between 5 and 10 per second, but the spikes showed no grouping in synchrony with the flashes. In general, these cells responded with either eye, although usually not equally. In ten cases the response to binocular stimulation was stronger, and in ten cases weaker, than the stronger response to stimulation of the eyes individually. Weaker responses may have resulted from the slight divergence which occurs when muscle relaxants are used and the consequent noncorrespondence of stimulation in the two eyes.

Responses of some cells to stimulation of one eye by movement in any direction were also reduced when both eyes were stimulated. Three cells, stimulated by movement in any direction, gave a nonrhythmic response which was much stronger for binocular than for monocular stimulation. These binocular effects again suggest that the responses originated in cells within the cortex.

A circular field stop, movable within the limits of the larger field, was used to determine whether responses of the various cells were specific to any region. In general, the rhythmic responses of on- and off-cells were strongly localized, while nonrhythmic responses showed much less localization and continued when the 5° field was displaced as much as 15° or 20°.

Luminance thresholds for response to the moving-line pattern, obtained with the use of neutral density filters, were found to fall between 0.001 and 0.01 mlam for all types of cells. Three units (one "on," one "off," one directional) stopped responding at luminances of from 5 to 14 mlam and resumed when luminance was again reduced. One neuron began to respond at 0.001 mlam for movement of the stimulus pattern from left to right. Response to both directions began at 0.004 mlam. For all units there was little change in response strength with change in luminance over the range in which any response occurred.

The effect on response of width of lines in the stimulus pattern was studied at a luminance of 0.5 mlam. The diffusing screen was located behind the pattern in order to achieve a sharper definition of the stimulus. Patterns were available with widths of 1°26′, 1°, 36′, 22′, 11′, and 5.5′. In no case could response be related to stimulus movement with certainty for patterns narrower than 22′. Usually, directional neurons did not respond to patterns narrower than 1°. All "on" and "off" neurons responded clearly to movement of the 1° pattern, and most to the 36′ pattern also. One unit responded clearly to movements of the 1° pattern in both directions but only from left to right with the 36′ pattern. These results probably were not limited by temporal resolution of the eye because pattern speed varied around zero. They do not afford a good measure of spatial resolution because sharpness of the retinal image was not controlled, but they do provide additional qualitative evidence as to the nature of the coding of information in cortical cells.

In the cat, neural elements which are excited specifically and uniquely by stimulus motion are apparently not found peripheral to the cortex (see *5*). Motion specificity is accompanied by response to retinal stimulation over a wide region and an accompanying reduction in the fidelity of response to temporal variations in stimulation at specific locations. These results must stem from convergence of many retinal cells on single cortical cells, but they do not fit any simple scheme. Restriction of "movement" cells to the higher visual centers, in contrast to the situation found in the frog, pigeon, and rabbit, may have some relation to the binocular vision of the cat, a capacity which frogs, pigeons, and rabbits lack.

GÜNTER BAUMGARTNER*
JOHN LOTT BROWN
Department of Physiology,
School of Medicine,
University of Pennsylvania,
Philadelphia 19104

ARNOLD SCHULZ
Department of Clinical
Neurophysiology, University of
Freiburg, West Germany

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6. Preliminary experiments indicate that the responses of certain cortical cells are altered qualitatively by general anesthesia. For this reason animals were maintained on a long acting local anesthesia, Depot-Novanaest in oily solution, which was injected subcutaneously and intramuscularly all around the head and at the point of exit of medial and lateral branches of the trigeminal nerve on both sides. We have found this drug to afford complete anesthesia of from 12 to 24 hours when used with human patients. Additional descriptions of the preparation are presented elsewhere: G. Baumgartner and P. Hakas, *Pflügers Arch.* **274**, 489 (1962); G. Baumgartner, J. L. Brown, A. Schulz, *J. Neurophysiol.*, in press.
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* Permanent address: Department of Clinical Neurophysiology, University of Freiburg, West Germany.

5 October 1964

Separation of the Salivary and Motor Responses in Instrumental Conditioning

Abstract. *If an instrumental conditioning schedule is arranged so that a dog must repeatedly perform a movement in response to one stimulus in order to secure the presentation of another stimulus, which is then followed by food, a virtually total separation of motor and salivary responses is observed. The first stimulus elicits the trained movement without salivation, and the second stimulus elicits salivation without instrumental responding. These experiments show a relative independence between classical and instrumental conditioned responses and clarify the rather complex relations between the two in the usual experimental procedure.*

In early papers by Konorski and Miller (*1*) a method was described for studying the relations between the salivary and the motor responses in instrumental conditioning. According to the views then held by these authors, the instrumental response produced its proprioceptive feedback which became a classical conditioned stimulus signaling the presentation of food. In consequence it was predicted that salivation should closely follow the instrumental response.

However, their own experimental data (*2*), as well as those of later workers (*3*), showed that although in many cases the predicted relation is in fact observed, in others large discrepancies exist between the two responses: the motor response may be either preceded by the salivary response, or the two responses may not even coincide at all. The origins of these discrepancies have been poorly understood, and the causal relation between the salivary and instrumental responses has remained obscure. The experiments reported here were designed to clarify this situation.

The subjects were four mongrel dogs trained in the following manner: first a classical conditioned response (for

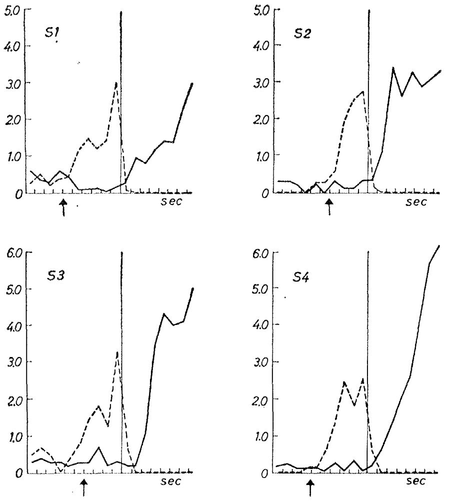

Fig. 1. Mean rate of lever-pressing (dashed line, presses per second) and salivation (continuous line, drops per second) during a typical session (about 15 trials) late in the training of each dog. The vertical line represents the onset of the classical CS, and the curves end at the time of reinforcement. The arrows indicate the median time (in seconds) of onset of the instrumental CS.

food) was established to a stimulus (hereafter called the classical CS), with a 1-second interval between the conditioned stimulus and the unconditioned stimulus (US). Then the animals were trained to perform an instrumental movement: pressing with the right forepaw a lever situated in front of and well to the right of the feeder, this response being reinforced with presentation of the classical CS and then food. When this task was mastered a second stimulus, the instrumental CS, was introduced, and subsequently only those instrumental movements performed in the presence of it were followed by the classical CS and then food. During subsequent training, both the instrumental CS and the classical CS were gradually prolonged until nine lever-presses occurred in the presence of the instrumental CS and the CS-US interval for the classical CS was 8 seconds. The instrumental CS was turned off immediately after the ninth press, and at the same moment the classical CS was turned on. Thus, the schedule involved two segments: the first segment required working for the second segment, and the second segment required only waiting for food.

The food reinforcement was a small portion of cooked meat and broth-soaked bread presented automatically. Recordings of salivation, begun only after the animals were well-trained, were obtained in the manner described by Sheffield (*4*), a cannula of polyethylene tubing being permanently implanted in the parotid gland. For three of the dogs, a light was used as the instrumental CS and a buzzer as the classical CS; for the fourth dog this arrangement was reversed.

Throughout the training the following behavior was observed in all dogs. The instrumental CS evoked a motor excitement of the animal, and this was accompanied by vigorous instrumental movements. Immediately after the instrumental CS was turned off and the classical CS was presented, the dog calmed down and waited for food, staring intently at the food bowl. The instrumental response was not performed in the presence of the classical CS (except, of course, occasionally immediately after the onset of the classical CS), although no precautions were taken to discourage the animal from such response.

The results with salivation were quite different. On most trials, there was either no salivary response to the instrumental CS or nearly none, although there was regularly a large salivary conditioned response to the classical CS. Often when the animal was salivating slightly during the intertrial interval, he would stop doing so upon the onset of the instrumental CS and lever-pressing. A reciprocal relation between salivation and the instrumental response was also observed in two dogs during the operation of the instrumental CS. These two animals would occasionally stop pressing the lever sometime during the instrumental CS, look toward the feeder and salivate, and then stop salivating when they finally returned to complete the ratio of presses. The typical relations between salivary and motor responses in each dog are presented in Fig. 1.

When these experiments had been completed, additional training was given to two of the dogs with the classical CS omitted and food presented immediately after the ninth press of the lever. Although substantial training was required, it was eventually possible to reach a state where salivation and instrumental responding were concomitant, as has been found in other studies in which there has been immediate reinforcement of the instrumental CR (*3*).

We have evidently found a method of complete, or nearly complete, separation of the motor and salivary responses in instrumental conditioning. This separation takes place when an instrumental response elicited by a given stimulus is a prerequisite for the presentation of a well-established classical CS, and when there is no close contiguity between the instrumental response and the place of feeding.

If we accept the well-documented thesis that instrumental responding for food reflects the presence of the hunger drive, the immediate conclusion to be drawn from our experiments is that conditioned salivation does not constitute a primary effect of that drive. This fact has not been previously observed because the instrumental response has always been experimentally intermixed with a classical CR elicited by the feedback from an immediately reinforced movement and by CS itself. Since in our experiments neither the instrumental CS nor the trained movement were followed immediately by food, the pure character of the instrumental CR could be revealed.

If instrumental responding and conditioned salivation reflected the same process, recording only one of these two responses would yield the same information as recording both. The present result, in showing a clear difference between the two responses and perhaps the rules governing them, emphasizes the necessity of studying both of them concomitantly in order to obtain a better understanding of learning processes.

GAYLORD D. ELLISON*
J. KONORSKI

Department of Neurophysiology,
Nencki Institute of Experimental
Biology, Warsaw, Poland

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* Present address: Department of Psychiatry, Yale University, New Haven, Conn.

8 September 1964