of phosphate to the host tissue is no greater in mycorrhizal than non-mycorrhizal roots.

Two mechanisms have been studied by which the ions trapped by the mycorrhizal sheath of fungus can be made available to the host. First, it has been shown by direct observation and photographic record that beech mycorrhizas have a life-period of about eight months only. Hence there is a periodic release of mineral-rich organic matter into the actual rooting region of the host. Secondly, there is in the tissues a metabolic turnover of phosphate, sensitive to oxygen and temperature, the net result of which is the movement of phosphate from fungus to host during periods when the rate of uptake is low. Hence, during periods of rapid release of minerals from newly fallen litter, nutrients may be trapped and accumulated in the fungal layer of mycorrhizal roots and, in the subsequent periods of slower mineral release, phosphate and perhaps other minerals are passed to the host. Laboratory physiological experiments, therefore, are providing a credible picture of the functioning of mycorrhizas in ecological conditions.

Dr. L. Leyton, of the Oxford Forestry Department, described detailed work on mineral nutrition of conifers which has been carried out in the same areas as that described by Dr. Dimbleby. His description of the soil profiles of sitka spruce forest in Yorkshire was exactly comparable with that of previous speakers, and his analysis of mor and mull again emphasized the deficiencies of available soil nutrients, especially of nitrogen. Significant increases of growth were obtained by the application of nitrogenous manures, and little increase was obtained with phosphate. Dr. Leyton described the technique of analysis of foliage to determine the nutrient status and mineral deficiencies of the site. On untreated soils, needle weight and nitrogen content are positively correlated, and the effects of the use of nitrogen fertilizers, removal of heather and mulching owe their efficacy in promotion of growth to increase of available nitrogen. Application of phosphate only affords a secondary stimulation.

The humus layer contains as much as 2 per cent of dry weight as nitrogen, so reasons were sought as to why this is not made available. Calcium deficiency is very marked, and it is possible that microbiological activity is limited by this factor. On the other hand, the soils in question are often water-logged in winter and dried out in summer. This adverse water régime may be counteracted by mulching, which results in a rapid increase of microbiological activity in the rooting layer.

The method of needle analysis has proved very valuable in this study, for it can be used to predict as well as to follow the effects of soil treatments on trees of any size. In all cases where treatments improve growth, an immediate response in needle colour and weight preceeds increased growth. The needles of the following year's crop are laid down in the buds of the current year, so that although immediate growth response to treatment is not observable, the constitution of the needles provides a satisfactory basis of prediction of growth in the future.

With these set papers as a background, the whole subject was discussed. Prof. Romell pointed out that the effects of liming are complicated because of the stimulation of white rot fungi above *p*H 4·5, and the lack of effect of lime treatments mentioned by Mr. Laurie and others might be explained by the trapping of nutrients by them. He asked about the stimulation of turnover in mor by hardwood litter, and Dr. Dimbleby and Mr. Murphy stated that it can occur and is associated with increase of faunal activity. Dr. Dimbleby spoke strongly in favour of developing stands of mixed tree species, but Mr. Hiley emphasized that adequate thinning of conifers would encourage ground flora, the detritus of which would have the required effect of reversing the tendency to formation of mor. He also described how mor develops under old oak stands and how felling of such stands and replanting with conifers may give rise to mull with an *Oxalis* and *Rubus* ground-flora. Dr. Harley pointed out that such a change might be the result of felling and planting rather than an effect of the conifers themselves. Mr. Laurie showed that there are still untouched problems concerning the factors leading to the aggregation of roots so characteristic of mor. He asked if some of the known effects of mycorrhizal and other fungi on the growth and branching of roots could be a factor in the process. Dr. Harley and Dr. Leyton suggested that a study of oxygen supply and water supply in the surface soil layers would perhaps be a better first approach to these problems, as both these factors greatly affect root-growth and activity. Prof. W. H. Pearsall, who was in the chair, commented that although there was clearly evidence that many of those present disagreed on various grounds with the planting of conifers on many sites in Great Britain, no battle had developed on this subject. The first problem in reafforestation, he said, is to make difficult sites productive and then to ensure that their soil tends to change towards mull rather than away from it. Britain is a region of brown forest soils, and present policy should be to re-establish them. No doubt it was felt that such a discussion would lead the meeting away from biology into economics, for in spite of this challenge no battle developed.

The meeting was a highly successful discussion of a most important subject, and indeed was a hard but valuable day's work for those who took part.

ANIMAL BEHAVIOUR

AT the recent meeting of the British Association in Oxford, Sections D (Zoology) and J (Psychology) held a joint discussion on "Animal Behaviour", which was attended by some four hundred members. The discussion dealt with the study of animal behaviour as it is practised by Konrad Lorenz and other zoologists who follow his lead. These investigators usually refer to themselves as ethologists, and the first two papers presented some of the features of their method, some of their findings, and some of their theoretical concepts. The third paper was given by a psychologist, who considered some of the relations between ethology and psychology.

Dr. N. Tinbergen (Department of Zoology and Comparative Anatomy, University of Oxford) opened the discussion with a paper on the bearing of the ethological study of animal behaviour on the study of human behaviour. He began by stressing the need for restraint in making comparisons between animals and men, and by saying that, in his view, the importance of Lorenz's work, and of ethology generally, lies not so much in any new theory of behaviour that has been put forward as in its particular type of approach. This approach sets great

store on careful observation and description of the behaviour being studied; on qualitative analysis as a prerequisite of quantitative measurement; on study of the whole behaviour in question, not merely of one particular part or phase or aspect; and on the preservation of a proper balance between study of the causation of behaviour and study of its evolution and survival value.

He then discussed certain aspects of the study of inborn behaviour—behaviour "as it appears before conditioning and other learning processes set in". Each animal has a limited repertory of movements, each of which is characterized both by its causes (internal and external) and by its overt motor-pattern. Ethology investigates both characteristics. In connexion with the begging response of the herring gull chick, for example, it has been shown, in relation to the stimuli, that, in eliciting the begging response, the red patch on the parent's beak (or a similar patch on a cardboard dummy) is of great importance, and that here, as elsewhere, "only very few of the receivable outside messages are influential"; and it has also been shown, in relation to the response, that it is an innate motor-pattern, since it is exhibited before the chick can have practised it and is non-modifiable and difficult to condition.

Similar studies of human behaviour are far more difficult, and often inadmissible. Yet there are perhaps indications of inborn mechanisms—specific responses to specific stimuli—in certain anti-predator reactions of human beings, in the infant's reaction to the mother's smile, and in other behaviour patterns.

Dr. Tinbergen also referred to ethological work on motivation. The motivation expressed in a movement can be recognized, he said, by the form of the movement, by the effect of the movement and by the specific factors attending its occurrence. Often there is mixed or ambivalent motivation, as in the alternating movements of attack and escape to be seen in animals and in boxers. There are also 'displacement activities'. These are patterns of behaviour that "do not belong to the motor pattern of the instinct that is activated at the moment of observation"; they are expressions of some other instinctive drive, and they act as outlets for a surplus of motivation, the discharge of which through the normal paths is in some way prevented—as when the aroused but baulked fighting instinct of domestic cocks finds an outlet in food-pecking movements. Although displacement activities are by no means rare in man, and may well have an important bearing on neurotic behaviour, they are not as easily identified in man as in animals, because, whereas a true displacement activity is always an innate pattern, in human behaviour learned patterns, like lighting a cigarette, or handling keys or handkerchief, also often function as outlets for displaced motivation.

In the second paper, Dr. R. A. Hinde (Ornithological Field Station, Department of Zoology, University of Cambridge) sketched five of the ways in which learning modifies inborn behaviour—"behaviour which appears without previous specific practice", as, for example, the 'mobbing' response of chaffinches to owls, which is elicited by a stuffed tawny owl in young chaffinches that have never seen an owl.

First, learning brings about changes in the stimuli that elicit a particular inborn response. Many studies, such as those of Wallace Craig and of W. H. Thorpe and F. G. W. Jones, indicate the importance that early experience may have in the development of behaviour that appears at first sight to be inborn. A particularly dramatic example of the effect of learning on the stimuli eliciting a response is provided by 'imprinting', as when the greylag gosling follows, and behaves towards, the first relatively large moving object that it sees as though it were its parent. In Dr. Hinde's view—and in this he differed from Lorenz—this process is probably not fundamentally different from other forms of learning.

Secondly, learning affects the stimuli which "guide the orientation of behaviour". Here only a few cases have been analysed; but, to take one example, Tinbergen has shown that the digger wasp makes a 'locality study' on leaving its nest, and learns the position of the nest in relation to certain landmarks (a ring of pine cones in one experiment); with the result that, if the landmarks are moved, the wasp repeatedly goes to the new position that they indicate, not to the real nest.

Thirdly, learning sometimes changes the motor-pattern of inborn behaviour. Such modification (except in the intensity of the response) is rare, if not impossible, in the inborn movements used by animals in locomotion, preparing food, nest-building, fighting, courting, and so on; but it occurs extensively in the movements underlying vocal utterances. The bullfinch, for example, can be taught to add whole new tunes to its repertoire.

Fourthly, there is the question of changes, due to learning, in consummatory stimuli—the stimuli to which the animal is particularly responsive while carrying out the instinctive or consummatory act in an inborn pattern of behaviour. Little is yet known about this kind of modification, but it would seem that it must be involved in 'imprinting', and must also be related to 'secondary reinforcement' as understood by Hullian learning-theorists.

Fifthly, Dr. Hinde referred to changes in responsiveness to a constant stimulus, and, particularly, to his work on the waning of the 'mobbing' response in adult chaffinches confronted with a stuffed predator. It has been shown, he said, that underlying this waning of responsiveness there are certainly two processes—one more or less independent of the stimulus and subject to fairly rapid recovery, the other specific to the stimulus and producing a more or less permanent decrement—and probably a third, which is linked to the stimulus and subject to rapid recovery.

In the last part of his paper, Dr. Hinde directed attention to three aspects of behaviour, which, he said, "are brought home rather more forcibly to the field ethologist than they are to the laboratory psychologist". These were: (*a*) that the nature, as well as the complexity, of the things an animal can learn seem often to be determined by its constitution; (*b*) that learning often occurs in animals without any of the conventional rewards, such as food, water or escape from pain, and in circumstances where "the perception of a particular situation seems to act as a reinforcing agent"; and (*c*) that animals are curious, and the analysis of this curiosity is "one of the most urgent problems awaiting both ethologist and psychologist".

To Prof. R. Knight (Department of Psychology, University of Aberdeen) had been assigned the task of discussing aspects of ethology that seemed of special interest to psychologists. He began by referring to matters about which ethologists and psychologists are agreed. Thus they both accept the

comparative study of behaviour, including the comparison of animal and human behaviour, as possible and useful. In 1951 Dr. Tinbergen wrote of "the almost universal misconception that the causes of man's behaviour are qualitatively different from the causes of animal behaviour", and no doubt this belief still has its adherents; but psychologists, no less than zoologists, may now be taken to accept the view that the comparative method is as appropriate in the study of behaviour as in anatomy, embryology, physiology or biochemistry. Again, both psychologists and ethologists proceed on the principle that behaviour, in Dr. Hinde's words, "is mediated by the nervous system, and every particular pattern of behaviour is mediated by a particular nervous mechanism or pattern of nervous activity".

The main differences, Prof. Knight suggested, between ethologists and many psychologists, especially American psychologists, relate to theory. Some of the difficulties that psychologists see in Lorenz's theoretical system have been expressed by D. O. Hebb and (though he is not himself a psychologist) by D. S. Lehrman, of the American Museum of Natural History.

Three of these difficulties may be put in the form of questions. First: Is the ethologists' use of the comparative method sufficiently strict? It would appear that Lorenz and Dr. Tinbergen do not always confine their comparisons to what is truly homologous, but are sometimes apt to assume that functionally similar behaviour patterns must be caused by fundamentally similar mechanisms; whereas in fact there is plenty of evidence that, at different evolutionary levels, functionally similar behaviour patterns often depend on mechanisms that are very different in origin and fundamental structure.

Second: Are the ethologists' criteria of innateness satisfactory? They ascribe innateness to all behaviour that appears without previous specific practice, and, in particular, to any behaviour pattern that appears in animals that have been raised in isolation from fellow-members of their species and prevented from performing the particular pattern in question. But, as Lehrman has pointed out, an animal isolated from others and prevented from practising a particular behaviour pattern is "not necessarily isolated from the effects of processes and events which contribute to the development of the particular behaviour pattern"; and cases (for example, the nest-building of pregnant rats) can be given of behaviour which satisfies the ethologists' criteria of innateness but is demonstrably dependent on the animals' previous experience.

Third: Are the ethologists on the wrong tack in looking for unitary, autonomously developing behaviour patterns? For heuristic and other reasons, many psychologists are averse from an approach which regards the development of behaviour as involving the maturation of specific behaviour patterns and of specific mechanisms underlying them. They prefer an approach which, while acknowledging the importance of the physical growth of various structures, regards the development of behaviour as a process in which at each stage new patterns of nervous activity, and consequently new patterns of behaviour, emerge from interaction within the organism and between the organism and its environment.

In the subsequent discussion, Dr. W. H. Thorpe (Department of Zoology, University of Cambridge) said that, in his view, Lorenz's theoretical scheme has greatly stimulated, clarified and simplified the study of behaviour. He referred particularly to its concept of the 'innate releasing mechanism', to its division of behaviour into flexible appetitive behaviour and the relatively rigid consummatory act, and to its distinction between 'directing' and 'releasing' stimuli. He also said that, although Lorenz's theory does take considerable account of innate or inborn behaviour, it is not anti-learning; indeed, it not only accepts the usual kinds of learning but also adds another—'imprinting'. Prof. C. W. Valentine (formerly of the Department of Education, University of Birmingham) said he wished to make it clear that not all psychologists, particularly in Great Britain, are unsympathetic to the idea of instinctive drives and inborn patterns of behaviour. Although the word 'instinct' has for many years been under a ban in American psychology, it is now beginning to reappear, and innate impulses and actions, as well as other constitutional factors, are receiving increasing attention in recent American work in educational and developmental psychology. Prof. T. H. Pear (formerly of the Department of Psychology, University of Manchester) welcomed ethology and its experimental field-studies of birds and a variety of other animals as helping to "break the domination of psychology by American laboratory studies of the rat"; but, while psychologists are right, he said, to be interested in animal behaviour, they must not let this interest so obsess them that they neglect the study of "civilized and sophisticated men and women".

REX KNIGHT

PAUL SABATIER, 1854–1941

By PROF. J. R. PARTINGTON, M.B.E.

PAUL SABATIER, the centenary of whose birth fell on November 5, was born of a modest family in Carcassone in 1854. In 1874 he passed high on the lists in the entrance examinations for the École Polytechnique and the École Normale Supérieure. His place (fourth) on the list of the Normale was higher and he chose to go there. In 1877 he was top of the list of graduates in his class. After a year as professor at the Lycée at Nimes, he had the good fortune to become assistant to Berthelot at the Collège de France, where he took his doctorate in 1880 with a thesis on the metallic sulphides. After a year at Bordeaux, he became assistant professor of physics, and in 1883 of chemistry, at Toulouse, becoming professor of chemistry there in 1884 at the early age of thirty. In Toulouse, in spite of an offer to succeed Moissan at the Sorbonne in 1908, Sabatier stayed for the rest of his life, and died there on August 14, 1941, aged eighty-seven*. He became dean of the faculty of science in 1905. He was an excellent and very popular teacher, and long after his retirement, in fact nearly to the end of his life, he continued to lecture. He became *correspondant* of the Academy of Sciences in 1901 and the first non-resident member in 1913. He was Nobel laureate in chemistry in 1912, Davy medallist of the Royal Society in 1912 and foreign member of the Society in 1918, doctor *honoris causa* of the University of

* *C.R. Acad. Sci., Paris*, **213**, 281 (1941); *Obituary Notices of Fellows of the Royal Society*, **4**, 63 (1942–44); *J. Amer. Chem. Soc.*, **66**, 1615 (1944).