Control of Timing Behavior by Contingent Photic Stimulation in Cats

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URAMOTO, I. Control of Timing Behavior by Contingent Photic Stimulation in Cats. Tohoku J. exp. Med., 1972, 106 (3), 253-263 — Cats were conditioned to press a bar for a food reward using a trace conditioning procedure. Comparison was made between two conditioning procedures. In one procedure, repetitive flashes were given contingently upon a correct response (Procedure B), and in the other no such photic stimulation was made (Procedure A). In the final stage of the conditioning, differences between two procedures were found; the distribution of response times was more concentrated with smaller means and variances in Procedure B than in Procedure A. Excitability of the visual cortex to a flash differed according to whether or not the flash was used as a response-contingent stimulus. To the response-contingent flash the primary component of visual cortical evoked potentials was augmented in amplitude with a reduction of peak latency. From these findings, temporal discrimination function of the animals was discussed. Behavioral correlates with modification of visual cortical evoked potentials were also discussed. —— contingent photic stimulation; conditioned response time; temporal discrimination

It was found in rats (Marx et al. 1955) and mice (Kish 1955) that a number of responses in conditioned bar pressing behavior increased when a light accompanied each response. Later this finding was confirmed by other investigators (Moon and Lodahl 1956, Kling et al. 1956, Forgays and Levin 1959, Berlyne et al. 1964), and the experiment in this line has been referred to as ‘light-contingent bar pressing experiment.’ McCall (1965) attempted to explain the reinforcing effect of response-contingent photic stimulation in terms of the stimulus-change hypothesis that increments and decrements in illumination would be equally reinforcing the conditioned behavior.

On the other hand, evidence has been accumulated that termination of CS acts as one of reinforcing factors in avoidance learning (Kamin 1956, Keenh and Nakkash 1959, Bolles et al. 1966). Recently Bower et al. (1965) showed in rats that when an auditory stimulus as CS was decreased in intensity following a conditioned response, the avoidance learning was facilitated. To explain these phenomena, Bolles and Grossen (1969) extended the stimulus-change hypothesis in such a way that an information on a stimulus change contingent upon the response, both intrinsic and extrinsic, was fed-back to subjects and acted as a reinforcing factor.

In the experiment to be reported here, cats were conditioned to press a bar

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for a food reward using a trace conditioning paradigm and attempts were made to examine how photic stimulation, given contingently upon the correct response, influenced the learning. It was found that when photic stimulation followed the correct response, both the means and variances of the response time tended to be smaller than in control. Also, examinations were made on how responsiveness of the cat visual cortex to a flash stimulus was changed when the flash was used as the response-contingent stimulus. A part of the data presented in this paper has been published elsewhere (Uramoto 1971).

METHODS

The animals were placed in an observation box (65 × 40 × 45 cm) and allowed to behave freely. One wall of the box had a window (10 × 15 cm) which permitted to introduce a flash from a conventional photic stimulator placed outside the box. Below this window there were provided a bar and a food tray. When the bar was pressed, a food pellet (a small fraction of the Quaker Oats Company's cat dry food) was presented on the tray. Near the box a loud-speaker was placed to sound a buzzer.

Before the conditioning the animals first learned to press the bar for the food reward, and then they were taught that the bar pressing was rewarded only when it was done after a buzzer tone was given as CS. This preliminary training was completed within about 10 days on the average. Then, the trace conditioning was started. The conditioning procedure for the first group of Ss (Cats 11, 12, 13, 21, 22 and 23) was as follows: The bar was locked for an initial delay of 10 sec from the onset of the buzzer lasting for 3 sec and the first bar pressing which occurred during 20 sec after the bar-locked time was followed by a pellet (UCS) (Procedure A), or after 5 msec by four flashes at 6 Hz and a pellet (Procedure B). In each procedure the trial was repeated at an interval of 90 sec. If the animals touched the bar during the bar-locked time, the response was taken as negative and the trial was abandoned. Each day they received 2-4 training sessions, each consisted of 20 trials. Each animal was conditioned three times in the order of A→B→A (Cats 21, 22 and 23) or B→A→B (Cats 11 and 13). The conditioning procedure was changed whenever the CR score remained above 90% in five successive sessions, or above 80% in ten successive sessions. The CR established under one procedure was extinguished before the animals were transferred to another procedure. The criterion of extinction was that the CR score remained below 10% in three successive sessions or below 20% in five successive sessions.

In the second group of Ss (Cats 41 and 42), the conditioning paradigm was slightly modified from that for the first group; the buzzer sounded for 1 sec and the initial delay period of bar-locking was 6 sec after the onset of CS. The first bar pressing which occurred during the subsequent 14 sec was followed by five flashes at 5 Hz and a pellet. The combination of flash and food reward was given regardless of whether or not the animals touched the bar during the bar-locked time. The inter-trial intervals was 60 sec. Each day the animals received two training sessions, each consisting of 50 trials. After the animals had been subjected to a total of six sessions, they received an extinction procedure of 3-4 non-rewarded sessions which was completed in two days. One extinction session consisted of 30 trials.

In the first group of Ss, a time of the first bar pressing from the onset of CS was measured by means of a pen recorder. A total number of bar pressings during each session was counted and two measures were calculated; the efficiency factor of bar pressing (E) and the reduction factor of redundant bar pressing (R). The former is defined as M/N, where M means the total number of rewarded bar pressings and N the total number of bar pressings, rewarded and non-rewarded, both being summed over the successive ten sessions. From the entire course of the conditioning two sets of successive ten sessions were taken; the first ten and the last ten. The efficiency factors for these two sets are
denoted as $E_i(=M_i/N_i)$ and $E_j(=M_j/N_j)$, respectively. The reduction factor $R$ is a relative difference of the total number of non-rewarded bar pressings between the first and last ten successive sessions, i.e., $R=(N_i-M_i)-(N_j-M_j)/(N_i-M_i)$.

Before the conditioning experiment, Cats 11, 12, 41 and 42 were prepared for recording evoked potentials of the visual cortex. Operations were carried out under Nembutal anesthesia (30 mg/kg, i.p.). In Cats 11 and 12 two stainless steel wire electrodes, which were aligned singly with a tip separation of 1.5 mm, were inserted into the visual cortex around a point of AP 0 mm and ML 2 mm. To the frontal bone a small screw was fixed as a ground electrode. In Cats 41 and 42 a screw was fixed to the bone overlying the visual cortex as a recording electrode and another screw to the frontal bone as an indifferent one. The third screw fixed near the indifferent electrode served to ground the animals.

In the animals so prepared, examinations were made on how evoked potentials of the visual cortex to photic stimulation were affected as the conditioning was carried out. This test experiment was performed in the inter-sessions of the conditioning. The animals were brought in a different room from that for the conditioning. They were placed in a box which was copied from the observation box for the conditioning. A buzzer tone similar to CS was given for one sec to Cats 41 and 42 and for 3 sec to Cats 11 and 12. Then, a single flash was delivered 4–8 sec from the onset of the buzzer in Cats 41 and 42 and 8–12 sec in Cats 11 and 12. The flash, delivered from the same photic stimulator as used for the conditioning, was given while the cat became attentive upon hearing the buzzer tone but remained quiet without overt movements. In Cats 41 and 42, 25–30 responses were recorded on film in one test experiment and their amplitudes were measured in each record. In Cats 11 and 12, 20 or 30 evoked responses were averaged by means of an on-line computer (ATAC-512, Nihon Kohden).

**RESULTS**

**Effects of response-contingent photic stimulation upon conditioned bar pressing behavior**

Previous workers have noted that bar pressing behavior or avoidance learning was accelerated when photic stimulation was introduced after responses. In the present study, however, no consistent difference was found in the rate of acquisition of CR between Procedures A (without photic stimulation) and B (with photic stimulation). This is shown in Table 1 representing the number of sessions needed for each animal to reach the criterion under each conditioning procedure. With regard to the number of sessions needed for extinction, there was no striking difference between the two procedures; usually extinction was reached in 10–20 non-rewarded sessions.

In earlier stages of the conditioning, all animals tended to press the bar during not only the bar-locked time but also the inter-trial interval. Since these bar pressings were not rewarded, they were redundant. As the conditioning was repeated, the animals learned to press the bar correctly in accordance with the

<table>
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<tr>
<th>Procedure</th>
<th>Cat 11</th>
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<th>Cat 21</th>
<th>Cat 22</th>
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<tr>
<td>B</td>
<td>46</td>
<td>85</td>
<td>81</td>
<td>A</td>
<td>87</td>
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<td>50</td>
<td>A</td>
<td>8</td>
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<td>24</td>
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* Cat 12 died after the first conditioning under Procedure B.
requirement of the conditioning procedure. In addition, the redundant bar pressings became less frequent. As the results of these two processes of learning, the efficiency factors of bar pressing (ratio of the total number of rewarded bar pressings to the total number of bar pressings, rewarded and non-rewarded) were increased from the first ten successive sessions to the last ten. This was true irrespectively of the type of conditioning procedure which the animals received (Table 2, E1 and E2).

### Table 2. Efficiency and reduction factors

<table>
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<th>Cat</th>
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<td>11</td>
<td>12</td>
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<td>N1</td>
<td>1189</td>
<td>543</td>
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<tr>
<td>N2</td>
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<td>226</td>
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<td>M1</td>
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<td>M2</td>
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<td>0.09</td>
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<tr>
<td>E2</td>
<td>0.43</td>
<td>0.79</td>
</tr>
<tr>
<td>R</td>
<td>0.81</td>
<td>0.91</td>
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All values were obtained from the first conditioning of the three in the order of A→B→A or B→A→B; values under Procedure B for Cats 11, 12 and 13 or under Procedure A for Cats 21, 22 and 23. Notations, see text.

If Procedures A and B are compared with respect to the reduction of the redundant bar pressings, a tendency will be seen that the reduction factor R is larger under Procedure B than under Procedure A. Since R is defined as a relative difference of the total number of non-rewarded bar pressings between the initial and last stages of the conditioning, a larger value of R means that there was a large difference between the two stages in the number of non-rewarded bar pressings. Thus, it seems likely that the response-contingent photic stimulation is effective in suppressing the redundant bar pressings. That the factor R turned out larger under Procedure B than under Procedure A is mainly due to the fact that in the earlier stage the cats conditioned under Procedure B showed more bar pressings than those under Procedure A (first row of Table 2). The discussion will be made later on this respect.

**Effects upon conditioned response time of contingent photic stimulation**

In the stage of preliminary training the cats used to press the bar immediately after hearing CS. These hasty responses were gradually suppressed as the training was repeated, although the cats still kept the tendency to press the bar very promptly. After the conditioning was started under either Procedure A or Procedure B, the timing of bar pressing after the bar-locked time (10 sec) became frequent. However, in the initial stage of the conditioning a considerable fraction of response times was still found less than the bar-locked time. This is seen in the left two histograms of response times in Fig. 1. These histograms are
Fig. 1. Distributions of response times in the initial five successive sessions (left) and in the final five successive sessions (right). Data were obtained from the first conditioning of the three in the order of A→B→A (bottom, Cat 23) or B→A→B (top, Cat 11). M and V denote mean and variance of the response times, respectively. Ordinates, number of responses. Abscissas, response time in sec. In the two histograms to the left the response times longer than 25 sec were collected in the rightmost columns.

composed of response times in the initial five successive sessions. The response times distributed very widely with peaks less than 10 sec. With regard to this, there was no marked difference between Procedures A and B. Repetition of the conditioning was effective in cutting the hasty responses. This is seen in the right two histograms in Fig. 1 showing the data obtained from the last five successive sessions. That the bar pressing before the bar-release was almost completely suppressed was equally seen under Procedures A and B. Furthermore, it is seen that the bar pressings with longer response times were also suppressed, thus the distribution of response times being more or less concentrated.

It should be noted that the distribution of response times in the last five successive sessions under Procedure A is different from that under Procedure B; the distribution under Procedure B is almost unimodal, whereas that under Procedure A is either unimodal or multimodal, and means and variances of the response time are smaller under Procedure B than under Procedure A (compare the right two histograms in Fig. 1). This is shown more clearly in Fig. 2 which includes the means and variances of the response time of all trials in the final five successive sessions of all conditioning period regardless of their sequences in any individual animals. The values obtained from Procedure B (open circles) were found in the lower section of the graph, while in the upper section there were values only from Procedure A (solid circles). Comparison between the two conditioning procedures in each subject reveals that the variances of the response time are consistently smaller under Procedure B than under Procedure A in all animals and, with one exception, the mean values show the same characteristic difference.
In an additional experiment it was investigated whether electrical stimulation of the lateral geniculate body (LGB) was effective as a response-contingent stimulus in the same way as photic stimulation. Two naive cats which had received a stereotaxic implantation of a bipolar electrode in the LGB were used. The LGB was stimulated for one second at 10 Hz with 0.05 msec pulses of 15 v in intensity. These parameters are similar to those used by Kiyono et al. (1970) and Swadlow and Schneiderman (1970) who succeeded in establishing CRs in animals by using electrical stimulation of the LGB as a CS. It was found that the LGB stimulation did not function in the same way as photic stimulation. The LGB stimulation neither brought the response time close to the bar-released time nor reduced the variance of response times.

**Augmentation of visual evoked potentials by pairing photic stimulation with a food reward**

The data from Cats 41 and 42 will be discussed first. In Fig. 3, visual evoked potentials (VEPs) to a single flash in Cat 41 are shown. In the VEPs there are two clearly distinguishable waves which are designated as a and b waves following Steriade and Ionescu (1967). Their peak times were about 22 and 45 msec, respectively. The amplitudes of the waves a and b (H_a and H_b, respectively) were measured and compared before and after the exposure to the conditioning.

Both H_a and H_b were significantly increased through the exposure to the conditioning with flash-contingency. Before the exposure to the conditioning the values of H_a and H_b were 204.2±50.9 μV and 189.5±70.7 μV (mean±s.d.), respectively. After six session (300 trials) of the conditioning, they became 286.3±81.6 μV and 300.0±123.2 μV, respectively, i.e., H_a and H_b values were increased by 140% and 154%, respectively. A statistical test of likelyhood (two tailed test)
shows that increases of 140% for H_a and of 154% for H_b are highly significant (both, P<0.001). Cat 42 manifested augmentations of 152% for H_a and of 164% for H_b (P<0.05 and P<0.001, respectively). After this enhancement of VEPs was found, Cat 42 received an extinction procedure. Then, it was again conditioned with the same paradigm as before but without contingent photic stimulation. After six sessions were finished, VEPs were again examined. According to the significance test, it can be said that the VEPs at this stage were about the same level as for the completely naive cat.

When individual records of VEP in Cats 41 and 42 were scrutinized, it was found that the positive peak latencies of the waves a and b in the conditioned state were slightly but definitely reduced as compared with those in control. This point was most clearly seen in Fig. 4 where averaged VEPs of Cat 11 are presented. Judging from the peak latency, the first downward and second upward deflections
seem to compose the a wave. The b wave was difficult to identify in this example. The top record (A) is a control taken before the cat was subjected to the conditioning procedure. The middle record (B) was obtained after 46 sessions of the conditioning under Procedure B had been carried out. In addition to the fact that the positive component of the wave a was increased about twice as large as the control, the peak latency was seen to be reduced by about 3.5 msec. After this record was obtained, the cat received the extinction procedure, and then it was reconditioned under Procedure A (without photic stimulation). After 17 sessions were carried out, the CR was recovered. The bottom record (C) was obtained at this stage. The positive component of the wave a was now brought back to the control level in amplitude as well as in peak time.

DISCUSSION

First, a discussion will be made on effects of contingent photic stimulation upon conditioned behavior. It was verified in the first group of cats that contingent photic stimulation brought about positive behavioral changes; differences between the two conditioning procedures were found in the distribution of response times in the last five successive sessions, and means and variances of the response time tended to be smaller under Procedure B than under Procedure A.

With respect to the temporal discrimination function, there have been many studies of timing behavior in rats using the differential reinforcement of low response rate schedule (Anger 1956, Kelleher et al. 1959, Ellen et al. 1964, Ellen and Butter 1969). These studies and others on monkeys (Brady and Conrad 1960, Stamm 1963) or rabbits (Suzuki and Saito 1970) have consistently indicated that animals responded at very short inter-response times in earlier stages of the training, and as the training progressed they tended to show longer inter-response times in accordance with requirements of the schedule. In the present experiment the animals were trained to press the bar after hearing CS and the response times were measured from the presentation of CS. It was found that the response times so measured were very short in the stage of preliminary training and in the earlier stages of the conditioning. Thereafter, they gradually tended to lengthen to fulfill the requirement of the conditioning paradigm. This characteristic tendency of prolongation of the response time seen in the present experiment is similar to the above-mentioned findings in the timing behavior. Therefore, it will be justified to say that the present experiment is primarily concerned with temporal discrimination in the animals. The present data indicate that temporal discrimination was performed more precisely under Procedure B than under Procedure A, suggesting that visual information on occurrence of the correct response contributed much to the temporal discrimination function of the CNS.

A number of "light-contingent bar pressing experiments" have confirmed that animals responded significantly more often than control animals when the intensity of cage illumination was changed as a result of bar pressing, and previous workers have noted that bar pressing behavior or avoidance learning was acce-
lerated by introduction of photic stimulation after responses (see Introduction). This may correspond to the present finding that bar pressings in the earlier stage of the conditioning were more frequent under Procedure B than under Procedure A.

It was shown that repetitive electrical stimulation of the LGB contingent upon bar pressing did not significantly improve the temporal discrimination. Kiyono et al. (1970) and Swadlow and Schneiderman (1970) demonstrated that LGB was effective as a site of CS in a conditioning paradigm. One might consider that LGB stimulation as a trigger of CR would be different in biological significance from that as in information of occurrence of correct responses. However, since the present experiment on the effects of response-contingent LGB stimulation was not extensive enough, a definitive conclusion must be reserved.

There are a number of experiments showing that cortical evoked potentials to sensory stimuli were modified with some behavioral correlates. Hernández-Peón et al. (1956) observed a decrease of click-evoked potentials when so-called distracting stimuli of non-auditory modality were introduced simultaneously with click. This was confirmed by other investigators (Hernández-Peón et al. 1957, Horn 1960, Kitai et al. 1965). Jane et al. (1962) reported the contraries that VEPs were augmented when an auditory stimulus was added to a visual stimulus. In the unitary studies it was evidenced that nonvisual stimuli could activate visual cortical cells and their discharges to a single flash were modified when other stimuli were simultaneously applied (Lömo and Mollica 1962, Horn 1965, Skrebitskey 1969). In the conditioning experiments many workers have reported that evoked potentials to photic or auditory stimuli as CS were augmented as the learning became complete (Fleming 1967, Khachaturian and Gluck 1969, Sommer-Smith and Morocutti 1970). In the same line as these findings, the present experiment revealed that VEPs to a single flash were augmented after the same flash had been used as a response contingent stimulus in the conditioning paradigm. In addition, the augmented VEPs were found to appear with a slightly reduced peak latency. This is similar to Steinberg's finding (1965) that the latency of VEPs to flash stimulation was reduced when distinct periods of arousal were increased by external stimuli.

The behaviorally correlated modification of the cortical evoked potentials has been considered to be due to a shift of attention or arousal level which results in an alteration of excitability of the specific sensory pathway through an altered ascending reticular activating influence (Ricci et al. 1967, Steriade 1968, Khachaturian and Gluck 1969). This concept will probably hold well in the present finding.

Acknowledgment

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References


