Fundamentals of Sensory Physiology

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Preface

In the field of sensory physiology we are concerned with what our sense organs – and the associated central nervous structures – can do and how that performance is achieved. Research here is not limited to description of the physicochemical reactions taking place in these structures; the conditions under which sensations and perceptions arise and the rules that govern them are also of fundamental interest. Sensory physiology thus demands the attention of everyone who wishes to – or must – delve into the potentialities and limitations of human experience.

Our aim has been to guide the student with minimal prior training in biology and the other natural sciences into the realm of sensory physiology. Where other areas of neurophysiology are involved, reference is made to the companion volume produced by the same publisher, ***Fundamentals of Neurophysiology*** (2nd edition in English, 1978); the two together present an integrated introduction to the fascinating world of the neurosciences, with emphasis on its neurophysiologic and sensory physiologic aspects.

This first edition in English was translated from the third edition in German, which appeared in 1977. The two earlier editions in German, published in 1973 and 1976, were particularly well received by students of physiology, medicine, biology, and psychology. In preparing the third edition, we have carefully revised the text, expanded it in some places, and provided new illustrations throughout thanks to the help of Mr. WOLF-RÜDIGER GAY and Mrs. BARBARA GAY of Stuttgart, Germany. The book has thus been both brought up to date and made more readable. On behalf of all the authors, I express sincere thanks for the help and support that has been extended to us from all sides, especially by our secretarial co-workers.

Regarding this edition in English, I owe many thanks to Dr. MARGUERITE BIEDERMAN-THORSON of Oxford, England, for her excellent translation. Finally, I am most grateful to the publishers, Springer-Verlag, and their staff for their close collaboration and for the care they have taken in preparing the book.

Kiel, Germany, June 1978 ROBERT F. SCHMIDT

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1. General Sensory Physiology, Psychophysics

J. Dudel

As an introduction to the particular aspects of sensory physiology treated in this book, we shall consider the subject of "general sensory physiology" – the principles underlying all sensory perceptions. Such generalization is both possible and useful, not least because the different sense organs very much resemble one another, both in their organization and operation and in their connections to the central nervous system (CNS). On the other hand, in studying human sensory perception one encounters the ***problem of subjectivity.*** That is, environmental stimuli and the respective responses of our sense organs correspond to statements by the subject about his sensations and perceptions. Even muscle physiology, for example, has a subjective, "psychological" side. The subject identifies himself with certain movements of his limbs; he "wills" them or "expresses himself" with them. But by comparison, the high-level mental aspects of sensory physiology appear far richer and more fascinating. We experience our sensations as highly personal events, on which our moods depend; in surroundings from which sensory stimuli have been excluded – in a state of "sensory deprivation" – we become mentally unstable and ill. A human being, then, is "nothing other than the sum of his experiences" (D. Hume). Indeed, certain philosophical schools have been so impressed by the strong subjective component in all sensory experience as to maintain that only the subject exists – that the "environment" is a product of the mind. The general ***psychophysical problem***, which so forcibly confronts us in sensory physiology, cannot be solved by the natural scientist, at least not yet. Psychophysical questions arise in very similar forms for all sense organs. Therefore a chapter on general sensory physiology should provide, along with a discussion of the basic organic mechanisms underlying sense-organ function, an introduction to the difficult questions of subjective sensory experience.

1.1. Basic Concepts in General Sensory Physiology

Sense organs. We experience our environment and the events taking place within our bodies not directly, and not in their entirety, but rather by way of specialized ***sense organs***. The best known of these organs are the eye, the ear, the skin as an organ of touch, the tongue as an organ of taste, and the nose as an organ of smell. Each such organ is so constructed that it responds to a particular range of environmental influences and passes on corresponding information to the CNS.

The ranges of stimuli to which the sense organs are specialized can be explained in phylogenetic terms. Only those environmental events are detected that were ***relevant to survival in the environment*** of the primates from which we are descended. Consider, for instance, the electromagnetic waves striking the surface of the body. We experience no sensation of γ rays, X rays, or ultraviolet light. We can see, with our eyes, only light of wavelengths between 350 and 800 nm, to which the earth's atmosphere is relatively transparent. By contrast, we do not see infrared light; bur we do sense long-wave heat rays by way of the heat sensors in the skin. Over the entire spectrum, radio waves elicit no sensations in humans. But other animals have adapted to habitats very different from ours by evolving other sense organs. For example, certain fish that live in very turbid water have a sense organ extremely sensitive to changes in electric field strength. With these they detect alterations in the electric field associated with pulses of current they themselves discharge. This information is used in orientation; the mechanism is like that of an echo-sounder or a radar installation.

Modality, quality, specific sensory stimuli. Each sense organ mediates sensory impressions that can vary in intensity but resemble one another in quality. A group of similar sensory impressions mediated by a particular organ is called a sense or, in a technically more precise term, a ***modality***. Such modalities include the classic "five senses": sight, hearing, touch, taste, and smell. But it is easy to list other modalities. The skin itself senses not only pressure and touch, but also cold and warmth, vibration and pain. In addition to these modalities, comprising sensory impressions arising from the ***external environment*** and acting at the surface of the body, there are others mediated by sense organs within the body which reflect ***its own state***. Examples of these are the sense of equilibrium and our knowledge of the relative positions of our limbs or the load on our muscles. Moreover, there are modalities associated with information about the state of our bodies of which we are not, or are only indirectly, aware. These include, among others, the osmotic pressure of the blood (thirst) or the blood's CO_2 tension (shortness of breath), as well as the amount of stretching of lungs and stomach. The definition of "modality" also holds for these interoceptive "senses." In each case they comprise a group of sensory impressions that resemble one another and are mediated by a particular kind of sense organ. The number of modalities, then, is far greater than five.

Within each individual modality, it is usually possible to draw further distinctions with regard to the kind of sensory impression, the ***quality***. For example, the modality "vision" can be subdivided into the qualities lightness (position on the gray scale), red, green, and blue. Corresponding qualities in the sense of hearing are the different pitches of tones; the qualities of taste are sweet, sour, salty, and bitter.

A sensory impression of a certain quality is elicited when the appropriate environmental factors influence the sense organ. The quality "sour" is sensed when acids contact the tongue. The factors that elicit sensory impressions of a certain quality are called ***specific sensory stimuli,*** or simply ***stimuli.*** The stimulus acquires its quality by virtue of the reaction with the stimulus-detecting cells of the sense organs, the ***receptors***. These cells are adapted to respond as strongly and specifically as possible to stimuli of their particular quality, both because of their positions and because of the presence of specialized cell organelles. The sense organs are located at sites exposed to their specific stimuli – the taste receptors on the tongue, and the light receptors in the retina of the eye, in the focal plane of a lens. The different kinds of receptor have special properties that guarantee the greatest possible effect of the specific stimulus quality. Again, take the visual cells of the retina as examples. Each contains a pigment that absorbs light of "its" particular quality. The details of this specialization of receptors for specific qualities are described in the next chapter. In general, the specific stimuli produce potential changes in the receptor cells, the receptor potentials (see Fig. 1-1); these in turn generate action potentials (cf. ***Fundamentals of Neurophysiology***, Sec. 2.4) that are conducted to the centers via afferent nerve fibers. These action potentials are the same for all sensory qualities. The quality of the information they contain is determined entirely by the receptor type from which the relevant nerve fiber arises. Even when such receptors are stimulated by a strong "unspecific stimulus" it is interpreted as specific: when struck on the eye we see light – "stars." As long ago as the last century Johannes Müller formulated the "law of specific nerve energies" to describe this phenomenon.

Quantity, threshold. Whereas the kind of sensory impression is given by its modality and quality, its intensity can be termed ***quantity***. The quantity of a sensory impression corresponds to the strength of the stimulus. Figure 1-1 shows the general nature of the response of a receptor to stimuli of increasing intensity. The receptor potential becomes larger, and the frequency of the triggered action potentials increases. Figure 1-1B shows the relationship between stimulus intensity and the response elicited from a receptor. Such relations can be determined at various levels of the nervous system, as well as for subjective impressions and perceptions. The point of origin of the intensity/response curve is always an important characteristic; this is the smallest stimulus that just produces a response, the ***threshold stimulus*** S_0. In the case of the receptor cell, this may be determined as the smallest stimulus that just elicits an action potential (Fig. 1-1); it can also be measured, for example, in the auditory organ as the lowest intensity of a tone that is just perceived by a subject. The form of the intensity/response curve is characteristic of different receptors as well as of different sensory impressions; this aspect of the relationship will be discussed further in later sections.

We have now become acquainted with a number of the basic concepts of sensory physiology: modality, quality, quantity, and threshold. Figure 1-2 illustrates the correspondence between these concepts and their organic substrate, again using the example of the organ of sight.

Sensory impressions are characterized not only by modality, quality, and quantity; they also have the property of occurring at a ***particular time and place***

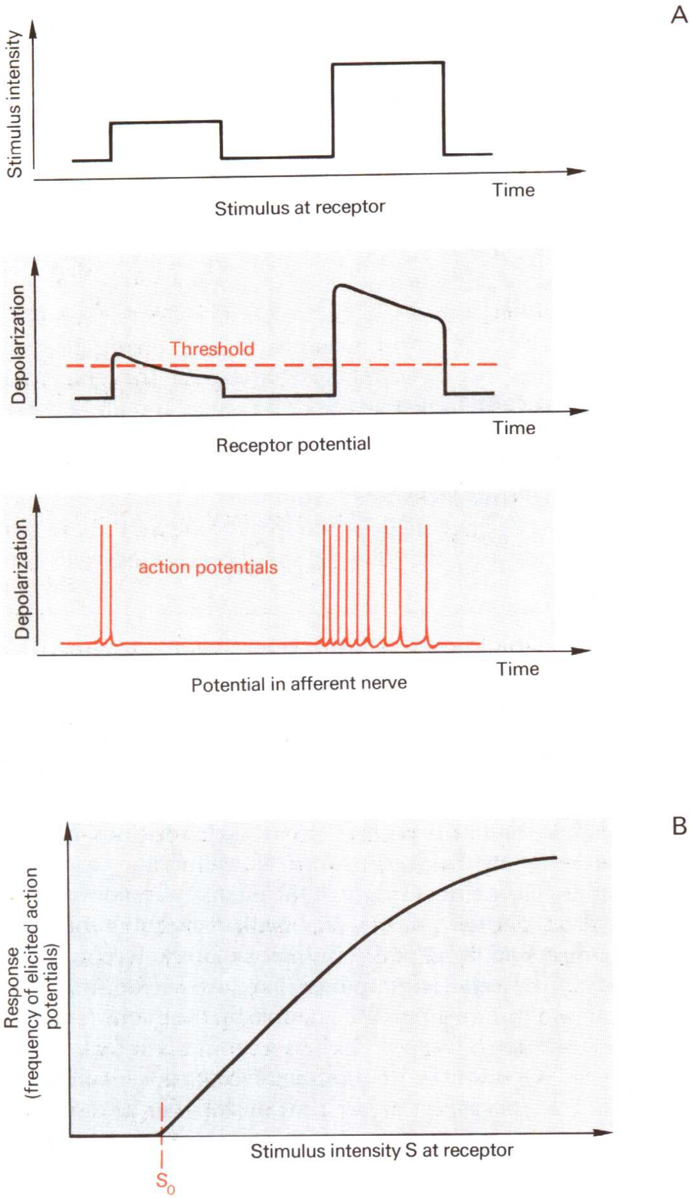

Fig. 1-1. (A) and (B). Relationships between stimulus intensity and frequency of action potentials. (A) Time course of the receptor potentials and action potentials elicited by two stimuli of different intensity. (B) Dependence of the frequency F of action potentials in a receptor upon stimulus strength S. S_0 indicates the absolute threshold intensity of the stimulus

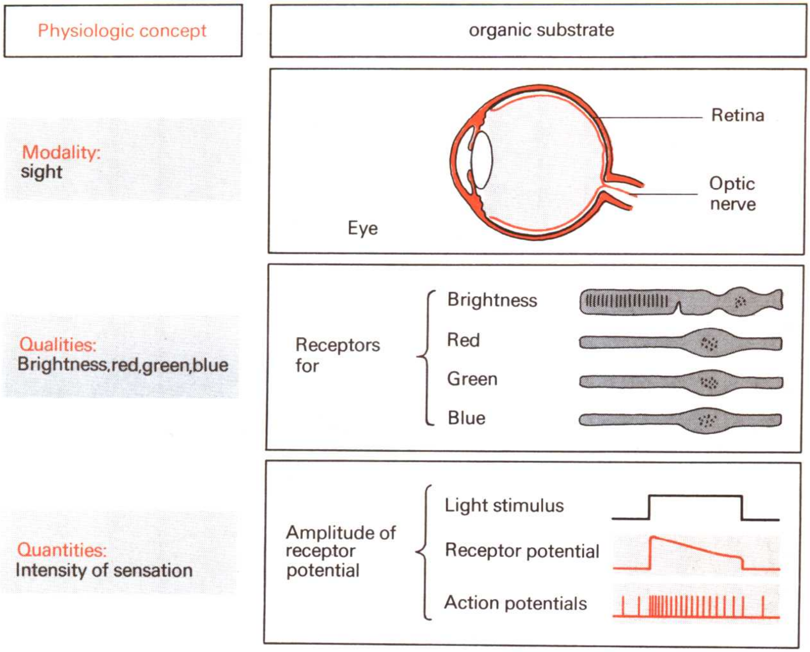

Fig. 1-2. Modality, quantity, quality, and their organic substrates; here the organ of vision is taken as an example

in the environment or in the body. Our eyes do not simply see light, but rather "pictures" of the space surrounding us. These pictures succeed one another in time, and they can also be recalled as having been associated with a particular point in time. The spatial and temporal aspects of sensory perceptions naturally correspond to the spatial and temporal properties of the stimuli.

Sensory impression, perception. The term ***sensory impression,*** which we have been using casually thus far, must now be explained more precisely. It is used to designate the simplest units, the elements of sensory experience. For instance, the perceived color "blue" and the taste "sweet" would be sensory impressions. It rarely happens that we receive such impressions in isolation; a combination of such sensory impressions is called a sensation. As a rule the pure sensation is accompanied by an interpretation, with reference to what has been experienced and learned, and the result is called ***perception.*** We express a perception when we say, "There is a chair".

Mapping between phenomenon and perception; objective and subjective sensory physiology. The chain of correspondences between the phenomena of the environment and their perception, indicated in the last paragraphs, is summarized in Figure 1-3. The boxes enclose basic phenomena of sensory

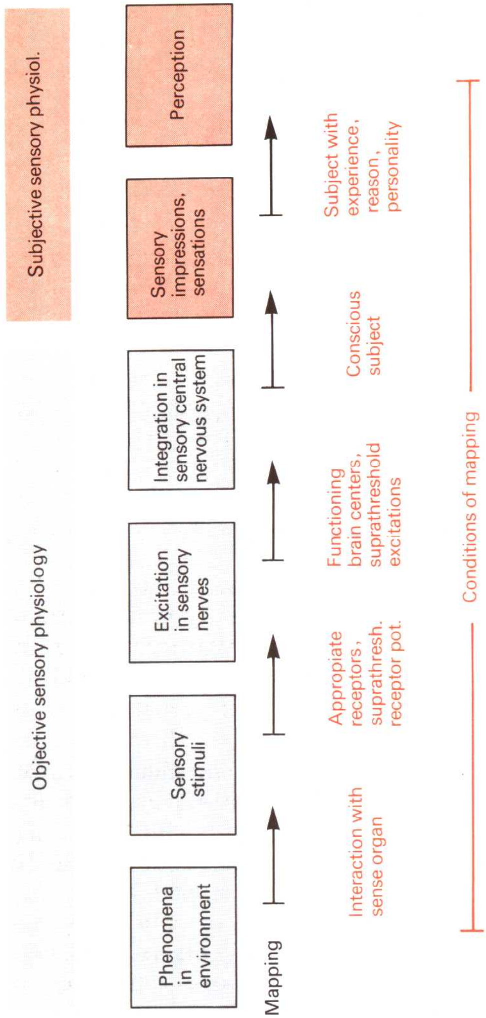

Fig. 1-3. Mapping in sensory physiology. The words in the boxes denote basic phenomena of sensory physiology, and the ***arrows*** between them indicate the "mapping." Below the basic phenomena, the conditions for mapping are shown

physiology at successive levels; they are joined by arrows which indicate correspondence, not causality. The arrows stand for a relation that is called "mapping." That is, the excitation in a nerve can be regarded as a mapping of a sensory stimulus, and perception as a mapping of sensory impressions. The concept "mapping" denotes that there is a defined and unique representation by which points on an object are associated with (or "mapped onto") points on another, or more generally in mathematical terms, a unique association between members of two sets ($x \varepsilon A \mapsto y \varepsilon B$). The object itself is not the cause of its representation; the mapping may occur by means of a suitable device, for example, an aerial camera which projects an image of the object onto photographic paper. The mapping therefore is not only characterized by the object, but also by the special mapping conditions, the surveyor's instruments, the scale, the kind of projection, or the symbols of representation for specific details.

Thus under the boxes that denote the different levels in Figure 1-3 are listed the conditions that hold for mapping in each case. Environmental phenomena (at the ***left*** in Fig. 1-3) are sensory stimuli only if they interact with a suitable sense organ. Similarly, Figure 1-3 indicates that the excitation sent from a sense organ to the CNS and processed there becomes a sensory impression or sensation only if the CNS is associated with a subject capable of consciousness. The mapping relationships indicated by the arrows in Figure 1-3, from environmental phenomena to the integrative processes in the sensory CNS, can in principle be described as physical and chemical processes in the structures of the body. This realm of sensory physiology is therefore called ***objective sensory physiology.*** By contrast, the mapping between these objective phenomena – a sensory stimulus and the subsequent responses of the nervous system – and a conscious sensation cannot be described in terms of physical and chemical processes. The realm of sensations and perceptions, as it is related to sensory stimuli, is therefore termed ***subjective sensory physiology.***

The proposition that subjective sensations and perceptions are not accessible to description in physicochemical terms must be qualified. From the point of view of the natural sciences, such an assertion is simply a statement of the present state of knowledge. The natural scientist will attempt to apply his methods to subjective phenomena as well, and there are impressive examples of success, as the discussion of ***psychophysics*** in Sections 1.3 and 1.4 shows. However, many professionals in other academic areas think that the response of the subject, the realm of the psyche, is fundamentally inexplicable in the framework of the natural sciences.

Sensory physiology, then, is divided into two parts: the description of the responses of the nervous system to a stimulus – objective sensory physiology, and analysis of the statements the subject makes about his sensations and perceptions – subjective sensory physiology. The terms ***objective*** and ***subjective*** in this context ought ***by no means to be taken as value judgments*** with regard to the correctness of a statement. The sentence "red is a warm color" can be just as "correct" as the sentence "the frequency of discharge in the sensory nerve fiber rises with the intensity of a sensory stimulus." As biologists, and especially as scientists who study humans, we must treat subjective statements about sensations and perceptions in just as unprejudiced a way as we do recordings of cell potentials. Section 1.3 will show that it is possible to make very precise statements, using the appropriate terms, about the objects of subjective sensory physiology; quantitative mathematical relationships can be established in this field as well. Even though the relation between stimulus and sensation can only be described by the term "mapping", and the qualitative distinction between physical stimulus and subjective sensory impression seems unbridgeable, the study of sensory physiology can employ the ***methods of behavioral physiology,*** briefly treated in the next section, to serve a certain ***mediatory function*** between physics and subjectivity.

By answering the following questions (designated by "Q" here and throughout the book) you can test your knowledge of the subject matter of the section. In deciding upon your answer, you should wherever possible not refer back to the text. Jot down your answers on a sheet of paper and then compare them with the Answer Key beginning on p. 257.

Q 1.1. A group of sensory impressions that resemble one another and are mediated by a particular sense organ is called .... When sensory impressions of different kinds can be distinguished within a modality, they are termed ....

Q 1.2. Identify the words in the following list that designate modalities with M, those that designate qualities with Q, and those that represent quantities with I.

a) Hearing ( )
b) Intensity of sound ( )
c) Red ( )
d) Taste ( )
e) Stretching of the lungs ( )
f) Sour ( )
g) Pitch ( )
h) Intensity of the color red ( )
i) Cutaneous cold sense ( )

Q 1.3. Choose the term that best describes the relationship between a sensory stimulus and the sensation:

a) Cause and effect
b) Objectivity
c) Mapping
d) Increase in specificity
e) Quality

1.2. Relation Between Stimulus and Behavior; Conditioned Reflex

The central nervous reactions elicited by a sensory stimulus may lead to responses of the whole organism, which may be directed outward or inward. If one hears an unexpected noise on one side, one turns the head in that direction; a deer in the woods behaves in just the same way. When monkeys in a zoo see their keeper at feeding time, they become restless and noisy. The appearance of some obstruction when we are driving causes us not only to brake and swerve aside; muscle tonus is also increased, and the heart beats faster. In all these examples, specific sensory stimuli have given rise to more or less complex changes in the activity of the animal or man. Such activities, usually ***interpretable as goal-directed,*** are in general termed ***behavior***. Changes in behavior resulting from a sensory stimulus can be described by an observer, and they can also be recorded by appropriate measuring devices. We regard such behavioral changes as explicable, in principle, by the responses of the animal's nervous system to the stimulus, even though we may not yet understand these responses in detail. Studies of behavior from the point of view of sensory physiology are thus a part of objective sensory physiology. Certain basic concepts and methods in this area, an area also in the domain of animal psychology and the psychology of learning, will be surveyed here.

Stimulus, behavior, reflex. If the hindpaw of a cat is stimulated painfully (for example, by pinching), it will pull the paw away by bending the joints of the leg. This behavior of the cat is called the flexor reflex in neurophysiology (cf. ***Fundamentals of Neurophysiology,*** p. 168). Part of an animal's behavior, then, consists of stereotyped reactions to certain stimuli, the ***reflexes*** (***Fundamentals of Neurophysiology,*** p. 106). Among the reflexes some (for instance, the flexor reflex) are ***innate*** or ***unconditioned,*** being based on fixed neuronal connections between receptors and effectors. But in the context of sensory physiology, the ***acquired reflexes*** are of particular interest. In these reflexes, the functional connection between receptors and effectors is formed by ***learning processes***. The animal learns to respond regularly to a certain stimulus with a certain activity. Such reflexes are also called ***conditioned***, because they are found only under the condition of previous learning. An example is the "automatic" braking by an automobile driver confronted with an obstacle.

Conditioning. The acquisition of conditioned reflexes by many animals can easily be examined in the laboratory. The first procedure for doing this was developed by PAVLOV, and is called the ***classic conditioning procedure***. In this method an unconditioned reflex is first triggered – for example, a dog is offered food, and the flow of saliva is thereby excited. Then the stimulus for the unconditioned reflex (the presentation of food in this example) is repeatedly accompanied by an arbitrarily selected second stimulus; for example, a bell may be rung at the same time the food appears. If this combination is repeated frequently, the dog will eventually respond by salivating when the ringing of the bell occurs by itself; at that stage, a ***conditioned reflex*** has been formed. That is, in the classic conditioning procedure the association between the adequate stimulus for an unconditioned reflex and an arbitrarily chosen test stimulus makes the latter a stimulus for a conditioned reflex.

This method of classic conditioning has the disadvantage that the experimental animal acquires the conditioned reflex passively by association. Conditioned reflexes can more easily be developed by the process of ***operant conditioning.*** In operant conditioning the desired response to a stimulus (i.e., the conditioned reflex that is the goal of the training) is rewarded – for instance, by a small amount of food. The reward ***reinforces*** the behavior, and the animal quickly learns to respond to the test stimulus with the correct conditioned reflex. The procedure of operant conditioning resembles that in other types of training, in which suitable rewards (or punishments) are used in connection with certain patterns of behavior. But ***in contrast to the training*** of horses or dogs, in operant conditioning the role of a human "trainer" is eliminated as far as possible. Conditioning is done by apparatus that automatically gives the stimulus, records the response, and presents the reward in accordance with the set criteria. A well-known example of such an apparatus was developed by Skinner and is called the "Skinner box"; this can be used to condition various kinds of small animals (Fig. 1-4). It consists of a cage for the experimental animal, with a stimulus display on the front wall. In the example shown this is a light. On the same wall a lever is mounted, and the animal is supposed to learn to press this lever when the stimulus is presented. A further attachment to this wall, in the cage of Figure 1-4, is a food container. An automatic device places a portion of food into the container as a reward, whenever the correct response, pressing on the lever, follows the selected stimulus.

Another element of the Skinner box in Figure 1-4 is a recording instrument that keeps track of the rate of correct responses to the test stimuli given repeatedly in a program over a certain time. From the record one can see how

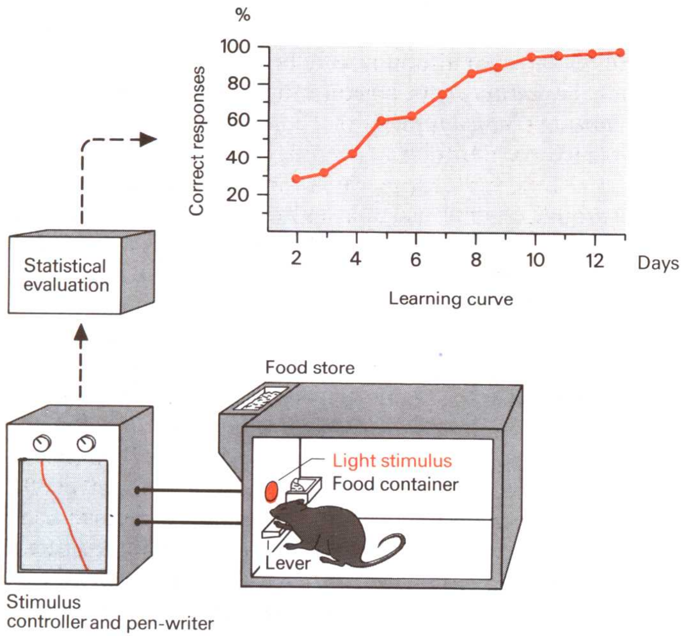

Fig. 1-4. Operant conditioning in a Skinner box. The experimental animal can respond to a stimulus presented via the controlling apparatus by pushing the lever, and is then automatically rewarded with food. The stimuli and their consequences are recorded on the pen-writer. Above the Skinner box is a learning curve derived from such records, with days since the start of conditioning on the abscissa and the percentage of correct responses to the test stimulus on the ordinate

rapidly and to what extent the conditioned reflex has been learned; the ***learning curve*** from such an experiment is shown at the top of the figure. On every day of the experiment (abscissa) the test stimulus was given 100 times, and the percentage of correct responses (ordinate) was recorded. The diagram shows that the curve rises during the first days, then flattens out and after about 10 days reaches a plateau of nearly 100% correct responses.

An advantage of devices like the Skinner box is that large numbers of them can be set up in parallel and that the experimental program – the test stimuli and the criteria for the correct response – for such an array can be automatically controlled. Today such experiments are usually controlled by computers, which also perform the statistical evaluation of the results. The test stimuli used in such programs can be varied over a wide range, which is particularly important in the experiments in sensory physiology that will now be discussed. The procedure of ***operant conditioning*** of reflexes, however, has also been used very successfully in ***other fields.*** Experimental psychologists study learning behavior, pharmacologists determine the effects of drugs on learning and on the performance of the conditioned reflexes, biochemists block enzyme systems, and neurophysiologists measure changes in the pattern of neural discharge during the learning process.

Measurement of dark adaptation by operant conditioning. As an example of the relation between behavior and sensory stimulus, we shall now consider in detail the way the method of operant conditioning can be used to determine the increase in sensitivity of the visual sense of a pigeon as it adjusts to darkness – the process of ***dark adaptation***. As you know from personal experience, we see "nothing" when we suddenly move from bright sunlight into a dimly lit room. But once we have spent some time in the room, we can gradually detect more and more objects in our surroundings; the sensitivity of our vision increases. We have ***adapted*** to the lower light level (for further discussion see Sec. 1.4). The experiment to be described now is designed to determine whether a similar dark-adaptation process occurs in the pigeon.

Before the experiment itself is begun, two conditioned reflexes are established: The pigeon pecks key A (in the arrangement of Fig. 1-5A) when it sees a stimulus light, and key B when it sees no stimulus light. Control of the stimuli in the apparatus is set up in such a way that closing of a contact by depression of key A reduces the intensity of the stimulus light somewhat, while closing of the contact at key B has the reverse effect. Now, when the stimulus light shines brightly at the beginning of the experiment the pigeon will peck key A, and it continues to do so until the intensity of the light becomes so low that it is no longer visible to the bird. When the pigeon sees no stimulus light, according to its previous training, it will peck key B. The stimulus-controlling arrangement then increases the light intensity, and key B will be pecked until the pigeon again sees the stimulus light. Operating both keys in this way, the pigeon will set the light at an intensity that fluctuates about the threshold intensity. Figure 1-5A, then, shows a method for the ***measurement of the absolute visual threshold*** of the pigeon, by means of two quite complex learned behavior patterns.