and apparently tetrodotoxin did not entirely eliminate the transient response in this preparation. However, in the records of Fig. 1 the steady-state component declines rather rapidly during the stimulus interval—in fact rather more rapidly than is typical—and the amplitude of the steady-state component was measured at the end of the stimulus period. If the amplitude of the steady-state component had been measured earlier in the stimulus period, the lower curve would be displaced upward to approach the minimum value of the transient curve. The argument is not crucial, because in several preparations tetrodotoxin abolished the transient component altogether for a variety of stimulus conditions and response amplitudes. This particular preparation (Fig. 1) was selected because the effects of the drug could be established and reversed very quickly. The double arrow in Fig. 2 indicates a brief injection of tetrodotoxin as the sea water was continuously exchanged. The drug inhibited the transient component of the graded response, and its effects were completely reversed in less than 60 seconds from the time that the drug was injected into the flow system. Solution exchange alone required intervals of this order of magnitude, since at least 60 seconds was necessary to clear the flow system when a dye was injected through the capillary.

Tetrodotoxin has been used to dissect the graded visual response (*7*), and it acted characteristically in blocking impulses in optic nerve fibers. The data suggested that the drug acts specifically on the neural processes rather than by uncoupling the neural system from the graded response. Tetrodotoxin appeared to discriminate between graded and neural processes on a quantitative basis. If C was the minimum concentration required to eliminate neural impulses, approximately $100C$ was required to abolish the transient component of the graded response. In general, concentration C had no measurable effect on the graded response.

The dosage characteristics of the drug varied considerably. The variation correlated perfectly with the use of three different batches of crystalline tetrodotoxin (Sankyo Corporation). The most potent batch was studied most carefully, and the drug blocked the transient component of the graded response at concentrations of about 10^{-7} g/ml. The intermediate batch blocked the transient graded response at 10^{-5} g/ml. The third batch eliminated the neural response at concentrations of 10^{-5} g/ml, but it did not block the transient graded response at maximum practical concentrations of 5×10^{-5} g/ml. Perhaps the variation between batches could be explained by differences in potency of several closely related chemical derivatives of tetrodotoxin (*1*).

The receptor potential of the pacinian corpuscle gradually declines in magnitude when subjected to relatively high concentrations of tetrodotoxin for prolonged periods (*8*). Occasionally a decline in the magnitude of the steady state component of the visual response of the *Limulus* eye was observed after prolonged exposure to tetrodotoxin. When the tetrodotoxin solution was replaced with normal sea water, the steady-state component stabilized at the lower amplitude but the effect on the transient response was reversed. That is, the difference between the maximum response amplitude and steady-state amplitude returned to its original value. For example, in a curve similar to that of Fig. 2, the difference between the open circles and the solid circles would be the same before and after application of the drug, while the solid circles would be displaced downward in an irreversible fashion after exposure to the drug (*7*, fig. 5).

Although unusual in its sensitivity to tetrodotoxin, the graded transient response of the *Limulus* eye exhibits two other properties which seem to be somewhat unusual among sensory systems. First the transient response can reverse the resting potential level of the sensory cell (*9*). Secondly, while graded over much of its range, the transient component exhibits regenerative properties over a portion of this range under a set of well-defined conditions (*10*).

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Voluntary Control of Microsaccades during Maintained Monocular Fixation

Abstract. *A contact-lens technique was used to record eye movements made by two subjects instructed either to "fixate" stationary white-light targets or to "hold" their eyes in position in the presence of the same targets. A marked reduction in saccade rate, frequently reaching zero throughout 9.8-second trials, was observed under the "hold" instruction.*

Microsaccades (very small, high-velocity eye movements) occur once or twice each second while subjects maintain fixation of a stationary target. These movements are commonly described as "involuntary" because they are observed after experienced subjects have been instructed to "fixate." The instruction to "fixate" has been considered to be equivalent to an instruction to hold the eye *still* once the image of a fixation target has been brought to some preferred position on the retina (*1*).

Microsaccades may serve an important visual function. Cornsweet, for example, showed that they return the retinal image of the fixation target object to some "optimal locus" from which it has drifted during intersaccadic intervals (*2*). This "optimal locus" is assumed to be the center of best vision. It seems possible, then, that microsaccades are executed in order to produce the best visual detail in the target image; and, therefore, the conventional instruction, "fixate," may, in fact, be different from an explicit instruction to "hold" one's eye still in the presence of a visible fixation target. If a subject chooses to ignore detail in the fixation target under "hold" instructions, microsaccades should be eliminated or reduced appreciably.

Eye movements under "fixate" and "hold" instructions were recorded by a contact-lens technique incorporating features which permit simultaneous and independent recording of rotations about the horizontal and vertical axes in Listing's plane, uncontaminated by torsions of the eye or translations of the head. The recording and fixation systems have been described in detail elsewhere (3).

Two experienced subjects participated in the experiments: R.S., one of us; and A.S., a graduate student at the University of Maryland. Both subjects were emmetropic and had acuities of 20:20 with the contact lenses in place.

In the first experiment subjects were instructed either to "fixate" or "hold" their eyes in position throughout 9.8-second recording trials in the presence of a round homogeneous disk of white light (5.4 or 31.2 minutes of arc) whose luminance was 1.0 mlam. Trials under each instruction with each target size were alternated. The experimenter presented a target of the appropriate size before each trial. The subject began recording when he felt that he had complied with the instruction given.

The results of this experiment were striking. Both subjects made very few saccades under "hold" instructions. Table 1 gives mean saccade rates under the four conditions (4). R.S. reduced his saccade rate with the small target under "hold" instructions to one-fourth the rate observed under "fixate" instructions. A reduction of one-third was obtained with the larger target. Similarly, A.S. reduced his saccade rates markedly with both targets under the "hold" instruction. R.S. made no saccades whatsoever on 22 percent of his "hold" trials. A.S. also succeeded in totally inhibiting saccades occasionally, although such trials were less frequent (6 percent) (5).

In view of Cornsweet's results noted above, it is of interest to compare the stability of fixation on trials when saccades were very infrequent with trials when they occurred often. If saccades are largely responsible for maintaining the eye in a preferred position, the variability of eye position should be greater on trials when saccades are very infrequent. Five trials with R.S. under each instruction with each target size were chosen for this analysis. The median saccade-rate trial and the two trials just above and below the median-rate trial were selected from each condition and were used to estimate the bivariate dispersion of the eye about its mean position.

The mean bivariate dispersion area (averaged over both target sizes) for R.S. under "fixate" instructions was 64 (min arc)^2 and 66 (min arc)^2 under "hold" instructions. Such area measures can be converted to standard deviations on an average meridian, which renders them easier to compare with older eye-movement research in which rotations on a single meridian (usually the horizontal) were recorded. The standard deviation for R.S. was 2.98 minutes of arc under "fixate" instructions and 3.02 minutes of arc under "hold" instructions. Clearly, the variability of the eye about its mean position on "hold" trials when saccades were very infrequent was not appreciably greater than on "fixate" trials. R.S.'s saccade rates and bivariate dispersion areas agree well with measures obtained several years ago when the same subject fixated similar targets. His saccades on the ten "fixate" trials that were selected for measurement in this experiment were very similar in extent to those reported by other investigators. The mean saccade vector magnitude (averaged over 155 saccades counted with both target sizes under "fixate" instructions) was 8.18 minutes of arc.

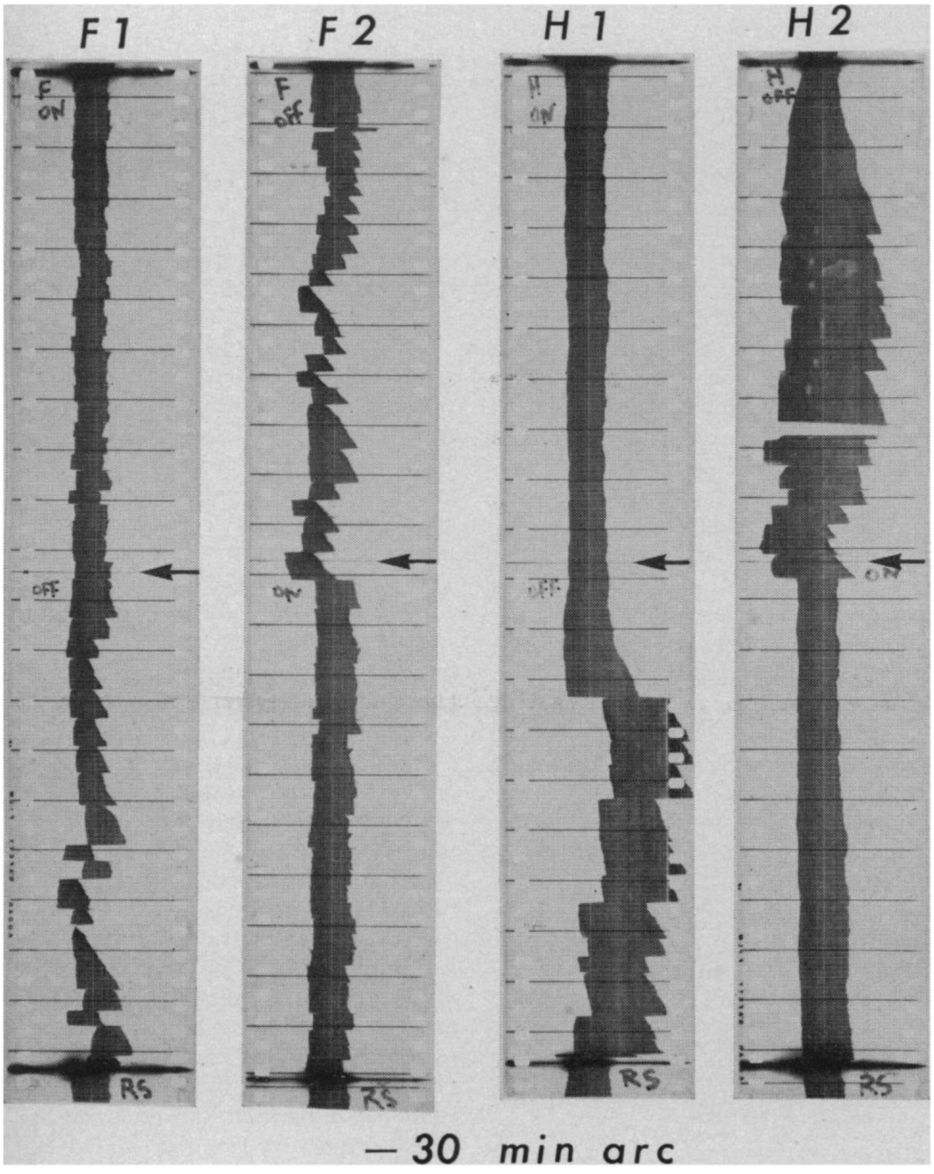

Fig. 1. Representative eye-movement recordings for subject R.S. when asked to either "fixate" or "hold" his eye for 21.3 seconds. The arrows point to a faint dark stripe on the film, signifying when a shutter either removed the target from view (*F1* and *H1*) until the end of the trial or allowed the target to come into view after 10 seconds (*F2* and *H2*). A 1-second time base is recorded as repetitive dark stripes across the film, and the recording trace was interrupted every 0.1 second (faint white lines). The position of the left edge of the trace is proportional to the position of the eye on the horizontal meridian, and the width of the trace is proportional to the position of the eye on the vertical meridian. The interruption in the recording trace in the 8tn second of *H2* occurred when the wedge of light drifted below the recording slit.

Table 1. Mean number of saccades per second (Rate) of subjects R.S. and A.S. viewing small (5.4 minutes of arc) and large (31.2 minutes of arc) targets under "fixate" and "hold" instructions. The standard deviations (S.D.) and number (N) of recording trials are given for each condition.

Instruction	Target	Rate	S.D.	N
	Subject: R.S.			
Fixate	Small	2.01	0.49	22
Fixate	Large	1.47	.70	25
Hold	Small	0.45	.50	20
Hold	Large	.50	.48	23
	Subject: A.S.			
Fixate	Small	1.40	0.34	48
Fixate	Large	0.86	.39	47
Hold	Small	.57	.26	49
Hold	Large	.33	.19	46

This mean saccade-vector magnitude is equivalent to a saccade whose extent on a single average meridian is 5.78 minutes of arc. The typical value for fixation microsaccades reported by other investigators is 5.6 minutes of arc, a value sufficiently similar to that observed in the present experiment to suggest that "normal" fixation patterns were produced by the instruction to "fixate."

A second experiment was performed to find out whether "fixate" and "hold" instructions could be maintained in the absence of a visible fixation target. Four kinds of trials were employed. Subjects were asked either to "fixate" or to "hold" for 21.3 seconds. On half of the trials under each instruction (*F2* and *H2*), the fixation target (5.4 minutes of arc at 1.0 mlam) visible during intertrial intervals was obscured by a shutter when the subject began recording. After 10 seconds the shutter opened and the target was visible for the remainder of the trial. On the other half of the trials (*F1* and *H1*) the target remained visible only for the first 10 seconds; the shutter then closed for the remainder of the trial. Both subjects served in this experiment; each recorded 36 trials, 9 under each condition.

Figure 1 shows representative recordings for R.S. Note in *F1* and *H1* typical "fixation" and "hold" performance in the first portion of the trial until the shutter removed the target from view. The second halves of the *F1* and *H1* trials show performance in the absence of any visible target object. Note that the variability of the eye about its mean position was considerably increased when the target was not visible (*6*). Also, even in the absence of a visible target, "hold" and "fixate" performances were different: there were more saccades when R.S. "fixated" an imaginary target than when he tried to "hold" his eye still in darkness. When the target disappeared at the onset of the trial and reappeared after 10 seconds (*F2* and *H2*), the results were virtually the same: a single large saccade corrected the position error noticed when the target reappeared and typical "fixation" and "holding" ensued.

These experiments suggest that microsaccades initiated during "fixation" may be under voluntary control. Subjects can inhibit them for prolonged periods when they are instructed to "hold" their eyes still. Furthermore, this inhibition of microsaccades does not, in itself, lead to increased variability of the eye about its mean position, which shows that there is an effective low-velocity corrective system for holding the eye in position on all meridians. Nachmias had previously shown that when a subject attempts to maintain fixation both saccades and drifts can contribute to position control of his eye. In his work, however, saccadic correction was most prominent; corrective drifts were observed on only a few meridians where saccadic correction was not effective (*7*). In the present experiments drift correction frequently takes over completely under "hold" instructions.

It is not known, at present, whether each microsaccade that is executed under "fixation" instructions is a voluntary act. We prefer at this time to assume that there is a microsaccadic system that is called into play when "fixation" is attempted. This assumption, however, is based exclusively on the very small size of these saccadic movements, and further experiments will be necessary to determine whether it is a system, rather than individual saccades, that is being called forth by an effort of the will.

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4. Three judges counted saccades. Agreement among judges was almost perfect. In those very rare instances where there was a disagreement, the count that went contrary to our hypothesis was accepted, that is, the lower value on "fixate" trials and the higher value on "hold" trials.
5. The differences in saccade rates were so large relative to the standard deviations that we felt formal statistical treatment was not necessary. The fact that saccade rates are lower with larger targets under fixation instructions has been reported previously (see Steinman *3*).
6. The increased variability in eye position found when a target is removed from view has been reported previously (see *2*, *3*, and *7*).
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Learning-Set Formation by Mink, Ferrets, Skunks, and Cats

Abstract. *The ability of mink, ferrets, skunks, and cats to learn to discriminate between objects was compared. Performance of mink and ferrets was similar to that reported for primates. This observation suggests that there is considerable overlap among mammals in ability to form learning sets.*

Interproblem learning, or the progressive improvement in learning consecutive, nonspatial, visual discrimination problems, is used to compare complex learning ability of mammals under laboratory conditions (*1*, *2*). While formation of learning sets has been observed in a variety of species, including rats, cats, and racoons (*3*), studies with primates (*2*, *4*, *5*) suggest that the latter are quantitatively superior to most carnivores in this type of learning. We investigated formation of learning sets in carnivores representing the mammalian mustelidae (weasel) family, a group whose complex learning abilities have not been systematically studied in the laboratory.

The subjects were seven mink and eight ferrets, skunks, and cats. Mink (*Mustela vision*), pearl variety, and ferrets (*Mustela furo*) were commercially developed strains. Skunk were *Mephitis* or striped variety. Animals ranged in age from 9 to 12 months. About half were males. Subjects were raised from infancy in laboratories and were fed canned cat