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OPERANT CONDITIONING OF EYE MOVEMENT IN THE MONKEY (*Macaca nemestrina*)[1]

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With the horizontal electrooculographic potential as the operant, four monkeys (*Macaca nemestrina*) were conditioned to move their eyes at high and low rates by initial use of fixed-ratio schedules of reinforcement, followed by a changeover to multiple schedules of fixed-ratio reinforcement and discriminated differential reinforcement of low rate. These differences in rate of eye movement were not observed in a control animal given the same patterns of discriminative stimuli and deliveries of the reinforcing agent independent of its eye movements.

Eye movement is a response which can be considered to occupy an intermediate position between involuntary and voluntary responses. It is controlled via the oculomotor nuclei, which are also involved in eyelid movement, a response that has been extensively studied using classical conditioning techniques. Although eye movement has occasionally been studied as a classically conditioned response (Deaux and Gormezano, 1963; Zikmund, 1964), operant conditioning of eye movement has not previously been reported. Operant conditioning of this response is of interest, particularly if low rates can be brought under control by a schedule, such as differential reinforcement of low rate (DRL), (Skinner and Morse, 1958; Wilson and Keller, 1953), in which only those responses which terminate interresponse times longer than some particular value (the DRL value) are reinforced. This might seem difficult for a response such as eye movement, in view of its partly involuntary nature and its high normal rate of occurrence compared with most skeletal responses.

Operant conditioning of eye movement was undertaken in four monkeys to study the effects of different rates of wakeful eye movement on rapid eye movements occurring during subsequent, low-voltage, fast-wave electroencephalographic (EEG) sleep (Meier and Berger, 1965); these effects will be reported elsewhere. In order to increase the likelihood of successfully controlling eye movements, several discriminative stimuli were employed, using techniques similar to those used by Hefferline (1958) in reinforcement of small muscle movement.

METHOD

Subjects and Surgery

Five monkeys, (*Macaca nemestrina*) 3 to 4 kg in weight, were used. Four of them (S-1, S-2, S-3, and S-4) were used as experimental subjects; the fifth (S-5) was used as a control.

All animals were stereotaxically implanted, under pentobarbital anesthesia, with stainless-steel screws and concentric electrodes for recording cortical and subcortical EEGs. Two flexible stranded stainless-steel wires, 0.2 mm in diameter and coated in silicone rubber, were bared for 30 mm at their ends and implanted into the dorsal neck muscles in order to record the electromyogram (EMG). Two holes, each 1.0 mm in diameter, were drilled 2.0 mm dorsal to the lateral margin of the orbital ridge of each eye. The ends of a second pair of flexible wires, which had been bared for 10 mm, were looped through these holes and tied back upon themselves. These leads served to record the horizontal electrooculogram (EOG). This method for recording eye movements depends upon the existence of a

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potential difference between the cornea and fundus of the eye. The EOG potential results from the spatial change of the corneofundal potential field as the eyeballs rotate with reference to the fixed periorbital electrodes (Kris, 1960). The free ends of the EMG and EOG leads were passed subdermally to the cranium. All electrode leads were soldered to terminal plugs (Winchester) anchored to the skull with acrylic dental cement in a conventional manner.

Apparatus

After a recovery period of at least two weeks, the monkeys were adapted to restraint in their home cages. A plastic collar placed around the neck allowed them to move only in a lateral direction. During all conditioning and recording sessions, two angle brackets were placed laterally at each side of the animal's head to prevent turning. In addition, a large wooden board was placed around the whole plastic collar to prevent lateral movement and to keep the monkey from interfering with its attached head cables or the apparatus in front of it (Fig. 1). This restraint system did, however, allow the animal to adopt a relatively normal relaxed posture.

Grape juice (Welch) was delivered to the monkeys through a metal tube, via a solenoid valve connected to a reservoir. The aperture at the end of the tube was small enough to maintain a continuous volume of liquid within the tube, so that when the solenoid was actuated fluid was instantaneously available. Three small 1.12-w lamps (G.E. 327) colored white, red, and green were suspended on a perpendicular panel 20 cm from the animal's face. A similar blue lamp was attached directly to the juice-tube 6 cm in front of the animal. These colored lamps served as discriminative stimuli. Recording cables were attached to the cranial electrode plugs and led to a plug-board connected to a Grass Model 6 EEG machine. The whole apparatus was placed in a dark, electrically shielded, sound-attenuating chamber, and the animals were observed through a closed-circuit infrared TV system.

The presentation of discriminative stimuli and programming of reinforcement schedules were controlled by solid-state logic modules

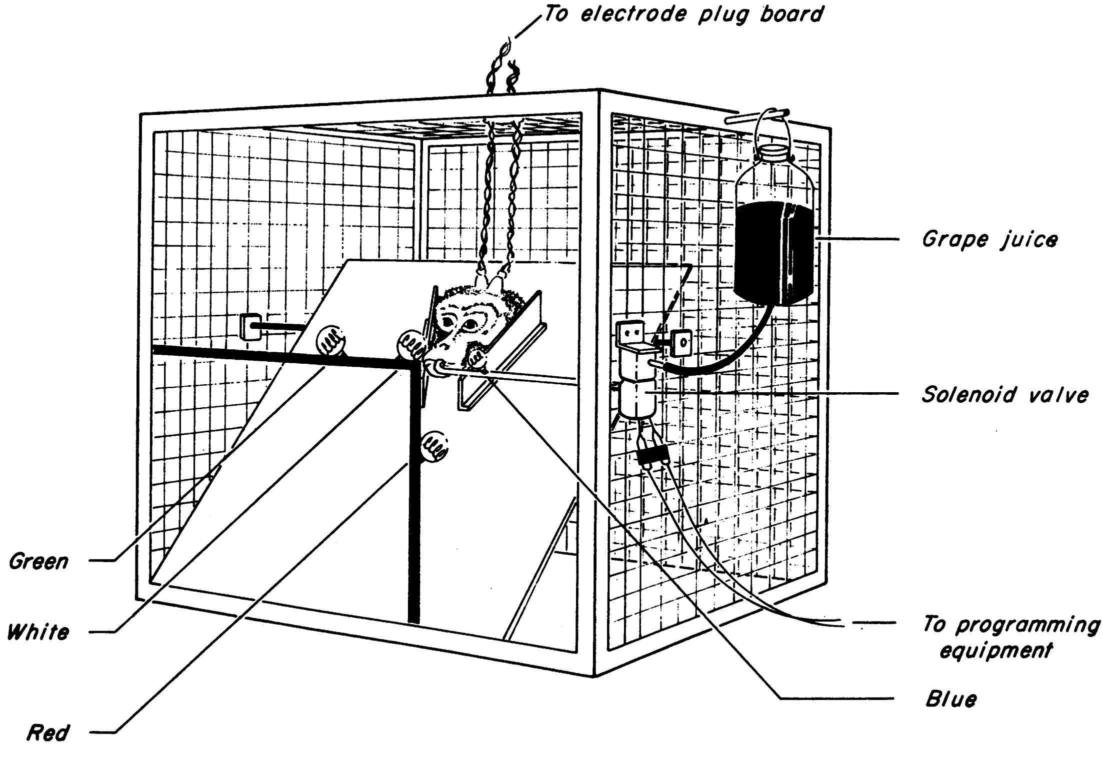

Fig. 1. Schematic illustration of the experimental apparatus.

(Applied Development Corporation). The output from the EOG channel of the EEG machine was fed to the input of a Schmitt Trigger so adjusted that a positive or negative EOG potential exceeding 200 μv in amplitude, via a time constant of 0.2 sec, was defined as a response. This relatively fast time constant was used so that eye movements which generated sufficiently large EOG potentials would activate the Schmitt Trigger irrespective of their starting position from rest. However, the use of a time constant rendered it impractical to attempt to calibrate the defined response physically, in terms of families of curves of angular deflection at various velocities of eye movement for each subject. From gross observations, the response represented a spontaneous fixational movement of the eyes of approximately 10 degrees. The Schmitt Trigger activated conventional timing and switching circuits appropriate to each schedule, and was also connected to a cumulative recorder.

Procedure

The monkeys were deprived of water for 12 hr before each session. Thereafter, water was offered at the end of each session and withdrawn when the animal had ceased to drink. On nonexperimental days, such as some weekends, water was freely available.

Fixed-ratio (FR) schedules, in which reinforcement was delivered after a fixed number of responses, and discriminated DRL schedules were compared in terms of rates and patterns of response. In order to control the eye movement response more effectively, several discriminative visual stimuli were utilized. Throughout both FR and discriminated DRL schedules, each response turned on the centrally located white light; this provided an external stimulus with each response in addition to internally generated physiological stimuli. The duration of the white light was determined by the length of time the response-generated EOG potential remained above 200 μv. Since the rise time and amplitude of the EOG potential varied with each eye movement, the duration of the white light varied dependently, but was usually about 60 msec. During FR schedules the red light was also continuously illuminated. During discriminated DRL schedules the green light was continuously illuminated; in addition, the blue light was illuminated when pauses longer than the DRL value were reached and was turned off by the next response with the delivery of reinforcement. It was anticipated that, apart from acting as an additional discriminative stimulus, anticipatory ocular fixations of the blue light might develop during training and thus help to improve performance on the discriminated DRL schedules. It should be emphasized that by using the blue light, the schedule was not a simple DRL schedule, according to customary usage of the term. The term DRL normally denotes reinforcement of an interresponse time exceeding some minimal value in the presence of an unchanging stimulus. The use of the blue light produced what may best be called a discriminated DRL schedule, but for the sake of brevity the abbreviation DRL will be used throughout this report.

The experimental subjects were first introduced to fixed-ratio schedules of reinforcement, beginning with reinforcement of every response (FR 1) and followed by progressive increases in the number of responses required for each reinforcement until a ratio of six (FR 6) was achieved. A changeover to multiple schedules of FR 6 and DRL 5-sec (*mult* FR 6 DRL 5-sec) was then made. A *mult* FR 6 DRL 5-sec schedule is one composed of alternating FR 6 and DRL 5-sec components. When effective control of the rate of responding on the *mult* FR 6 DRL 5-sec schedules was established, the subjects were next given, for six successive sessions on each, isolated schedules of FR 6 and of DRL 5-sec. The order of the two isolated schedules was counterbalanced for the four monkeys. A two-day period separated the two series of sessions during which the monkeys were retrained on the schedule presented second.

The quantity of juice emitted for each reinforcement was varied by means of a timer that controlled the duration of the interval for which the solenoid was opened. The timer was set at 0.04 sec during the FR schedules and 0.10 sec on the DRL schedules, delivering 0.08 cc and 0.18 cc of juice, respectively. Thus, as a result of the different rates of reinforcement on each schedule, the monkeys received approximately the same quantities of juice under the two conditions by the end of each session.

Each session lasted from 2 to 4 hr, depending upon performance. Three-minute periods of timeout, in total darkness and in which responses were not reinforced, began each experimental session. With the exception of the sessions of isolated schedules of FR 6 and DRL 5-sec, timeout periods occurred randomly thereafter, at intervals of 6 to 120 min, with durations varying randomly from 1 to 60 min. A timeout always separated successive elements of the *mult* FR DRL schedules. During the sessions of isolated FR 6 and DRL 5-sec schedules, timeout periods were not reintroduced after the 3-min timeout which began the session.

Monkey S-5 was used as a "semi-yoked" control. For this purpose, two magnetic tape recordings of the EOG of Monkey S-3 were made, one during its last session on an isolated FR 6 schedule and one during its last session on an isolated DRL 5-sec schedule. Later, the output of the tape recorder was connected to one channel of the EEG machine. The output of this channel was fed to the input of the Schmitt Trigger which activated the programming apparatus; the gain was set so that the amplitude of the EOG potentials at this point was the same as when they had been recorded from Monkey S-3. Monkey S-5 was placed in the experimental apparatus and its EOG leads connected via another channel of the EEG machine to a second Schmitt Trigger that activated the cumulative recorder. Amplification was set so that a response was defined as in the experimental subjects. Using this arrangement, each of the two tape recordings was replayed as described for six successive sessions, making 12 sessions in all, with the programming apparatus set exactly as it had been when the equivalent sessions with Monkey S-3 were recorded. The EOG of Monkey S-5 could thus be recorded while the animal was exposed to the identical stimuli and reinforcements as Monkey S-3 had been during its isolated FR 6 and DRL 5-sec schedules, but independently of Monkey S-5's own eye movements. Thus, it was possible to examine any direct effects of differences in the discriminative stimuli and frequencies of their illumination, together with differences in the magnitude and frequency of delivery of grape juice, on the rate of eye

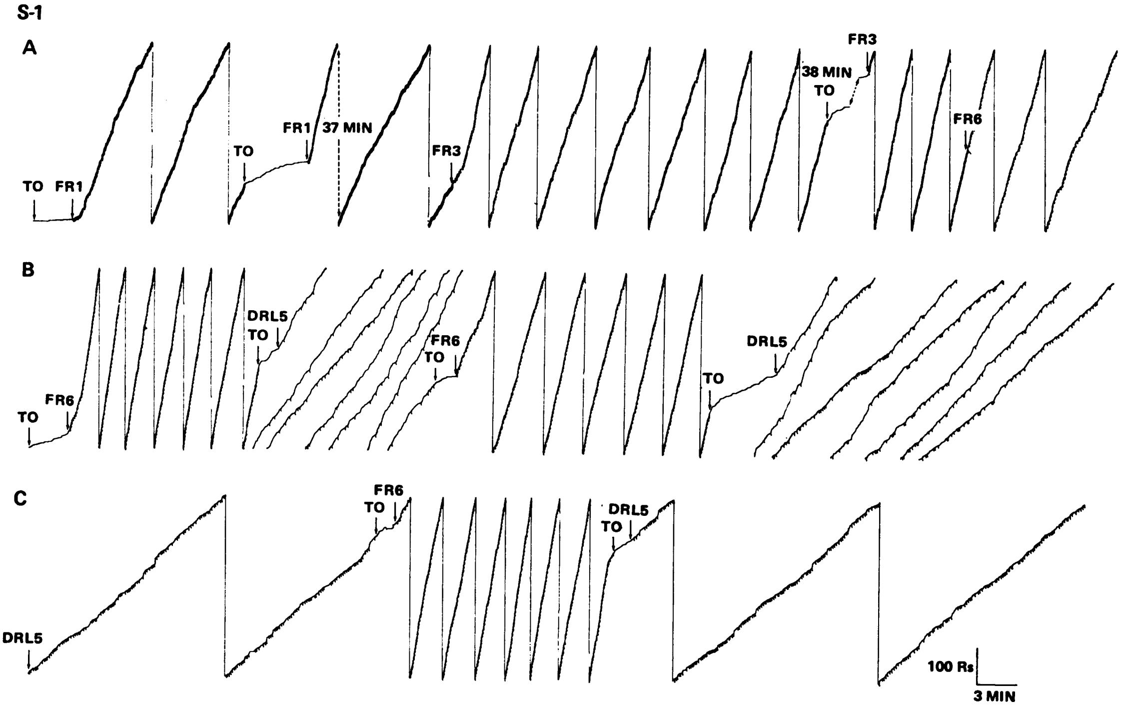

Fig. 2. Cumulative records illustrating various stages of conditioning of eye movement in Monkey S-1. A, beginning of Session 1, with introduction of the FR 1 schedule, followed by progressive increases in the fixed ratio to FR 6. B, introduction of the *mult* FR 6 DRL 5-sec schedule at the beginning of Session 2. C, later performance on the *mult* FR 6 DRL 5-sec schedule in Session 5. In Fig. 2 through 7, each downward pen deflection represents delivery of reinforcement, and the abbreviation, DRL, refers to a "discriminated DRL" schedule. For the stimulus conditions in effect during each schedule and periods of timeout, see text.

movement during the FR 6 and DRL 5-sec schedules.

RESULTS

Figures 2 to 5 show the similar development of control of rate of eye movement in each of the experimental subjects. The introduction of FR 1 schedules at the end of the initial timeout rapidly increased rate of eye movement (Fig. 2A, 3A, 4A, and 5A). Subsequent periods of timeout decreased response rate. A stable high rate of response on FR 1 schedules was established in all subjects within the first experimental session. The fixed ratio was then progressively increased by steps from FR 1 to FR 6 until a high stable rate of response on the FR 6 schedules was obtained in Monkeys S-2, S-3, and S-4 by the end of the second session (Fig. 3B, 4B, and 5B), and in Monkey S-1 by the end of the first session (Fig. 2A).

After establishing stable high rates of eye movement on the FR 6 schedules, *mult* FR 6 DRL 5-sec schedules were introduced. The DRL 5-sec element was introduced after a brief timeout period which followed an initial FR 6 element (Fig. 2B, 3C, 4C, and 5C). The illumination of the green light produced a burst of eye movement at a rate close to that exhibited during the prior FR 6 element. However, the absence of reinforcement soon led to a decrease in response rate in all animals except Monkey S-2, which steadily continued as this schedule was maintained. As the response rate decreased, the rate of reinforcement and the ratio of number of reinforcements to number of responses increased progressively. Performance stability on the subsequent FR 6 element of the schedule was hardly affected by the experience with the DRL 5-sec portion, although the rate of response was lower than during the initial FR 6 element (Fig. 2B). Continued experience with the *mult* FR 6 DRL 5-sec schedules during subsequent sessions led to decreased rate and increased constancy of response during DRL 5-sec components (Fig. 2C, 4E, and 5D).

The immediate use of a 5-sec pause for reinforcement on the DRL element of the *mult*

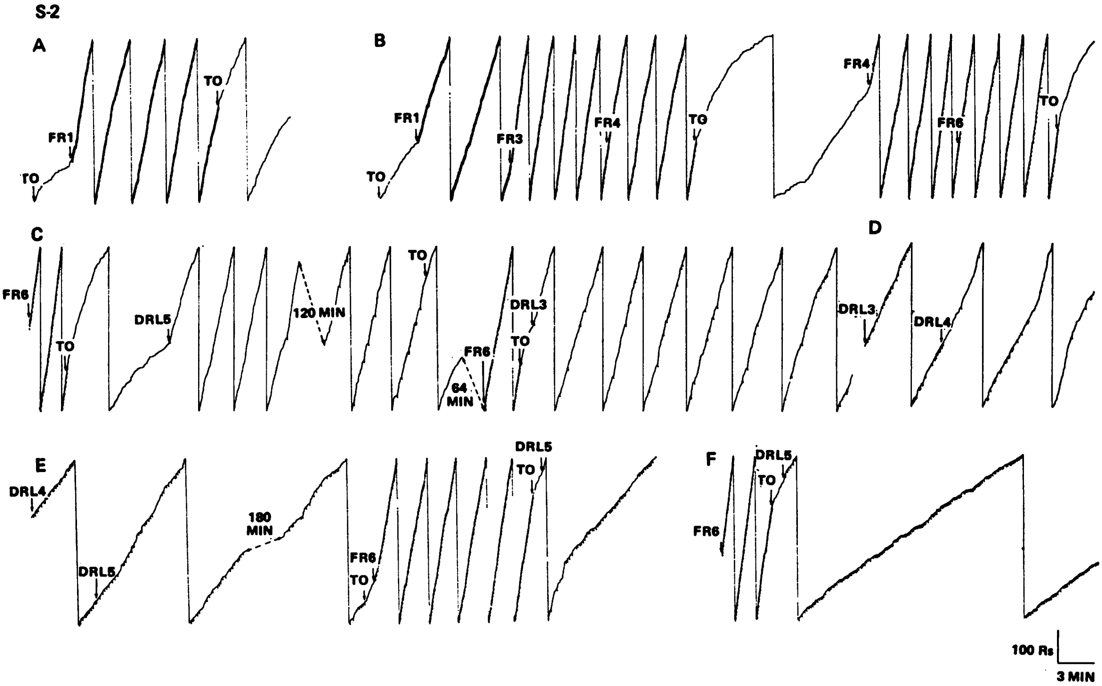

Fig. 3. Cumulative records illustrating various stages of conditioning of eye movement in Monkey S-2. A, introduction of the FR 1 schedule at the beginning of Session 1. B, performance during progressive increases in the fixed ratio, from FR 1 to FR 6 in Session 2. C, introduction of the *mult* FR 6 DRL 5-sec schedule, followed by substitution of a *mult* FR 6 DRL 3-sec schedule in Session 3. D, increase in the DRL interval from 3 sec to 4 sec in Session 4. E, increase in the DRL interval from 4 sec to 5 sec in Session 5. F, final performance on the *mult* FR 6 DRL 5-sec schedule in Session 8.

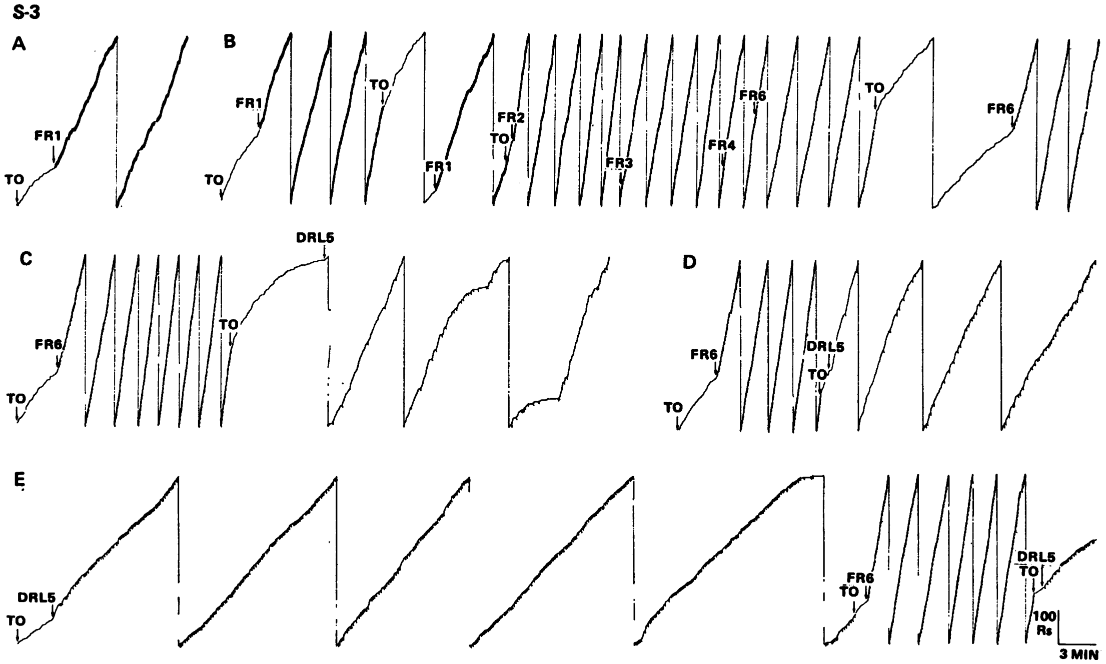

Fig. 4. Cumulative records illustrating various stages of conditioning of eye movement in Monkey S-3. A, introduction of the FR 1 schedule at the beginning of Session 1. B, performance during progressive increases in the fixed ratio from FR 1 to FR 6 in Session 2. C, introduction of the *mult* FR 6 DRL 5-sec schedule at the beginning of Session 3. D, later performance on the *mult* FR 6 DRL 5-sec schedule at the beginning of Session 5. E, final performance on the *mult* FR 6 DRL 5-sec schedule at the beginning of Session 8.

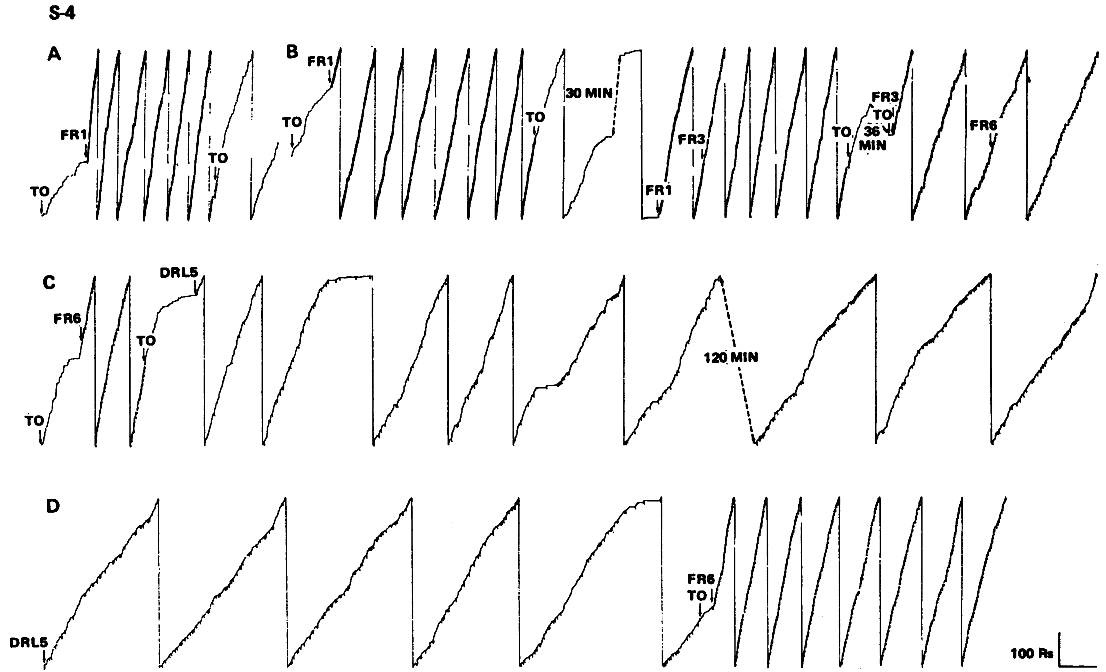

Fig. 5. Cumulative records illustrating various stages of conditioning of eye movement in Monkey S-4. A, introduction of the FR 1 schedule at the beginning of Session 1. B, performance during progressive increases in the fixed ratio from FR 1 to FR 6 in Session 2. C, introduction of the *mult* FR 6 DRL 5-sec schedule at the beginning of Session 4. D, final performance on the *mult* FR 6 DRL 5-sec schedule in Session 10.

Table 1

Rate of Response (per Min) during the Different Schedules and Periods of Timeout (TO)

	Mult FR 6 DRL 5 Schedules[a]			*Isolated Schedules*[b]			
Subject	*TO*[c] *Darkness*	*FR 6 Component Red and White Lights*	*Discriminated DRL 5 Component Green, White, and Blue Lights*	*TO*[c] *(FR 6) Darkness*	*FR 6 Red and White Lights*	*TO*[c] *(FR 6) Darkness*	*Discriminated DRL 5 Green, White, and Blue Lights*
Experimental							
S-1							
Mean	12.1	215.4	28.8	17.5	142.5	12.0	23.8
σ	—	—	—	4.8	24.1	4.8	1.8
S-2							
Mean	28.7	234.8	30.0	71.2	206.8	48.5	27.4
σ	—	—	—	18.6	26.3	10.7	2.6
S-3							
Mean	26.3	226.1	38.9	37.6	186.9	18.6	33.2
σ	—	—	—	15.0	47.0	5.5	2.4
S-4							
Mean	66.7	206.8	77.9	60.2	125.8	47.5	27.6
σ	—	—	—	21.2	8.0	9.4	2.3
Yoked-Control							
S-5							
Mean	—	—	—	80.3	40.2	73.5	54.6
σ	—	—	—	14.3	4.2	21.9	5.2

[a] Mean rate of response during the last session on *mult* FR 6 DRL 5-sec schedules.

[b] Mean and standard deviation (σ) over each series of sessions on isolated DRL 5-sec and isolated FR 6 schedules.

[c] Measures taken from the 3-min timeout period which began each session.

FR 6 DRL 5-sec schedule, failed to produce a significant decrease in response rate even after a long period of time, in Monkey S-2 (Fig. 3C). A 3-sec interresponse time was, therefore, substituted in a *mult* FR 6 DRL 3-sec schedule for this animal. Effective control was established on the DRL 3-sec element by the end of the second session on this *mult* FR 6 DRL 3-sec schedule. The DRL value was then progressively increased from 3 to 4 sec and from 4 to 5 sec during subsequent sessions (Fig. 3D and E), with the result that this monkey eventually exhibited the greatest difference in rate of response on each component of the *mult* FR 6 DRL 5-sec schedule by the end of its eighth training session (Fig. 3F, Table 1).

All four experimental monkeys responded for extended periods of 2 hr or more, at stable differential rates on the *mult* FR 6 DRL 5-sec schedules, after from 6 to 10 training sessions. The mean ratios of response rate during the FR 6 and DRL 5-sec elements varied from 2.7:1.0 in Monkey S-4, to 7.8:1.0 in Monkey S-2, respectively (Table 1).

When the experimental subjects were subsequently given isolated DRL 5-sec schedules, performance improved markedly. Figure 6B, taken from subject S-1, illustrates the increased stability and decreased rate of response, with increased ratio of reinforcements to responses, on an isolated DRL 5-sec schedule compared with previous performance on the DRL 5-sec components of the *mult* FR 6 DRL 5-sec schedule (Fig. 2C). This improvement in performance was seen in all the experimental animals on their first experience with the isolated DRL 5-sec schedule, whether or not this had been preceded by experience with the isolated FR 6 schedules.

In addition to differences in rates of response described above, the patterns of response were strikingly different during the FR 6 and DRL 5-sec schedules or schedule components. During the isolated FR 6 schedules and FR 6 components of *mult* FR 6 DRL 5-sec schedules, the subjects would move their eyes vigorously to and fro, while keeping their mouths clamped to the end of the juice tube. The upper EOG record of Fig. 6A illustrates the brief pauses which occurred after each

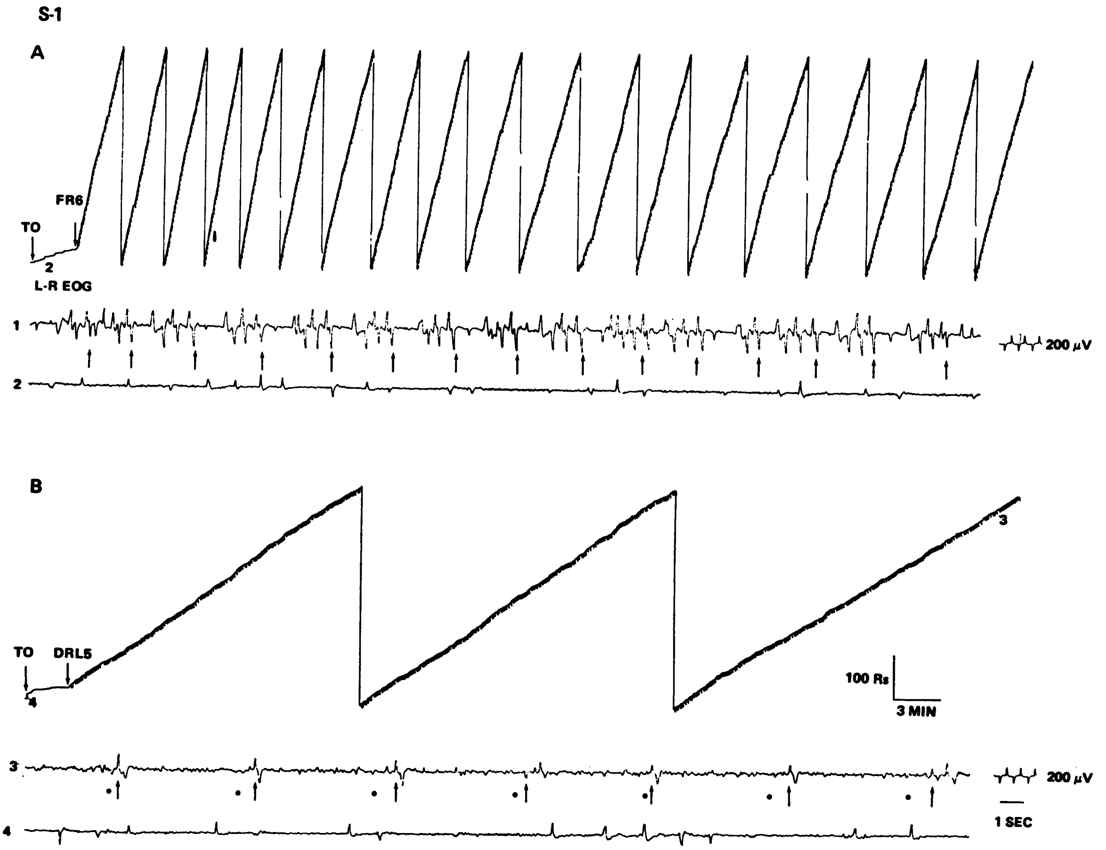

Fig. 6. Cumulative records of eye movement responses in Monkey S-1 at the beginning of two different experimental sessions on: A, an isolated FR 6 schedule and B, an isolated DRL 5-sec schedule. Electrooculographic (EOG) records appear below each cumulative record, illustrating the different patterns of eye movement during each schedule and periods of timeout. The points of time in the cumulative records at which the EOG tracings were taken are indicated by the numerical codes. The vertical arrows indicate presentations of reinforcement; during the DRL 5-sec schedule, each onset of the blue light is represented by a black dot.

reinforcement, so that bursts of eye movement to left and right generated clusters of six alternately positive and negative potentials. By contrast, during isolated DRL 5-sec schedules and DRL 5-sec elements of *mult* FR 6 DRL 5-sec schedules, the monkeys would fixate on the blue light until it went on, then would rapidly move their eyes to right or left, producing reinforcement, and would finally fixate on the blue lamp again until its next illumination. As mentioned earlier, this behavior was anticipated in the experimental design and was the reason for deciding to use the blue light as an additional discriminative stimulus. While watching the blue light the monkeys might or might not apply their mouths to the end of the tube, but would do so the moment the lamp lit up, while they made the appropriate eye-movement response. The upper EOG record in Fig. 6B was typically generated by the above behavior, showing biphasic potentials generated by lateral movements of the eyes with returns to center separated by intervals of just over 5 sec. The irregular patterns of eye movement shown by the EOG tracings during timeout periods (Fig. 6) were distinct from the more regular patterns of eye movement during both FR 6 and DRL 5-sec schedules. However, the mean rate of eye movement during timeout periods which preceded isolated FR 6 schedules tended to be higher than during timeout periods which preceded isolated DRL 5-sec schedules (Table 1).

The behavior of the "semi-yoked" control monkey, S-5, was strikingly different from that of the experimental monkeys. Thus, the rate of eye movement remained relatively close to

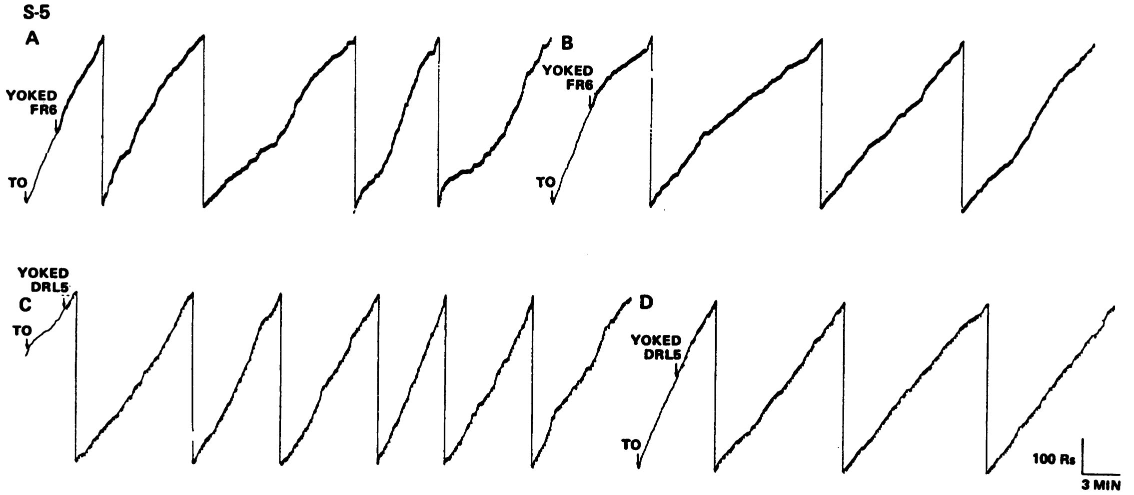

Fig. 7. Cumulative records of eye-movement responses in the control monkey S-5 during: A, the beginning of Session 1 on the yoked FR 6 schedule, B, the beginning of Session 6 on the yoked FR 6 schedule, C, the beginning of Session 1 on the yoked DRL 5-sec schedule and D, the beginning of Session 6 on the yoked DRL 5-sec schedule. The records illustrate the slightly higher rate of eye movement during the yoked DRL 5-sec schedules than during the yoked FR 6 schedules.

the levels of the initial timeout periods during both the FR 6 and DRL 5-sec yoked-control schedules (Fig. 7, Table 1), and the rates of eye movement during each of them bore little resemblance to the rates during the equivalent experimental schedules in Monkey S-3. In fact, the small differences that did exist in rate of eye movement during the yoked-control schedules were opposite in direction to those during the experimental schedules of Monkey S-3 (Table 1). Thus, the rate of eye movement during the initial DRL 5-sec yoked-control schedules (Fig. 7C) was somewhat greater than the mean rate during the initial FR 6 yoked-control schedules (Fig. 7A). These differences progressively diminished by the sixth session of each yoked-control condition (Fig. 7B and D). Therefore, the higher rate of eye movement during the FR 6 experimental schedules, compared with that during the DRL 5-sec experimental schedules, could not be due simply to differences in the stimulus parameters or differences in magnitude and rate of reinforcement. The different contingencies of the stimuli and reinforcements must have been the factors controlling eye-movement responses under the different schedules.

DISCUSSION

The present results demonstrate that eye movements can be controlled by different schedules of reinforcement. That the high and low rates of eye movement obtained during *mult* FR 6 DRL 5-sec schedules, and during isolated schedules of FR 6 and DRL 5-sec, were not caused by differences in stimulus and reinforcement parameters, was demonstrated by the absence of similar effects in a "semi-yoked" control animal given the same patterns of stimuli and deliveries of the reinforcing agent, but independent of its eye movements.

To judge from the overt behavior of the experimental subjects, the blue light was effective in lengthening interresponse times during DRL schedules, but its presence may not have been necessary for the development of that response pattern. Similarly, the white light which flashed on with each eye movement may not have been vital to the conditioning of eye movement under both the FR and DRL schedules. The white light was intended to provide the subjects with an exteroceptive stimulus additional to the proprioceptive stimuli generated by each eye-movement response. A similar technique was originally used by Hefferline (1958). Using visual feedback from a meter, subjects were trained to make a movement of the masseter muscle so small that, although detectable in the EMG, they were unable to report its occurrence. In a subsequent study (Hefferline, Keenan, and Harford, 1959) in which an invisible thumb twitch served, via the EMG, to postpone aversive noise stimulation, a group of subjects who were given visual feedback produced more reinforcements than those without feedback. However, in both studies, when the visual feedback was removed at a later time, the subjects were able to continue the effective performance with proprioceptive stimuli alone.

Operant techniques may have application to studies of eye movement and their role in the development of visual perception in addition to their value in investigations of eye movement during sleep. It has been shown that small, saccadic components of eye movements are necessary for the continuity and stability of visual perception (Pritchard, 1964). These saccadic movements are presumably respondent in nature. Held (1965) and Held and Hein (1963) demonstrated the importance of operant behavior of the peripheral skeletal apparatus under visual observation for the development of normal visuo-motor coordination. The development of visual perception itself probably involves operant learning. The oculomotor control necessary to bring peripherally projected retinal images to the fovea and maintain them there under stable fixation would seem to be a learned operation. Once the image has been brought to the fovea, the small saccadic, respondent eye movements become physiologically necessary for stability of perception (Pritchard, 1964). Thus, the ontogeny and adaptability of visual perception may involve operant learning of eye-movement control and integration of it within the efferent-afferent-reafferent system described by Held (1965).

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