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THE GSR OF MONKEYS DURING ORIENTING AND HABITUATION AFTER SELECTIVE PARTIAL ABLATIONS OF THE CINGULATE AND FRONTAL CORTEX*

DANIEL P. KIMBLET, MURIEL H. BAGSHAW and KARL H. PRIBRAM

Stanford University, School of Medicine, Palo Alto, California, U.S.A.

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Abstract A previous report of depression of the galvanic skin response component of the orienting reaction after amygdalectomy despite behavioral deficits in habituation, prompted this study.

Two frontal lobe lesions were investigated for effect on GSR reactivity to tones. The lateral frontal cortex lesion was found to depress the GSR orienting reaction whereas the medial-frontal-anterior cingulate lesion did not. Additional analysis of the control records in terms of lability-stability ratings showed that the lateral frontal Ss maintained a level of reaction lower than that of initially stabile or "rerun" stabilized controls.

The conclusion of the previous report, i.e. that autonomic indicators of orienting may serve as a registration component of the behavioral reaction to novelty is supported and extended.

1. INTRODUCTION

IN ANOTHER study of this series [1], amygdalectomy was found to impair markedly the GSR component of the orienting reaction to sound stimulation. The suggestion was made that the GSR component of orienting signified a process necessary to habituation since amygdalectomy had previously been found to interfere with behavioral habituation.

This study examines further the neural substrate involved in this process. Several studies have shown that frontal lobe resections alter a monkey's behavioral response to novelty [2, 3]. Is the GSR component also affected by these lesions? If so, is the GSR depressed or absent as it is after amygdalectomy? And, if it is depressed, what can be learned about the process signified by this GSR component of orienting?⁺₄

2. MATERIALS AND METHODS

2.1. Subjects

Twenty-two immature rhesus monkeys served as Ss. They had been Ss in object and pattern discrimination experiments but had never been exposed to pure tone stimuli.

Group CI--Fourteen animals received no surgery and were run once. (This group is the same control group reported in the preceding study.)

Group CII—Five of the above who were given one additional run.

Group LF-Four animals received bilateral lateral frontal cortex lesions.

Group MF—Four animals received bilateral medial frontal cortex lesions.

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Now with Department of Psychology, University of Oregon.

[†]Since this study was completed two reports of changes in galvanic skin response following frontal lesions in man have become available in the literature: LURIA, A. R. and HOMSKAYA, E. D. Neuropsychologia 1, 1963, and LURIA, A. R., PRIBRAM, K. H. and HOMSKAYA, E. D. Neuropsychologia 2, 257, 1964.

2.2. Surgery

2.2.1. Group LF. The lateral frontal isocortex section ablation lesions were performed bilaterally in one stage under nembutal anesthesia; the posterior limit of the lesion included the rostrol bank of the arcuate sulcus and extended anteriorly to include the frontal poles. Reconstructions of the lesions are shown in Fig. 1.

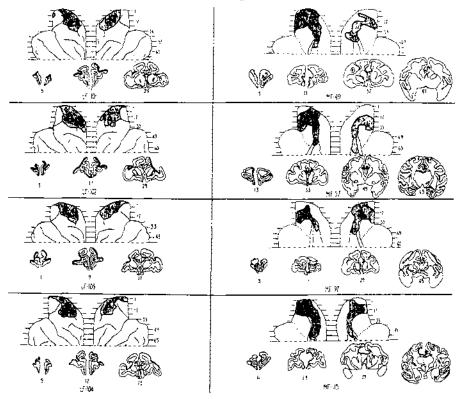


FIG. 1. Reconstructions of the lesions of the lateral frontal cortex (LF) and medial frontalanterior cingulate cortex (MF). Dark areas denote the lesion.

2.2.2. Group MF. Four animals received bilateral medial frontal isocortex suction ablation lesions. The lesions included the anterior cingulate cortex as well. Reconstructions are shown in Fig. 1.

2.3. Apparatus

The identical apparatus was used as in the previously reported study mentioned above. A Grayson-Stadler twin oscillator delivered pure tones of either 1000 c/s (77 dB) or 1500 c/s (81 dB) through a Jensen coaxial speaker in the ceiling of a sound-shielded experimental box. A dim shielded light allowed constant observation of the S via a one-way glass window. GSR's were measured with a Fels Dermograph (Model 22A) and recorded on an Esterline Angus graphic ammeter (Model AW).

2.4. Procedure

The S was transferred to a Foringer primate chair and securely restrained at the neck and waist. Zinc-zinc chloride disc electrodes with zinc-sulphate electrode paste was secured, one to the shaved leg and the other to the sole of the foot, with Elastoplast bandage. The legs were comfortably tied to the footrest to eliminate gross motor activity. After a ten-minute adaptation period in the closed box one of the pure tone stimuli (1000 c/s or 1500 c/s, 2 sec) was presented repeatedly at irregular intervals and only when the animal was quiet. Mean intertrial interval was 30 sec. All head, body, arm, leg, and eyelid movements as well as vocalizations were recorded by foot switch by an observer. After 50 presentations of the original tone a habituation criterion of four consecutive no responses was instituted, after which two presentations of the other, novel, stimulus were given. The original stimulus was then again presented to the four no response criterion, after which two more trials of the novel tone were presented.

Fourteen control animals (Group CI) were tested in the above manner once, and of these, five (Group CII) were tested twice. The two operated groups (Group MF and Group LF) were tested twice and the results for the second run are reported here.

2.5. Scoring

Records were discarded on which more than 30 per cent of the trials were contaminated by movement. A response was scored when a drop in resistance of 500Ω or greater occurred within 5 sec after the onset of the stimulus. Amplitude of response was measured from the start of the deflection to the peak.

Lability-stability scores were obtained by counting the number of spontaneous fluctuations (SF) in baseline skin resistance over a two minute period of pretest resting record. Ss scoring greater than the mean for 12 control animals were called "labile" and those scoring less than the mean, "stabile".

3. RESULTS

3.1. Experiment I: The effect of selective partial ablations of the frontal cortex

The lateral frontal group had a markedly reduced rate of response to both the original tone and the novel tone compared to the CII and medial frontal groups (Fig. 2). Even on

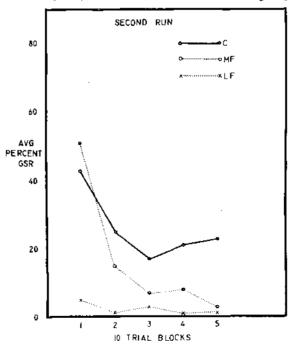


FIG. 2. Curves for % GSR response to the first fifty presentations of the original stimulus on the second run for the normal (CII), medial frontal (MF), and lateral frontal (LF) groups.

Block 1 trials, responses of the lateral frontal group were infrequent. These lateral frontal Ss were not entirely unreactive, however. GSR's occurred frequently after eyelid opening and slight body movements which were too small to produce electrode displacement artifacts. The percent response curve (Fig. 2) for the MF group appears depressed in blocks

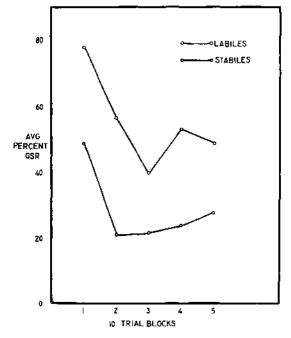


FIG. 3. Curves for % GSR response on first fifty trials of the first run for the labile (L) and stabile (S) groups of the normal (CII) group.

3-5 compared to the CII groups. However, this difference may be explained by the fact that Ss that compose the MF group were relatively low in their responses on the first run relative to the CII group, but the fall in their response rate on the second run was comparable to that shown by the CII group. Further, Table 1 shows that the MF group scored well above the LF group in mean responses per 50 trials and in median trials to four no responses—scores comparable to those of the CII group. In addition, all Ss of the MF group responded well to the first presentation of the novel tone and their overall response rate to the total of four novel stimulations were like that of the CII group. By contrast, the LF group showed few responses to any of the four novel tone presentations—and all of these few responses were made by one S.

3.2. Experiment II: Decreased reactivity and "stability" in the control group

The differences in effect between the MF and LF lesions suggested that it might be fruitful to ascertain whether the depressed GSR reactivity of the lesioned Ss was in any way similar to the individual differences in GSR reactivity in the initial control run or to changes in reactivity produced by a second exposure to the experimental procedure in unoperated animals.

LACEY and LACEY [4] have shown that the frequency of spontaneous GSR fluctuations is an indicator of relative autonomic lability in human Ss. Therefore a means of scoring short periods of pretest resting records of the control group was sought. The scoring adaptation method of KOEPKE and PRIBRAM [5] was used. They used graduate students as

Table 1.							
	Group	N	Run	X total R, 50 trials	Md. trials to 4 NR	$\overline{\mathbf{X}}$ % response to 1st novel tone	$\overline{\mathbf{X}}$ % response to all 4 novel tone
(CII)	Control II	5	2nd	9.8	7-0	100	50
(MF)	Medial-frontal	4	2nd	8.3	13-0	100	60
(LF)	Lateral–frontal	4	2nd	1.0	1-5	25	31
	Mann-Whitney U Te	st		MF vs. CII=7, n.s.	CII vs. MF=7, m		
				LF vs. CH=2, $p < 0.0$	05 CII vs. $LF=3, p$	=0.026	
(CI)	Control I	14	1st	21.5	28.5	91	85
(L)	Labile	6	İst	22.0	70.0	100	85
(S)	Stabile	6	lst	11-0	20-0	100	83
	Mann-Whitney U Te	5t		L vs. $S=3, p < 0.05$	L vs. S=3, p <0		

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Ss and found that the number of spontaneous fluctuations per minute was a reliable method for differentiating labile and stabile Ss who showed significantly different rates of habituation of the GSR to auditory stimuli.

Of 14 Ss in the control group of the present study a mean spontaneous fluctuation rate of four per minute was found for 12 scorable records. Since distribution of individual scores about the mean was found acceptable (Kolmogarov-Smirnov distribution statistic D=-0.0369), the six animals scoring above four spontaneous fluctuations per minute were termed "labile" and the six animals scoring below four spontaneous fluctuations per minute, "stabile". These two groups showed distinctly different rates of GSR response to the first 50 trials of the initial tone. The percent response curves across ten trial blocks (Fig. 3) show that labile Ss respond more frequently and habituate more slowly than do stabile Ss. (Rank correlation coefficient between SF scores and trials to first four consecutive no responses-0.7, p < 0.01.) Table 1 also shows labiles (22R) scoring higher in mean R in 50 trials than stabiles (11 R), and labiles scoring 70 trials to the 4 NR cf, to 20 trials for stabiles.

Amplitude measures in the first 50 trials showed a group difference for the first two trials when labiles had higher median amplitude responses (5100 Ω) than stabiles (1500 Ω). After the first two trials both groups showed median amplitude of 2100 Ω .

When the novel tone was introduced both labile and stabile groups reacted 100 per cent of the time with high amplitude responses (median 5400 Ω). This amplitude compared with a median of 2250 Ω for the last response before the initial tone. On the second presentation of the novel tone (on the very next trial) the number of Ss responding remained high for both groups but the median amplitude of responses returned to the previous level. When mean number of responses to all four novel stimulations were averaged, the rate of response remained high for both groups (Table 1).

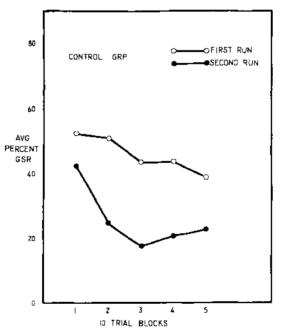


FIG. 4. Curves for % GSR response on the first fifty trials of the first run compared to the second run for the normal Ss (CII) who were run a second time.

Control Group II habituation curves are graphed in Fig. 4 for first and second runs. This group, relatively labile on Run 1, changes to the stabile range on Run 2. Table 1 shows that the mean R in 50 trials on Run 2, (9.8), is very similar to the stabile group on Run 1 and median trials to 4 NR (7.0) are also nearer the stabile range.

The Cll group showed a 100 per cent response to the first novel tone on the second run but the rate dropped to 50 per cent when all four novel presentations were scored, evidence of habituation of response to the novel tone.

In general, then, monkeys do show individual differences in the degree of GSR reactivity in the resting record and these differences are reflected in rates of habituation of GSR responses to auditory stimulation. A repeat run shows that the rate of response shifts towards lower levels but the shape of the original habituation curve (high in the first 10 trials) persists. Orienting to a novel stimulus is identical for both "labile" and "stabile" monkeys on a first run and is only slightly depressed on a second run in both groups.

4. DISCUSSION

The aim of this experiment was to extend the examination of the neural substrate involved in the GSR component of orienting and habituation and to analyze further the process which this reaction might signify. Selective partial ablations of the cingulate and frontal cortex were made and the incidence of GSR during orienting to tone found markedly depressed by the lateral frontal lesion only. The question arose whether this depression of the GSR merely reflected an increased stability and thus lowered reactivity of the "lateral frontal" Ss.

To this end the records of 14 unoperated Ss were analyzed and grouped into "stabile" and "labile" subjects. Further, both operated and unoperated groups were given repeat runs in order to determine whether repeated exposure to the situation would "stabilize" their responsivity. The results showed that such repetitions did indeed affect the "habituation" parts of the records - but not the responses to initial and novel presentations. And it is these that are altered by lateral frontal ablation.

This result is consonant with the hypothesis derived from the experiment on the effects of temporal lobe lesions on the GSR component of orienting and habituation, viz., that the GSR component, also absent in amygdalectomized monkeys, signifies something other than orienting *per se*. Perhaps registration of the orienting is involved. The result of the frontal lobe study makes it clear that the changes in GSR observed are not due merely to making the operated Ss more stabile or even hyperstabile, since "stabile" unoperated Ss and unoperated Ss stabilized by a second run continue to respond initially and to novelty with a GSR. Further, monkeys with lateral frontal lesions react behaviorally to novelty even more strongly than do their controls [3]. Also, amygdalectomized Ss are slow to habituate behaviorally [6] as if the novelty of the event had failed to register and thus remained for a prolonged time truly "novel".

Should this interpretation of the significance of the GSR in orienting and habituation be supported further, two components of the orienting reaction should be distinguishable... one cortical, related to performance; the other, autonomic, related to "registering" the novelty of the event. The "registration" component would serve as an indicator that some central mechanism has been so reset that subsequent input events will be handled more selectively on the basis of immediately prior events. The results of this study support the conception that responses of the autonomic nervous system signal that such resetting has occurred.

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Résumé—Cette étude a été inspirée par un travail antérieur sur la dépression de la réponse électrodermale, composante de la réaction d'orientation après amygdalectomie malgré les déficits comportementaux de l'habituation.

Deux types de lésions frontales furent étudiés pour juger de leur effets sur la réactivité électrodermale aux stimuli sonores; lors des lésions du cortex fronto-latéral la composante électrodermale de la réaction d'orientation était diminuée tandis que elle ne l'était pas après lésion médio-fronto-antérieur cingulaire. Une analyse ultérieure des enregistrements chez les contrôles en termes de moyenne de labilité-stabilité montrait que les sujets latéro-frontaux conservaient un niveau de réaction inférieur à celui des contrôles initialement stables ou stabilisés après des applications répétées.

La conclusion du premier travail, c'est à dire, que les indicateurs du système autonome de la réaction d'orientation peuvent servir de composantes d'enregistrement de la réaction comportementale à la nouveauté, est confirmée et même étendue.

Zusammenfassung—In einem vorausgegangenen Bericht wurde von der Abschwächung der galvanischen Hautreflextätigkeit berichtet, die sich unter Orientierungsaufgaben einstellte. Es handelte sich dabei um Fälle nach Ausschaltung der Mandelkerne, die man wegen bestehender Verhaltensstörungen entfernte. Die nachfolgende Studie stellt eine Ergänzung hierzu dar.

Zwei frontale Schädigungsbilder wurden auf das Verhalten des galvanischen Hautreflexes nach vorausgegangener Tonreizung geprüft. Laterale Schädigungen des Stirnhirns fielen durch Verminderung der galvanischen Reflexantwort bei Orientierungsbemühung auf, während medio-fronto-anteriore Läsionen und solche des Gyrus zinguli ein derartiges Bild vermissen liessen. Zusätzlich liess die genauere Analyse der Kontrollableitung hinsichtlich von Labilitäts- und Stabilitätskomponenten erkennen, dass fronto-laterale Hautreflexe ein niederes Reaktionsniveau gegenüber anfänglich stabilen oder von aussen her stabilisierten Kontrollfällen besassen.

Das Ergebnis dieser Befunde wird so interpretiert, dass offenbar eine selbständig tätige Einrichtung die Hinweise zur Orientierung gibt und damit die Registrierungsdaten für die Verhaltensreaktionen auf neue Umweltbedingungen liefert.