal lesions produce a more considerable impairment than the dorsolateral lesions, and that the performance at the variable intertrial interval schedule is more affected than that at the fixed intertrial interval schedule. Briefly, the most considerable impairment of inhibitory performance in the alternation test is found after medial prefrontal lesions at the variable intertrial interval schedule. Initially the inhibitory CRs are totally abo-

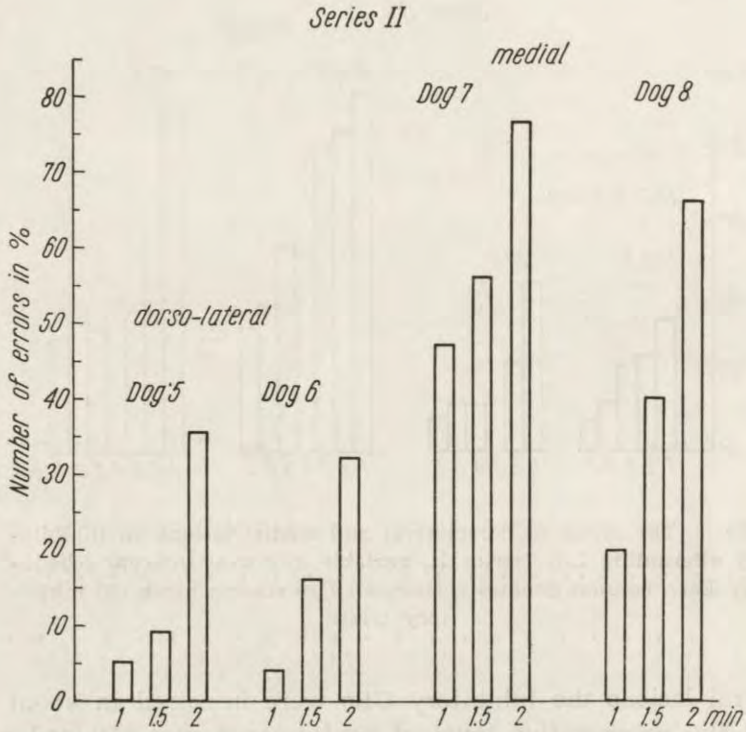

Fig. 4. The distribution of errors in inhibitory trials depending on the length of intertrial intervals in dogs after dorsolateral and medial prefrontal lesions (series II). Each column denotes mean number of errors in 10 session block for 1.0, 1.5 and 2.0 min. intertrial intervals

lished, and the subsequent recovery is never complete. On the other hand, lesions of the dorsolateral prefrontal cortex produce a negligible impairment of inhibitory in the alternation test used at the fixed intertrial interval schedule. The effects following the medial lesions at the fixed interval schedule and those following the dorsolateral lesions at the variable interval schedule take the medium course. However, the performance of the latter animals appears to be more affected than that of the former ones.

The analysis of distribution of errors in the variable interval group of dogs has revealed that the longer the interval preceding the inhibitory trial, the more likely is affected the inhibitory performance on this trial after operation. Thus, the inhibitory CR after a 2 min. interval was impaired most severely, whereas that after 1 min. interval was impaired most slightly. Since in the alternation test the intake of the reinforcement food on the positive trial determines the type of the inhibitory trial, it becomes understandable that a long intertrial interval makes the inhibitory task more difficult than a short intertrial interval. This explains the impairment of the inhibitory CRs after the 2 min. intertrial interval following a dorsolateral prefrontal lesion which, as shown by earlier studies, appears less harmful for inhibitory performance than a medial prefrontal lesion.

Our results seem to be in a good agreement with the earlier results of Brutkowski (1959) concerning the effect of prefrontal lobectomies on alternation test, as well as with those of Brutkowski and Dąbrowska (1963) concerning the effects of partial prefrontal lesions on a differentiation test. Brutkowski (1959) has shown that the more difficult is the type of the alternation task, the stronger the impairment after the prefrontal lobectomy. Further, Brutkowski and Dąbrowska have shown (1963, 1964) that if the intertrial intervals are short (15 sec.), the differentiation task appears more difficult than that if the intervals are long (1 min.) Moreover, these authors have shown that if short intertrial intervals are used, the differentiation is impaired even after a dorsolateral prefrontal lesion. It may be thought that in the alternation task the long intertrial intervals make the inhibitory task difficult. The problem of whether the impairment of inhibitory CRs after dorsolateral prefrontal lesions is qualitatively or quantitatively different from that after medial prefrontal lesions is open.

SUMMARY

1. The effects of dorsolateral and medial prefrontal lesions on an alternation task at a fixed or variable intertrial interval schedule were studied.

2. Whereas the positive CRs were not or slightly affected by both types of lesions, the inhibitory CRs were more or less severely impaired depending on the placement of the lesion and the type of the alternation task.

3. The most severe impairment of the inhibitory CRs followed the medial lesions when the alternation task was used at a variable interval schedule; the slighest impairment followed the dorsolateral lesion at a variable interval schedule and the medial lesion at a fixed interval schedule. The effect of the dorsolateral prefrontal lesions on an alternation task used at a fixed interval schedule was very negligible.

4. In the variable interval schedule, the most affected were those inhibitory trials which followed the positive trials after 2 min. interval, less affected were those after 1.5 min. interval, and the least affected were those following 1 min. interval.

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Acta Biol. Exper. (Warsaw), vol. XXV, No. 4, pp. 387—394, 1965

THE EFFECTS OF BILATERAL LESIONS IN PRECRUCIATE CORTEX ON SIMPLE LOCOMOTOR CONDITIONED RESPONSE IN DOGS[1]

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(Received April 7, 1965)

In our previous papers on the function of what is called a premotor area in dogs (Stępień et al. 1960, Stępień et al. 1963) we have shown that bilateral ablation of this area caused distinct disturbances in alimentary instrumental conditioned reflexes (CRs). Following premotor (precruciate) ablations, disorders in responses to conditioned stimuli (CSi) and / or disinhibition of responses to inhibitory CSi were observed. No motor disturbances were otherwise noticed. Moreover, all animals remained as skillful as they were before the operation. Our interpretation of this phenomenon was that the animal encountered difficulty in performing two antagonistic movements in quick succession, that is, turning its head towards the source of CS and lifting the foreleg.

To elucidate this problem more extensively, it would be advisable to change the experimental procedure by substituting a manipulatory CR for the locomotor response. Since the source of the CS could be placed far from that of the food tray, one may expect that the orienting reaction toward the stimulus would be more pronounced. This is the subject of the present paper.

MATERIAL AND METHOD

The experimental group consisted of 18 adult mongrel dogs in which locomotor positive as well as inhibitory CRs to acoustic stimuli were established in a special experimental room (Fig. 1). The food tray was situated about 2 meters in front of the starting platform. The sources of the positive and inhibitory CSi

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were placed on the left and right side, 2 meters from the platform. In some animals, the sound of a buzzer was the positive and the beating of a metronome the inhibitory CS. In others, the metronome was the positive and the buzzer the inhibitory CS.

In the preoperative conditioning, a „go-no go" method was used. All the animals were trained to run from the platform to the food tray in response to a positive CS, reinforced by food, and not to go to the food tray when the non-reinforced (inhibitory) CS was given. The experimental session consisted of 9 trials in which only 2 or 3 inhibitory CSi were presented. Occasionally, the so-called indifferent acoustic stimuli were also applied.

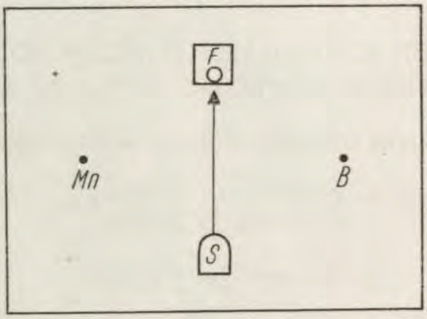

Fig. 1. Experimental setting. F, food tray; S, starting platform; Mn, metronome; B, buzzer

After both positive and inhibitory CRs were firmly established, an operation was carried out under general Nembutal anesthesia. The cortical tissue was, under aseptic conditions, bilaterally removed by subpial aspiration. The extent of ablations of the precruciate area was determined according to the descriptions by Adrianov and Mering (1959) and Kreiner (1964).

For the purpose of surgery the animals were divided into 4 groups. In group I (7 dogs: D-1 to D-7), the whole medial precruciate area and, in group II (3 dogs, D-8, D-9, D-10), only its anterior part was removed. In group III (6 dogs), only the posterior part of the precruciate area, i.e., a strip, lying on the anterior edge of the cruciate sulcus, was destroyed: in 2 dogs (D-11, D-12), the lesion extended to the medial, as well as to the dorsal part of the area investigated; in 2 animals (D-13, D-14), only the medial part and, in 2 others (D-15, D-16), only the dorsal part was removed. In group IV (2 dogs, D-17, D-18), the gyrus proreus was ablated. The extent of lesions, verified in a postmortem examination of brains is presented in Fig. 2.

The experiments were resumed a week after the surgery and to avoid retraining were performed once a week or even once in two weeks.

RESULTS

Following ablations of precruciate area, all animals remained skillful and no paresis was observed. On the other hand, their reactions to the CSi were more or less impaired.

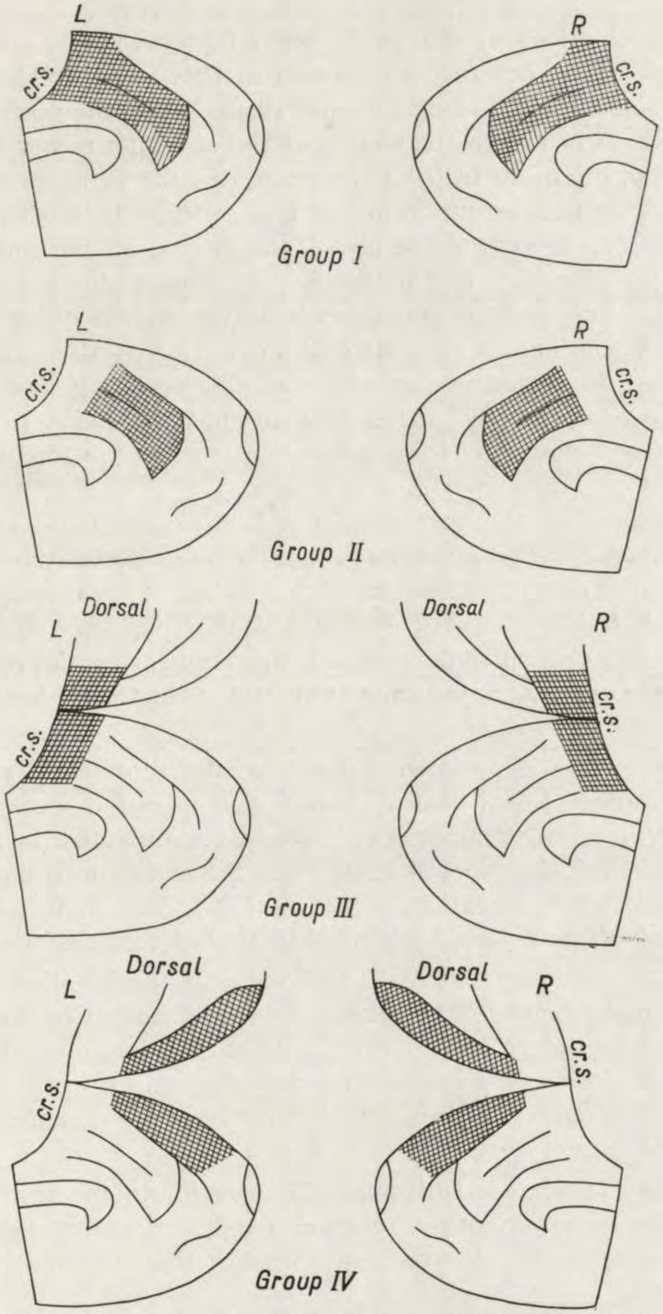

Fig. 2. Location of lesions. L, left hemisphere; R, right hemisphere; cr. s., cruciate sulcus. Striped areas show the extent of lesions in different groups of animals. In groups I and II, lesions are situated on the medial aspect of hemispheres, in groups III and IV, on both the medial and dorsal aspects. In 2 dogs of group I (D-4, D-6) a small antero-inferior part of the precruciate area was spared

Group I: ablations of the entire medial precruciate gyrus. A week after the operation, severe disturbances in CRs were displayed by the animals brought into the experimental room. When the positive CS was given, they briskly ran to the source of the stimulus rather than to the food tray and, intensely sniffing the apparatus for 10 or 20 seconds, remained there as long as the stimulus was continued. It often happened that the arm of the metronome struck the animal on the nose. The dog reacted by jumping back and thereafter, returned to the metronome and sniffed again. The animals remained near the source of CS, nosing it, even when the stimulus was discontinued. Afterwards, when the dog stopped being interested in the source of CS, he left it and, instead of going to the food tray, began to walk around the room. In fact, none of our animals, belonging to this group, approached the food tray during the first postoperative experimental session.

Two weeks after the operation (the 2nd experimental session), the animals behaved in the same way, that is, they nosed the metronome or the buzzer when it was operated but when it was stopped, it was only in some trials that they approached the food tray. A week later (the 2nd or 3rd experimental session), the animals continued to run to the source of CS but, also in some trials, they ran to the food tray even though CS was still acting.

During the next experimental sessions, the directional reaction toward CS (running to its source) ceased and, about 8 weeks after the operation, it disappeared, or was only slightly manifested. In response to CS, the animal ran the shortest route from the platform to the food tray, as he did before the operation, or he started to run in the direction of the source of CS and then, very quickly turned towards the food tray.

In contrast to these evident disturbances in the reaction to positive CSi, the animals' behavior in response to inhibitory CSi was more or less the same as before the operation. When the inhibitory CS was given, the animals either remained on the platform, or ran to the food tray (the symptom of disinhibition) but they never approached the source of the inhibitory CS.

In response to what is called indifferent stimuli, the animals displayed only the usual orienting reaction or directional response to the source of the sound but it was much weaker than the reaction evoked by positive CSi.

Group II: ablations of the anterior part of medial precruciate area. In this group, similar but weaker disturbances in CRs were observed. Even during the first experimental session (one week after surgery), the dogs could stop nosing the source of CS and run to the food tray when

CS was still acting. However, in some trials, the animals sniffed the buzzer or metronome throughout its operation and did not go to the food tray.

The directional reaction to the CS ceased gradually and, about 5 weeks after the operation, it disappeared almost completely.

The response to inhibitory CSi and to indifferent stimuli was much the same as that, observed in animals of group I.

Group III: ablations of posterior part of precruciate area (lying on the edge of cruciate sulcus). In the 2 dogs (D-11, D-12) in which the lesion stretched on to the medial, as well as to the dorsal aspects of the hemispheres, the responses to positive and negative CSi were similar to those, observed in animals of group II. The disturbances in CRs were pronunced but not very strong and, after 5 weeks, they disappeared almost completely.

In the other 4 animals in which only a medial (D-13, D-14), or only a dorsal (D-15, D-16) strip of the cortex, lying in front of the cruciate sulcus, was destroyed, no impairment of CRs was revealed.

Group IV: ablations of the proreal area. In this group, no disturbances in solving the task were observed.

The results, concerning the reactions to positive CSi, are presented in Fig. 3.

DISCUSSION

The results of our experiments show that, in spite of their unchanged motor skillfulness distinct disturbances of the preoperatively well-established locomotor CRs are produced in dogs by the bilateral ablation of the precruciate area. It has been shown that the most severe impairment of CRs occurred after the resection of the entire precruciate cortex, located on the medial aspect of the hemispheres. Partial ablations of the investigated area on the medial, as well as on the dorsal aspects of the hemispheres resulted, as far as our task was concerned, in much weaker disturbances or could even be harmless (dogs: D-13. D-14, D-15, D-16). A graphical picture of the anatomo-functional relations is presented in Fig. 4.

A bilateral removal of the proreal area produced no disturbances in the learned movement. It is known that a lesion of this area results in a severe impairment of delayed responses (Ławicka, Mishkin, Kreiner and Brutkowski, unpublished).

An unusually strong directional reaction to the CS was the most striking change in the animals' behavior observed after the ablation of

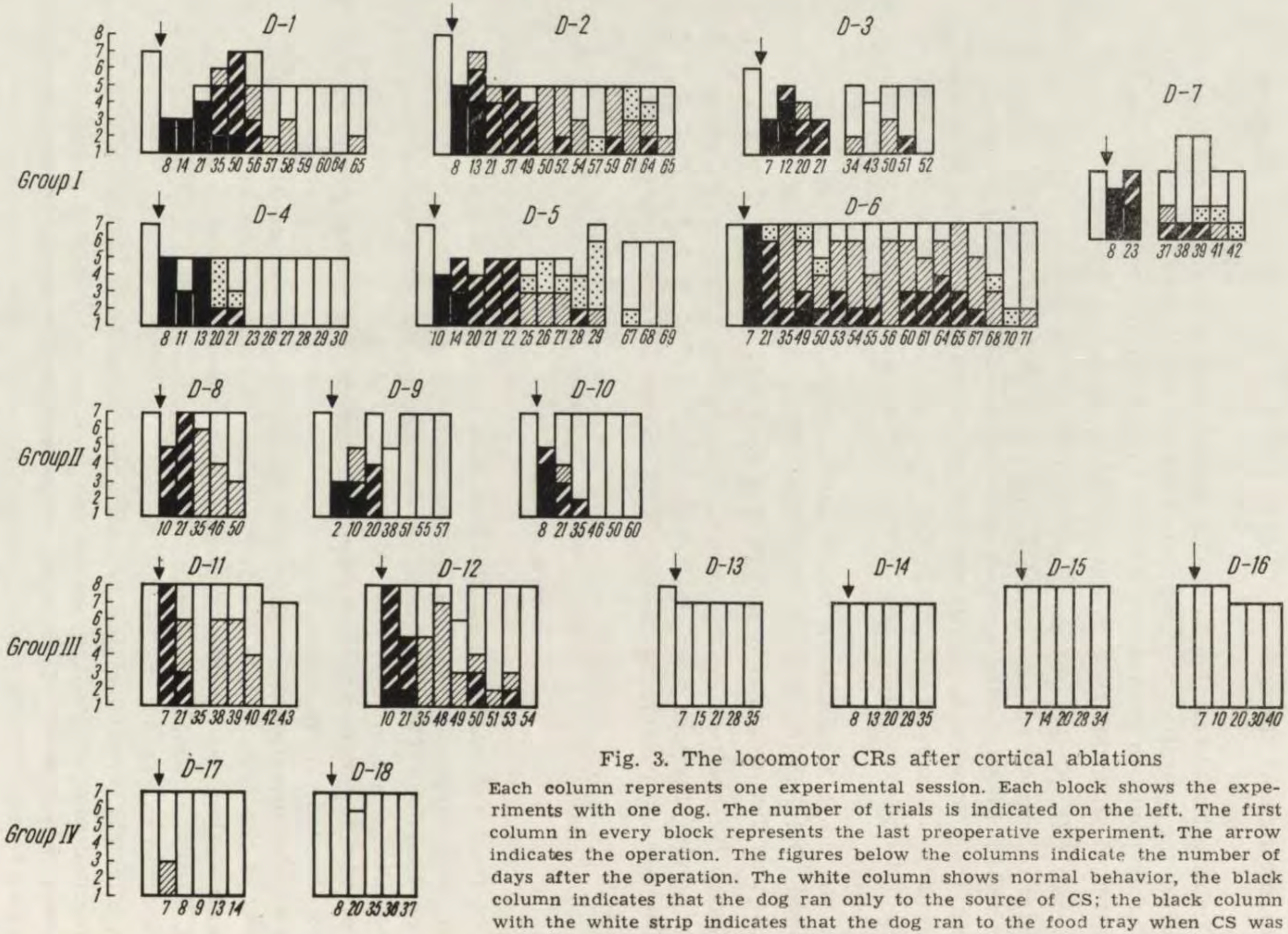

Fig. 3. The locomotor CRs after cortical ablations

Each column represents one experimental session. Each block shows the experiments with one dog. The number of trials is indicated on the left. The first column in every block represents the last preoperative experiment. The arrow indicates the operation. The figures below the columns indicate the number of days after the operation. The white column shows normal behavior, the black column indicates that the dog ran only to the source of CS; the black column with the white strip indicates that the dog ran to the food tray when CS was stopped; the striped column, the animal ran to the source of CS and then to the food tray; the dotted column, the dog started to run towards the CS but quickly turned to the food tray.

the precruciate area. It was manifested by running to the source of CS and nosing it persistently. This directional reaction was pathological since it has never been observed in normal animals. No normal dog was ever seen to put his nose to the metronome or to sniff repeatedly the metronome despite being struck by it. We suggest to call this peculiar response to CSi „the food CS magneto-reaction".

Since the experiments were performed rarely, this pathological reaction improved gradually without the need of retraining. For instance, a notable improvement was observed in some dogs (D-3, D-5 and D-7) after a 2- or 3-week interval in testing. The compensation was slower following ablations of the entire medial precruciate area and quicker following ablations of the sole anterior or posterior part of the area investigated.

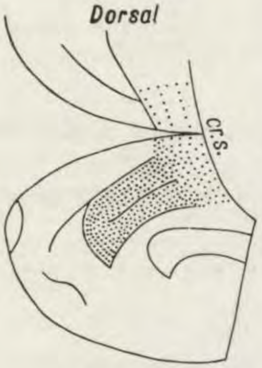

Fig. 4. The anatomo-functional relations between the location of the lesions and the food CS magneto-reaction. The density of dots shows the strength of food CS magneto-reaction, following ablations in this area

A question arises as to the mechanism of the food CS magneto-reaction. Our first impression was that it is simply a strongly-manifested disinhibition of the orienting reaction. This reaction, evoked in our experiments only by positive CSi, speaks against such an interpretation. It was provoked by neither inhibitory CSi nor indifferent stimuli. Thus, we are inclined to believe that the stimuli, associated with the food reinforcement evoke the described pathological reaction, following lesions of the precruciate areas. It is unknown whether or not the same reaction is produced by CSi signaling defensive US.

Another question is: why, in the early postoperative period, the animals did not run to the food tray and later, when the CS presentation was over, they did it. It seems that the food CS magneto-reaction has interfered with the performance of the learned locomotor movement in the same way as it did in the experiments during which lifting the foreleg was a CR. An attempt to elucidate the possible mechanism of this disturbance will be the subject of further research. It is also necessary to elucidate whether or not the food CS magneto-reaction is only a function of the lesion of the precruciate area.

SUMMARY

Locomotor positive (reinforced by food) and inhibitory CRs to acoustic stimuli were established in 18 dogs. In 7 animals, the medial precruciate area was removed bilaterally. Following this lesion, a strong directional reaction to CS (running to its source and sniffing it) and a marked disturbance in performance of preoperatively trained movement were observed. These manifestations gradually declined without retraining. From the very beginning, the reaction to inhibitory CSi was more or less normal. The pathological reaction towards the source of CS has been called „the food CS magneto-reaction". In 9 animals, fllowing more restricted bilateral lesions in the precruciate area (both in the anterior and caudal part), a similar but weaker or no food CS magneto-reaction occurred. After bilateral ablations of the proreal area (2 dogs) no food CS magneto-reaction was seen.

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Acta Biol. Exper. (Warsaw), vol. XXV, No. 4, p. 395, 1965

Book Review

Oxygen in the Animal Organism. I. U. B. Symposium Series, Vol. 31. Proceedings of a Symposium held under the joint auspices of the International Union of Biochemistry and the International Union of Physiological Sciences, London, 1963. Edited by Frank DICKENS and Eric NEIL. Pergamon Press, Oxford-London-Edinburgh-New York-Paris-Frankfurt, 1964, XVIII + 694 pp. illustr.

It is well known that molecular oxygen is indispensable for animal life; it is often forgotten, however, that oxygen may be toxic. These two and many other aspects of oxygen in the animal organism have been discussed at a symposium held at Bedford College, London, in September 1963. A seven hundred page volume contains all 32 main papers read at the Symposium, together with the discussions which followed each paper. The topics covered by the Symposium were numerous and manifold, from the electronic structure of the oxygen atom (J. S. Griffith) to the evolutionary aspects of biochemical adaptations (J. Lascelles and D. L. Gilbert) and oxygen utilization at elevated gravitation (A. G. H. Bjurstedt).

Two articles are concerned with oxygen stores and supply in man (by H. Rahn) and in aquatic animals (by J. Krog). A series of papers deals with the nervous regulatory mechanisms of respiration and circulation, the response to hypoxia and the aerobic work capacity (speakers: M. deBurgh Daly, D. J. C. Cunningham, Per-Olof Åstrand, A. B. Otis and D. E. Gregg). A separate session has been devoted to the respiration and oxygen supply in the foetus and the new-born (G. S. Dawes, K. W. Cross and J. Mestyán). Chemical aspects of oxygen transportation by blood and the structure and properties of O_2 binding pigments are considered by three papers (by F. J. W. Roughton, C. Manwell and E. Antonini). Oxygen exchange between blood and tissues is described by R. E. Foster and some aspects of the respiratory metabolism of the tissues are discussed in three papers by J. M. Lowenstein, T. P. Singer and B. Chance. The relationship between oxygen supply and the functioning of the heart, the brain and the kindney is described in detail by D. E. Gregg, K. Kramer and C. F. Schmidt. Finally, the oxygen toxicity and the effect of oxygen on tumor growth and on the radiation damage are the subject of another series of articles by J. W. Bean, R. Gerschman, N. Haugaard, Z. M. Bacq and L. H. Gray. There are also a few papers which deal with special problems such as oxygen secretion in the swimblader (J. B. Steen), the mutability of Michaelis constant as related to the oxygen tension (R. B. Fisher) and methodic problems of P_{O_2} measurements (D. B. Cater and I. Longmuir).

The book as a whole contains a large portion of information which may be very useful for both a physiologist and a biochemist interested in the respiration and the respiratory metabolism in man and animals.

Lech Wojtczak, Warsaw, Poland

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CONTENTS — VOL. XXV

No. 1

PHYSIOLOGY OF THE HIGHER NERVOUS ACTIVITY

ANIMAL BEHAVIOUR

No. 2

NEUROANATOMY

PHYSIOLOGY OF THE HIGHER NERVOUS ACTIVITY

No. 3

NEUROANATOMY

PHYSIOLOGY OF THE NERVOUS SYSTEM

PHYSIOLOGY OF THE HIGHER NERVOUS ACTIVITY

ELECTROPHYSIOLOGY

No. 4

NEUROANATOMY

PHYSIOLOGY OF THE HIGHER NERVOUS ACTIVITY