Mass action and Pavlovian conditioning

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The acquisition and extinction of a classical Pavlovian conditional nictitating membrane response was investigated in four surgically hemidecorticated and seven normal albino rabbits. The acquisition and extinction performance of the lesioned animals was not significantly different from that of the normals.

Three major lines of evidence suggest that Pavlovian conditioning (associative learning) and instrumental learning (contingency learning) are normally mediated at different levels in the mammalian brain. Subcortical structures are apparently adequate for the acquisition and retention of Pavlovian conditioning whereas instrumental learning requires neocortical involvement in these processes (Russell, 1966a). Firstly, instrumental learning is readily lateralized to one cortical hemisphere in the functional split-brain (Bureš & Burešová, 1960; Ross & Russell, 1964; Russell & Ochs, 1963) as it is in the surgical split-brain (Sperry, 1961; Meikle et al, 1962). Classical conditional respiratory responses (Meikle et al, 1962; Ross & Russell, 1967) and passive avoidance responses (Bureš et al, 1964), on the other hand, are not lateralized in either type of split-brain preparation. This suggests that the storage and/or retrieval of Pavlovian conditioning can occur subcortically. Secondly, it has been reported that both surgical and functional lesions impair the acquisition of instrumental learning in accordance with Lashley's principle of mass action (Lashley, 1929; Plotkin, 1967; Travis & Sparks, 1963; Saavedra et al, 1963). Acquisition of Pavlovian conditioning is unaffected by depletion of neocortex (Bloch-Rojas et al, 1964; Burgoyne et al, 1967; Mysliveček et al, 1961; Ross, 1964) and does not appear to conform to the principle of mass action (Russell, 1966b). Thirdly, retention of prior instrumental learning is abolished by functional or surgical decortication (Russell & Ochs, 1963; Pinto-Hamuy, 1961). In contrast to this there is perfect retrieval of previously established classical conditioning under these conditions (Belenkov, 1961; Mogenson & Peterson, 1966; Russell, Kleinman, & Plotkin, 1968).

The present experiment was designed to test the construct validity of reports that the course of Pavlovian conditioning is not affected by extensive cortical lesions. The response system utilized was the nictitating membrane of the albino rabbit (Gormezano, 1966), using a delay conditioning paradigm.

Method

Following an extensive unilateral craniotomy and opening of the dura, hemidecortication was performed by subpial aspiration in six albino rabbits. The lesion area was packed with gelatin sponge soaked in dilute chloramphenicol solution and the scalp incision closed. Pentobarbitone sodium anaesthesia was used throughout. Six to 18 weeks were allowed post-operatively for recovery. Eight normal and the six hemidecorticate rabbits were then prepared for conditioning by placing a silk suture in the nictitating membrane of the right eye. During testing the arm of a rotary potentiometer was connected to the suture by means of fine wire so that any movement of the membrane caused a resistance change. This alteration in resistance produced a voltage change, via a Wheatstone bridge circuit, that was then amplified and displayed as a deflection on the upper beam of a dual beam oscilloscope. The lower beam was used as an event marker. The oscilloscope display was recorded photographically.

A 1000 cps tone that raised the noise level of the experimental chamber from 82 to 103 dB (SPL, C scale) was the conditional stimulus (CS) and a 3 mA electric shock delivered post-orbitally via skin electrodes was the unconditional stimulus (US). The tone was presented for 300 msec when 200 msec of shock was delivered. The two stimuli ceased simultaneously 500 msec after CS onset. The intertrial interval was fixed at 80 sec. On each of five days of training each animal received 36 tone-shock pairings and five probe (tone alone) trials. Probe trials were distributed

regularly every tenth trial so that the first and last trial on each day was a probe. Then followed two days of extinction, on each day of which each animal received 41 unpaired tone trials.

Any deflection of 4 mm or more on the upper beam of the oscilloscope that occurred after CS onset and less than 20 msec after US onset was counted as a conditional response (CR). Pilot studies showed that the unconditional membrane response occurs with a latency of 20-40 msec and no membrane UR was ever noted to tone alone. Halfway between each conditioning trial one traverse of the two oscilloscope beams was recorded on film exactly as on a conditioning trial so that an estimate of spontaneous responses during a comparable time interval could be obtained. Two hemidecorticate animals and one normal were discarded during training due to damage sustained through struggling in the restraining harness. This left three animals with right sided lesions and one with a left sided lesion in the hemidecorticate group.

Results and Discussion

The results are given in Fig. 1 in which CRs on both normal and probe trials are summed and presented as a percentage of the total number of possible daily CRs during acquisition and in blocks of 10 trials for the two days of extinction. In view of the apparent inferiority of the acquisition of the normal animals the four best responders were selected from them and used as an additional comparison group. Using the weak criterion of $p < 0.25$, analysis of variance showed no significant differences between any of the three groups during acquisition. All groups showed good extinction on Day 1 and substantial spontaneous recovery on Day 2. No differences between groups reached normally acceptable levels of significance during extinction. However, the tendency suggested by inspection of Fig. 1 for the hemidecorticate group to extinguish at a faster rate than normals does receive some support from the analysis of variance performed on the extinction scores. The number of CRs produced in extinction by the hemidecorticate and "best" normal groups differed at the 10% level of significance on Day 1 ($F = 5.902$, $df = 1,6$) and at the 25% level on Day 2 ($F = 2.422$, $df = 1,6$). Differences between the "all" normal and hemidecorticate groups, however, did not achieve even the 25% level of significance until the last two blocks of trials on extinction Day 2 ($F = 1.546$, $df = 1,9$).

The study as it stands involves no control for sensitization or pseudoconditioning. However, subsequent observations on the same animals showed that when the tone was again made positive (paired with shock) and unreinforced presentations of light were substituted for half the tone trials a perfect differentiation was manifest from the outset. When the significance of the two stimuli was switched both hemidecorticate and normal animals achieved a good reversal of CR distribution. These results indicate that the data given in Fig. 1 also represent true conditioning. Spontaneous responses were observed on 0.674% of intertrial sample runs for all normal animals, 1.09% for "best" normals and 0.365 for the hemidecorticate group and so do not constitute a serious source of spurious CRs. Detailed histological verification of the lesions is not yet complete but gross anatomical observation suggests that the removal varies from 60 to 85% of the hemisphere. No correlation was evident between individual acquisition performance and extent of post-operative recovery, laterality or size of lesion.

Thus extensive unilateral neocortical lesions appear to have no adverse effect on acquisition or extinction of the conditional nictitating membrane response under the present experimental conditions. As far as acquisition is concerned, this finding extends the similar observations of Bloch-Rojas et al, 1964; Burgoyne et al, 1967; Mysliveček et al, 1961; and Ross, 1964, utilizing different response systems and conforms to the thesis that neocortical mass is not a critical factor in the mediation of classical conditioning.

The postulation of a subcortical basis for Pavlovian conditioning does not deny the importance of cortex in analyzing complex stimuli (Diamond & Neff, 1957) or the possibility that cortex is involved in the finer adaptation of Pavlovian conditional responses to the environmental conditions upon which their elaboration is

Fig. 1.

based (Asratyan, 1965). However, given that the stimuli are capable of being adequately encoded by subcortical structures, the same structures are capable of utilizing inputs to form the basis of the associational analysis that underlies Pavlovian conditioning. In contrast to this it seems that, under similar stimulus conditions, neocortical tissue is involved on a mass action basis in the contingency analysis of response consequences which enables instrumental learning to take place.

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