.e. in the state of rigor. We have demonstrated a logical extension of the classic length tension relationship to the 'contraction' due to the rigor state, thereby drawing attention ot its dependence (amongst other things[7,9]) on the sarcomere length.

[13] We thank Dr. DARCY GILMOUR for discussions and comments. This work was supported by grants from the Australian Research Grants Committee and The National Heart Foundation of Australia.

Zusammenfassung. Bei Glycerin-extrahierten Fasern des Kaninchen-Psoas-Muskels wurde ein der normalen isometrischen Kontraktion ähnlicher Zusammenhang zwischen Sarkomerenlänge und -spannung für die Kaliumkontraktur festgestellt.

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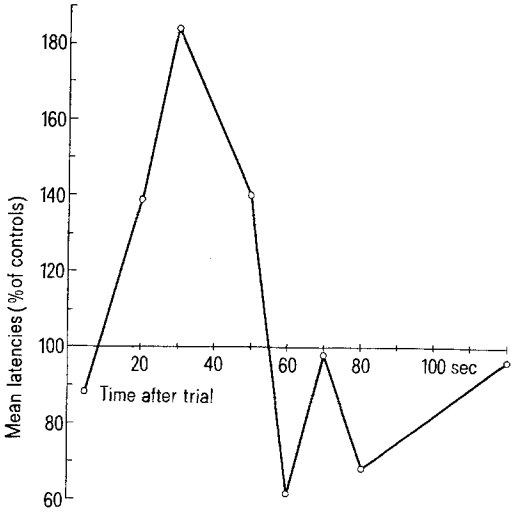
Facilitation of Learning by Reward of Post-Trial Memory Processes

A wide variety of treatments administered during a critical period following a learning experience have been shown to exert an effect on subsequent performance of the learned task. For example, memory can be disrupted by posttrial electroconvulsive shock[1-3], cortical and hippocampal spreading depression[4-6], drugs[7-9], brain stimulation[10-15], and other treatments; or can be facilitated by drugs[7,16,17] and by stimulation of the reticular formation[18,19] and perhaps other brain structures[20].

The critical post-trial period during which memory can thus be influenced has traditionally been considered to represent a period of memory 'consolidation' which is still widely thought to be coded in terms of active electrophysiological processes. Since various studies have shown that electrical activity of the brain can be directly controlled by operant conditioning procedures[21-27], we have hypothesized that memory consolidation per se can be brought under control of reward, and in the present study provide evidence that it can be reinforced by access to food. This hypothesis rests on the proposition that the 'period of consolidation', as defined by post-trial manipulations, reflects a labile, dynamic process which can be considered as a 'response', and thus susceptible to contingencies of reinforcement.



Effect of food reward on passive avoidance learning. Abscissa represents times after the conditioning trial when 1 min access to food was given to the experimental groups. The step-down latencies are expressed in terms of mean percent of each control group on the ordinate. (e.g. the 30 sec reward group remained on the platform 84% longer than its control group).

Materials and methods. The subjects were albino mice of the inbred C3H/He/Gif COB strain, outbred from Charles River Mouse Farms ICR COBS. They were kept in groups of 20 animals per cage with ad libitum access to food and water. They were kept at all times on a reversed 06.00–18.00 h 12 h light/dark cycle.

The passive avoidance step-down equipment consisted of a box with 50 × 50 cm high walls with a grid floor made of 6 mm diameter stainless steel bars spaced 13 mm apart (7 mm interbar distance). In the middle of the box was a 1 cm high, 67 mm diameter round wooden platform. Fitted over this platform was a removable 20 cm long, 68 mm diameter plastic tube. The electric foot shock across the grid consisted of a scrambled 1 sec duration

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Effects of post-trial reward on one-trial passive avoidance learning

Reward onset (sec)	Step down latencies				No. of animals	Retest latencies (% of controls)
	Baseline Control	Experiment	Retest Control	Experiment		
<5	14.86 ± 7.32	12.91 ± 5.64	27.53 ± 50.53	24.29 ± 50.77	111	88.2
20	13.73 ± 7.46	13.88 ± 6.93	26.78 ± 45.04	37.17 ± 62.33[a]	125	138.8
30	14.59 ± 7.62	14.02 ± 7.07	22.30 ± 24.70	41.04 ± 72.99[a, b]	127	184.0
50	13.98 ± 8.35	13.76 ± 6.92	27.70 ± 43.17	38.70 ± 68.46[a]	100	139.7
60	12.67 ± 7.40	12.88 ± 8.70	18.65 ± 31.98	11.41 ± 7.64[a]	126	61.2
70	15.04 ± 7.96	14.84 ± 8.95	27.09 ± 52.36	26.61 ± 43.64	126	98.2
80	12.72 ± 7.25	13.09 ± 6.24	23.20 ± 56.49	15.76 ± 24.66[a]	100	67.9
120	17.38 ± 8.28	16.78 ± 9.11	37.08 ± 65.11	35.81 ± 63.24	112	96.6

Mean baseline and retest stepdown latencies of the experimental (reward) and control groups are given in sec with standard deviations. The right column expresses retest stepdown latencies of the reward groups in terms of percentage of their control groups. [a] $p < 0.001$, F_{max}-test. [b] $p < 0.01$, slippage test.

2 mA current limited by a constant current unit. Special feeding boxes (for reinforcement) consisted of two 140 × 92 × 75 mm red plastic boxes with transparent plexiglass lids. The experimental room was maintained at 23 °C at all times, and illuminated by a diffuse overhead neon light during the experiments.

Procedure. To test our hypothesis, 927 mice were trained in the one-trial passive avoidance step-down task and given reward at various times after the learning trial. Prior to the learning trial all animals were deprived of food for 16–18 h. The learning trial consisted of placing the animal onto the wooden platform and recording the latency of its descent onto the grid. When all 4 limbs touched the grid, it received a scrambled foot shock. Except for the < 5 sec reward group, the animals were thereupon immediately placed into a waiting chamber (a ceilingless box, which, otherwise, looked like their home cages).

The < 5 sec reward group was placed immediately into the 'reward-boxes' where they had 1 min access to food. The other groups were placed into these reward boxes 20, 30 ,50, 60, 70, 80 or 120 sec after the learning trial. The control groups underwent the same procedure except that no food was available in the reward boxes. Thereafter the animals were returned to their home cages where the normal ad libitum food and water schedule was resumed after 1 h. 24 h later they were retested in the step-down apparatus, whereby the step-down latencies were recorded. A trial was terminated if an animal remained on the platform for 5 min. The animals were always run at the same time of day.

Results. A facilitation of memory should have resulted in longer step-down latencies. Since the results indicated that about 50% of the animals did not manifest any learning whatsoever in the step-down task, it was expected that reward of consolidation would increase the latencies of the learners, but not of the nonlearners. A facilitation of memory should, therefore, result in an increased variance together with increased mean latencies of the reward groups as compared with the non-reward control groups. The tests commonly used for such data are the F_{max}-test and the K-sample slippage test[28]. The Table shows the baseline and retest latencies of the experimental (reward) and control groups. According to the slippage test, reward administered 30 sec after the foot shock led to a significant increase in the step-down latencies upon retest ($p < 0.01$). According to the F_{max} test, reward given after 20, 30, and 50 sec showed significantly longer latencies ($p < 0.001$). It may be worthy noting that, at 60 and 80 sec delays, reward had the opposite effect of decreasing the step-down latencies ($p < 0.001$, F_{max}-test*. This could be interpreted as reflecting 2 opposing effects – reward of consolidation and reward of step-down behaviour – whereby the effect of reward of consolidation predominates at 20, 30, and 50 sec delays, and the residual effects of reward of stepping-down shortly thereafter.

Discussion. We have shown that food reward administered during a critical period after a passive avoidance trial facilitates performance upon recall, but not when given before or after this period. These data are in accord with traditional criteria for defining a labile post-trial period of memory 'consolidation' and provide evidence that the underlying process, whether one of 'consolidation' or 'retrieval'[29,30], can be brought under the control of reinforcement, i.e. that it can be conceptualized as an 'operant response'.

It should be emphasized that if the reward had acted upon the overt response (step-down behaviour) instead of on the memory process, we should rather have expected opposite results, namely a decrement in retest performance, with the shortest step-down latencies resulting from immediate reward and a gradual increase in latencies ensuing with increasing delay of reinforcement. We can assume that the postulated dual effects of reward (on the overt response and on the memory process) interact, and thus that our facilitation curve reflects these opposing tendencies.

Presumably the period of facilitation we obtained does not reflect the duration of the consolidation process, since we must assume, by tradition, that reward is maximally effective upon completion of the response, which in our case is supposedly some memory process. Hence, it would follow from such considerations that in our experiment the active memory process involved terminated at around 30 sec, the maximal period of facilitation by reward.

The implications of this hypothesis and data are that, apart from its traditional role in leading to strengthening of a response, reward can also directly influence the

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'consolidation' of a reinforced response. The reciprocal, that consolidation can be suppressed or prevented by punishment, would be a logical consequence of this hypothesis.

It would be desirable in the light of this hypothesis to re-evaluate the various treatments known to facilitate and inhibit consolidation in terms of their possible rewarding and aversive effects, and thus to investigate the usefulness of a theory which tries to account for the modifications of memory processes by post-trial manipulations in terms of mechanisms of reinforcement and punishment, which would open the possibility of integrating 'memory-consolidation' theory with 'behaviour-modification' theory.

Zusammenfassung. Unter Verwendung einer passiven Vermeidungsreaktion mit Futterbelohnung nach verschiedenen Zeitintervallen zwischen 0 und 120 sec konnte gezeigt werden, dass Belohnung 20, 30 und 50 sec nach dem Fusschock signifikant verbessertes Lernen bewirkt. Diese Daten unterstützen die Hypothese, dass Gedächtnisprozesse – konzeptionell als operante Reaktion aufgefasst – durch Belohnung modifizierbar sind.

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[31] Research supported by the Swiss National Science Foundation Grant No. 3.8790.72.

Rhythmic Activity in Frog (*Rana pipiens*) Visual System

Oscillatory potentials have been demonstrated in the visual system of the frog[1,2] and many other visual systems[3–5]. These oscillations were observed in the retina and optic nerve. For a given species, the frequency of these oscillations was found to be constant despite changes in light intensity[3,4]. The oscillatory potentials are generated by the synchronous discharge of retinal ganglion cells. In the cat, the rhythmic potentials occurred after the onset of illumination as well as its offset[5]. In the present experiments, the occurrence and pattern of the rhythmic potentials was studied in *R. pipiens*.

Methods. 29 specimens of *R. pipiens* were used. The frogs were anaesthetized by immersion in 0.1% tricaine methanesulfonate[6]. The sciatic and branchial nerves were severed to inhibit movement. The frogs were pinned onto a holder, covered with a damp sponge, and presented 95% O_2-5% CO_2[7]. Recordings were made either extracellularly from class III cells of the left retina or from the right optic tectum[8]. All recordings were made on awake frogs which had been dark adapted for 1 h before commencing the experiment. The electrodes used were metal filled, and had tip diameters of 2–5 μm[9].

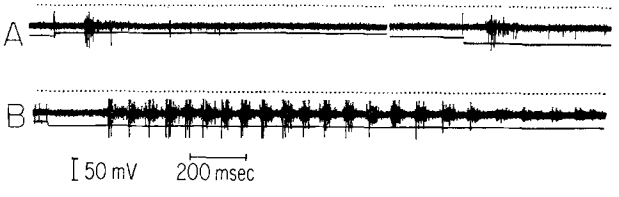

Fig. 1. Recordings of the off-response. Both flashes 30 sec duration. Trace A photopic level stimulus; trace B mesopic level stimulus.

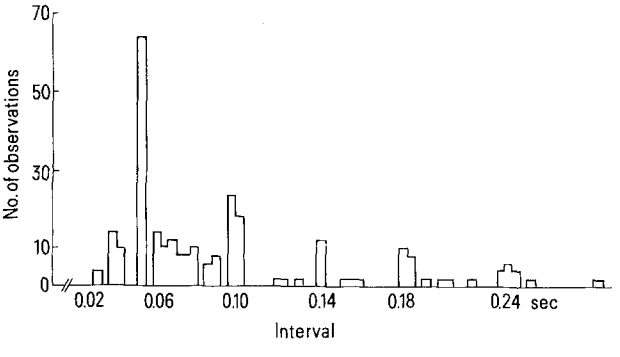

Fig. 2. Interval histogram of interspike intervals excluding the intervals shorter than 0.02 sec. The interspike intervals tend to cluster at interval of 0.048 sec, 0.096 sec, 0.144 sec, and 0.192 sec. Histogram based upon mesopic level stimulus of 30-sec-duration.

The frogs were placed behind a screen which covered the visual field of the left eye. A drop of water was periodically presented to the left eye to prevent drying. The light stimuli covered the full range of intensity levels from scotopic to photopic. The durations of the stimuli ranged from 0.05 to 90 sec duration. The responses to the stimuli were monitored auditorally and visually as well as recorded for later playback and photography.

Results. The results are based upon 686 recordings from class III cells. One-third were activity recorded from the tectum; the remainder were extracellular recordings from class III cells in the retina. Within a narrow range of stimulus intensities and flash lengths, when stiumli were presented to a previously dark adapted retina, a rhythmic bursting firing appeared. The pattern was most clearly observed in response to the extinguishing of a 30-sec-period of illumination using a 3.6 neutral dentisity filter. Calibration of this filter demonstrated the stimulus to be approximately 0.02 lux. This value falls in the mesopic range[10]. The pattern was occasionally observed in response to a slightly brighter stimulus (3.2 N.D. filter) of the same duration.

The firing pattern can be seen in Figure 1. Interval histograms were generated by measuring the interspike intervals between single cells spikes in response to the

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