Jan de Wilde Voordrachten

ANIMAL MOTIVATION

voordracht
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door

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Ladies and gentlemen,

When I received the invitation to give this first Jan de Wilde Memorial Lecture, I was surprised, honoured, and moved, all at once. Jan and I did not see each other very often but there grew up between us over the 37 years since we first met in Stockholm in 1948, an unspoken personal bond, based on shared attitudes to many things such as the inseparability of pure and applied science, and likewise of ecology and physiology, not to mention internationalism. Needless to say I much admired his research, but equally the incredible energy he devoted to so many constructive activities, and his less public role as a catalyst of wise policies in both pure and applied entomology. I also grew very fond of him, and cannot believe he is gone.

One major achievement of his was to launch the study of insect-plant relations as a research field in its own right: this too was an interest we had in commin. The huge international symposium to be held in Pau this July is truly another memorial to Jan de Wilde. The theme of this lecture lies in a relevant field, behaviour, which has also grown massively over the same years, having been launched internationally by another remarkable Dutchman, Niko Tinbergen. De Wilde's main personal research interest was not of course in behaviour; but as an eco-physiologist he always fostered it in his laboratory, first in Amsterdam and then there in Wageningen. The key point about him in this context is that, as a true physiologist, he simply took it for granted that behaviour *is* physiology (its highest integrative level), not animal psychology. That attitude of De Wilde's is also my starting point today.

A famous American insect physiologist, V.G. Dethier, who is well known in this Department as a collaborator of Louis Schoonhoven's, did personally work for many years on behaviour - the feeding behaviour of blowflies - as well as on the underlying physiologocal mechanisms. Unlike De Wilde he had close relations with colleagues in Psychology and his view of behaviour was not always as straightforward as De Wilde's. This very fact makes the evolution of his ideas on motivation in insects and animals generally an illuminating story for anyone trying to get to grips with that confusing but important subject.

A Quest in Vain

We have Dethier's own word for it that his personal motivation through all those years of masterly analysis of a fly's feeding behaviour, was much more than every scientist's natural curiosity:

> "The purpose underlying the foregoing analysis of the fly was not to study the fly *sui generis*. It was to hold a different glass to the problem of motivation, to ascertain whether or not it occurred in an organism whose evolutionary appearance predated that of man, to discover whether or not its expression lay within the capabilities of a relatively simple nervous system, to enquire into the reality of motivated behavior as a separate class." (Dethier 1966)

In other words, as he explained, what concerned him was whether motivation emerges as a causal factor in behaviour only in more complex animals, and even then, only at the higher levels of their complex nervous systems.

There were, however, dyed-in-the-wool, Mechanist, Behaviorist opponents of such subjective, anthropomorphic terms still around, notably T.C. Schneirla. They had dominated the field for the first half of the century and still claimed motivation was an unnecessary and misleading assumption. Because he did not believe this Dethier proceeded, as no one else has, to give their claims a full fair test by rigorous and exhaustive experiments designed to reveal how far a fly's feeding behaviour could be explained in ordinary physiological terms without having to invoke motivation as a special, separate kind of causal mechanism. At some point this endeavour could fail and the unexplained residue would then *be* motivation, isolated and analysable at last.

But that point never came. The upshot of Dethier's unremitting quest was that no such unexplained residue could be found in the fly. Not only that: he could not pin-point any such residue in accounts of feeding behaviour in the rat, either, although the rat is a much higher animal and its feeding behaviour has been a standard model of motivated behaviour.

What is motivation?

The issue at stake here was not really what motivation is. As Tim Halliday wrote in his chapter on Motivation in the recent 3-volume, multi-authored textbook *Animal Behaviour*, there is no consensus on that. The meanings attached to motivation range all the way from the near-supernatural to the strictly Mechanistic. Most, although not all, contemporary zoologists share Halliday's Mechanistic view:

> "At best, intervening variables are labels for unknown physiological processes... The ultimate aim of much research into motivation is to identify and understand how such processes work, so that concepts such as hunger, thirst and drive become unnecessary." (Halliday 1983).

Until that day dawns - and this is the root of the problem - they make free-and-easy use of many terms embodying such concepts. Coming from psychology, these are in origin subjective terms, as distinct from objective ones that do not refer to introspective evidence but rather to external observation of behaviour: the only kind of evidence we have from animals.

However, most zoologists disclaim any subjective connotation when applying these psychological terms to animals. They say the terms are purely metaphorical: no more than a convenient, shorthand way of describing the adaptive *function* of any behaviour. That is so say the terms do not refer to the present-day or "proximate" causes of the behaviour but to the evolutionary or "ultimate" causes of its survival under natural selection. An "ultimate" cause thus refers to the outcome of the behaviour, the useful *end* that it achieved for the animal; whereas the "proximate" cause of the same action are those that bring it about here and now, its physiological mechanism.

Although these two kinds of cause are obviously quite distinct, many people, from Tinbergen in the fifties and sixties to J.R. Krebs today, have pointed out that it is easy to confuse them and fall into teleology which is the mistaking of ultimate causes for proximate ones. The reason is simple. We human beings are conscious of the likely outcome of any action we take. We consciously intend to achieve it. For us, that achievement is the purpose of the action and the purpose is for us therefore the present, proximate cause of our action, even though we may know nothing of its real proximate, physiological causes. Without thinking, we cannot very well avoid attributing similar motivation to animals.

Nevertheless this admitted risk of confusing the two kinds of cause is generally ignored because subjective, "mentalist" language is so powerfully attractive to us. It is the language we constantly use to describe our own and our fellow human beings' behaviour.

That is the behaviour we know much the best, and we have an extraordinarily rich vocabulary for it. Indeed, N.K. Humphrey plausibly maintains that natural selection favoured the evolution of consciousness because it was the main instrument of our exceptionally elaborate and highly successful social interaction. However that may be, one consequence of our consciousness is that we readily and unthinkingly describe all behaviour as purposeful because in ourselves, it is.

It is true that teleological way of thinking about animal behaviour is genuinely useful in research just because it does attempt to identify what each behaviour achieves for the animal. We all want to have some idea of that even if our main interest is in proximate causes. It often suggests what known kind of causal mechanism could be employed in the given task, and that can then be looked for. However, that incidental value of mentalist language is of no help when we wish to characterize motivation as a separate class of proximate cause of behaviour. This is exceedingly difficult because the concept of motivation remains fuzzy, elusive and controversial.

So, from the many criteria found in the literature - varying responsiveness, endogenous activity (the essence of motivation according to Dethier), drive, drive reduction (satiation), goal-directeness, etc. - Dethier carefully assembled an inclusive definition. He translated all the psychological attributes into physiological-behavioural equivalents in order to uncover any difference between the mechanisms of motivated and non-motivated behaviour:

> "Motivation is a specific state of endogenous activity in the brain which, under the modifying influence of internal conditions and sensory input, leads to behavior resulting in sen-

sory feedback or change in internal milieu, which then causes a change (reduction, inhibition, or another) in the initial endogenous activity." (Dethier 1964)

But the quest for motivation thus objectively defined drew a blank, since as he said this definition "would construe all behavior as motivated". Motivation was therefore a superfluous concept. "Certainly", he added in 1976 after some further years of experimental analysis, "the concept adds nothing to our understanding of the fly's feeding behavior."

Unnecessary impediment

Undismayed by this setback, Dethier turned hopefully to what he thought would be a more rigorous criterion, operant conditioning, which the psychologist P. Teitlebaum had proposed as the acid test for motivation in animals. I think Teitlebaum was wrong about this but need not go into it here because Dethier himself made no further reference to it after 1966. Another, more plausibele interpretation that Dethier later cited from another psycohologist, R.C. Bolles, was that motivation simply means learning; but this again would make the concept of motivation redundant. Nevertheless, through the sixties Dethier still kept an open mind on the major question of mental activity in the fly his lack of any positive evidence of it, and defended his continuing quest:

"We might do well to accept the dualistic methodology ... namely, to use, in addition to behavioristic and physiological analyses, concepts about physiological events which come to us through common sense, intuition, introspection, sensation, and perception ... Perhaps these insects are little machines in a deep sleep, but looking at their rigidly armored bodies, their staring eyes, and their mute performance, one cannot help at times wondering if there is anyone inside". (Dethier 1964)

As the quest continued through the seventies, however, he became dissatisfied with this equivocal position. He made a close scholarly examination of existing ideas on the subject and eventually reached this conclusion:

"Analysing the concept ... suggests it may have outlived its usefulness ... Perhaps motivation ought to be a poetical expression not to be taken seriously." (Dethier 1981)

This was a sceptial but gentle formulation that left everyone to decide for themselves whether or not to use mentalist terms like motivation. The majority see no real dichotomy between reflexes and more complex behaviour and, believing that mentalist terms are mere metaphors that do negligible harm, still think it is convenient to maintain a dichotomy of terms. W.T. Keeton spoke for this majority in his well known textbook "Biological Science' :

"there is no difference in kind between simple reflexes and more complex reactions .. but .. applying the term 'reflex' in such a broad manner makes it synonymous with 'behavior', which does not help us at all. It is customary, therefore, to restrict the term 'reflex' to relatively simple and automatic responses to stimuli and to designate more complicated behavior patterns by other terms." (Keeton 1967)

That sounds like plain common sense - until we notice that those "other terms", after all, are different in kind from reflexes. "Reflex" is an objective term referring to proximate causation, whereas "motivation", "goal-directed", etc. are subjective terms really referring to ultimate, evolutionary causation. Thus Keeton re-introduced the very dichotomy he had just disavowed. But he evidently did not realize he had done that and this failure to recognize the implicit dichotomy of proximate causes is still very widespread as we shall see.

By 1982, Dethier's disillusionment with psychological concepts in the study of animal behaviour was complete. He now flatly rejected the conventional assumption that they do negligible harm:

> "the concept of motivation ... has not only outlived its usefulness as an analytical scaggolding but has become an impediment to our understanding of the behavior it purports to explain." (Dethier 1982)

"An impediment": that is Dethier's unfashionable but valid point. Contrast that unequivocal statement of his with the more common one to the effect that concepts like motivation are useful at the start of a study of some behaviour sequence, but become unnecessary and irrelevant as causal analysis proceeds. Dethier's point is that they become not just irrelevant but positively counter-productive, because they do mistake ultimate for proximate causes. Most people have missed this point, as Keeton did.

Cartesian dichotomy

How did that blind spot arise? Whatever motivation has been taken to mean, the underlying issue has never been that. As Dethier saw, it is whether motivation and other such internal processes really do make up a *separate class* of proximately causal mechanism in behaviour. The idea that they are a separate class goes back to long before Descartes but he articulated it so clearly, in the language of his time, that it has come to be called Cartesian Dualism.

Descarte restricted the idea to man. In this century it was Konrad Lorenz who boldly extended the dichotomy to all animals. Internal energy accumulation and external stimulation, he wrote, "are two absolutely heterogeneous causal factors"; and he insisted upon:

> "the peculiarity and independence of endogenous activity as a distinct physiological process ... an independent, particulate function of the nervous system which ... is, at the very least, equally as important as the reflex." (Lorenz 1950)

The dichotomy is usually expressed less starkly nowadays but it is often implied, for example in Halliday and Slater's Introduction to the first volume of their book:

> "As animals become more complex ... the problem of changing motivation crops up ... While single actions may appear in much the same form every time ... sequences of different activities are seldom repeated in exactly the same order ... This is also a good reason why changing motivation often has to be invoked." (Halliday and Slater 1983)

If motivation crops up only in complex animals and even there does not always have to be invoked, then there must exist behaviours that are not motivated. Obviously there would be no dichotomy without that idea of a *non*-motivated class of behaviour. So the idea deserves closer scrutiny than it usually receives in discussions of motivation including Dethier's.

Non-motivated Behaviour

Turning our attention to non-motivated behaviour has one substantial advantage. Whereas motivated behaviour is multivalent and controversial, the meaning of non-motivated behaviour is clear and agreed in the psychological and ethological literature.

It is said to be made up of "simple reflexes" characterized by one property conveyed in many ways: "stimulus-bound", "push-button", "S-R" (stimulus-response), "automatic", "rigid", "invariable", "inflexible", "stereotyped", "lacking endogenous neural activity", and so on. Early in his quest, Dethier himself had described non-motivated behaviour as "complex chaining of simple reflexes with invariable S-R relationships", and wrote of "reflex physiology with its assumption of neurological silence in the absence of overt stimulation."

The seldom recognized fact is that this picture of reflex action is no more than a relict from the early decades of this century when militantly Mechanist zoologists over-reacted to the previous Vitalist obscurantism. *Determined to get rid of that, they over-simplified* understandably but grotesquely, enabling Lorenz and Tinbergen to ridicule them. Their model of reflex action still survives as the antonym of motivated behaviour, but it bears no resemblance to the real reflex action which the mammalian physiologist C.S. Sherrington had already explored in depth. He summed it up in the title of his classic 1906 book: "The *Integrative* Action of the Nervous System" (my emphasis). He insisted that the "simple reflex" was an abstraction. So too did the insect physiologist V.B. Wigglesworth; and the psychologist J.E.R. Staddon has recently recapitulated the ample evidence that

> "Sherrington's concept of the reflex is far from the simple, inflexible, push-button caricature sometimes encountered in introductory textbooks" (Staddon 1983)

That is an understatement. Unfortunately the push-button caricature is by no means confined to introductory texts. It is all-pervasive, providing the only logic behind the ubiquitous use of "motivation" to mean some non-reflex mechanism.

Staddon continues:

> "To be sure, there is always a stimulus and a response; but the ability of the stimulus to produce the response depends on the reflex threshold - and the threshold of each reflex depends not only on the state of many other reflexes but also on higher centers, which retain the effects of an extensive past history ... The function of reflexes is the *integration* of behavior, which would be impossible without well-defined rules of interaction".

Staddon has since put in a nutshell the historic mistake of the Mechanist (now called "radical") Behaviourists, when he said:

> "psychologists emphasised the wrong aspect of reflexology, attending to the stimulus-response property of reflexes, and not to reflex integration - the principles by which tendencies to action combine to produce overt behavior." (Staddon 1986)

Zoologists have made just the same mistake. Consequently, "reflex action" seems to them to exclude most of behaviour, and to exclude above all the making, storing and using of spatio-temporal "maps" in the brain by the integration of conditioned reflexes. That process is currently known as cognition or thinking even in animals: a good example of the confusion created by subjective terms since to most of us cognition and thinking are conscious mental activities far removed from reflex action. But the psychologists such as H.S. Terrace who have led the recent revival of interest in this cerebral function do not mean that at all. For them, consciousness is quite another matter and they call Cartesian dualism a "spectre" which they are *not* raising.

Another psychologist, C.R. Gallistel, has presented a fresh synthesis of proximate behavioural causation challengingly entitled "The Organization of Action", and based explicitly on

Sherringtonian reflex physiology. These animal psychologists (unlike most zoologists up till now) are moving in the same general direction as Dethier in turning back to build anew upon the achievements of the pioneer behavioural physiologists: not only Sherrington, but also Pavlov, G. von Holst, Paul Weiss and others. Their achievements were effectively set aside for many decades by psychological, ethological and even some physiological students of animal behaviour. Witness K.D. Roeder writing in 1962:

> "Old standbys, such as the reflex and the morphological center, have become peripheral in their significance."

On the other hand concurrent advances in neurophysiology quickly made nonsense of the supposed lack of endogenous activity and the related idea of a fixed one-to-one relation between input and output in reflex action. Suffice it to recall Roeder's own forceful statement:

> "To consider means whereby endogenous factors are prevented from preempting the output of a neuron, so as to leave some control to sensory input, seems as important as it is to determine the basis of endogenous activity." (Roeder 1963)

If, therefore, motivation, when looked at objectively, is not something that comes in only at higher levels, then it becomes an unnecessary, misleading concept just as it did for Dethier from his own experimental evidence.

The knee-jerk, and the recoil from a hot stove, and a few other instant responses are cited routinely to illustrate the supposedly simple, push-button character of reflexes. But they are not typical. They do of course show relatively constant input-output relations and may be relatively simple in having short first-order arcs through the spinal cord. But they also have collateral arcs up through the brain that can modulate and even inhibit them, as when someone acts bravely under the dentist's drill. They are what Sherrington called "strong reflexes" that override all their rivals unlike "weak reflexes" such as grooming which are easily overridden. A reflex can be innately strong, as with the hot stove; or it can become strong through social reinforcement like recoil from a cockroach; or it can come out strong simply because the stimulus is "supernormal" like the sudden stretch of the patellar tendon that produces a knee-jerk. Strong reflexes are but one end of a long spectrum.

In sum, non-motivated behaviour has no physiological reality, so there is no dichotomy of behavioural mechanisms. The still prevailing, gross misapprehension of reflex action sustains a false dichotomy between it and the rest of behaviour.

Survival of the Unfit

How can that false dichotomy have lived on to this day? When the pioneer ethologists' observations became widely known in the 1950's it was at once obvious to everyone that they could not conceivably be accommodated by the push-button model of behaviour. There was undeniably something more, and the Mechanist behaviourists' vocabulary had no words for this enigmatic something. In the result, psychological terms once discredited by the behaviourists but reintroducted by the ethologists, rapidly acquired scientific legitimacy among students of animal behaviour and even some physiologists such as T.H. Bullock and G. Hoyle. Just because these concepts were quite separate from reflex action as it was generally misconceived, they did not displace the push-button caricature of reflexes: they simply supplemented it. In this way the caricature and the dichotomy lived on unscathed.

The most telling evidence for internal "energy" accumulation, drive and motivation came from the pioneer ethologists' observations described as *Vacuum* and *Displacement* activities, for these are activities that appear "spontaneously", that is to say in the absence of the stimuli that normally elicit them. They are glaringly non-reflex by definition, on the push-button model. Tragically for the future, no one seems to have noticed at the time that this phenomenon had been observed more than half a century earlier by Sherrington in spinal reflexes. He called such occurrence "spontaneous reflexes", which is not as self-contradictory as it sounds since the activities in question were normally observed as responses to stimuli: exactly paralleling the ethologists' observations of whole animals.

Spontaneous reflexes seem to depend on the principle of reflex interaction that Sherrington called *post-inhibitory rebound* or *successive induction*. This principle has now been recognized as operating at the neuronal and whole-animal levels as well as at the spinal reflex level. A reflex action can occur without the usual stimulus provided it has been kept inhibited for long enough by a stimulus that elicits an antagonistic reflex. That this prior work is still ignored shows how strongly entrenched the push-button caricature of reflexes still is.

Even Staddon seems to have overlooked spontaneous reflexes when he said "To be sure, there is always a stimulus ..." No doubt he meant a stimulus in the behaviourist's usual one-sided sense of an external and excitatory one, but the effective stimulus for a spontaneous reflex is *inhibitory*, and this obscures the reflex nature of the "spontaneous" action. Although as Sherrington said "inhibition is *so-equally* with excitation a nervous activity" (my emphasis) it is hard for an observer to keep this in mind.

Our natural tendency is to think only of the excitation - what the animal is doing - because that is how we think of our own behavior. The concurrent inhibition of everything the animal is not doing is then easily overlooked: out of sight, out of mind. Yet what the animal will do next depends not only on what new stimuli the on-going behaviour brings in (the chain-reflex principle) but also on after-effects of the on-going behaviour including the "priming" of rival behaviours inhibited by it (antagonistic induction).

For instance, when what appear to be "irrelevant", "displaced" activities are attributed to "thwarting" or "frustration" this concentrates an observer attention on the absence of an expected stimulus, as if that alone caused the behaviour. This is simply because that absence is uppermost in our minds when we feel frustrated. We do not think of the likely causal role of other stimuli that are present and capable of eliciting quite different activities, but were temporarily inhibited by the on-going one. Yet the real cause of some new activity being performed when the on-going activity is "thwarted" may well be the "priming" of it while it was inhibited by the on-going one. The subjective terms used to describe the behaviour again obscure its reflex nature.

The cost of convenience

That is one example of the harm done by mentalist terms in the analysis of animal behaviour. As Dethier perceived, almost alone among current writers, the assumption that mentalist descriptions of animal behaviour do negligible harm is untenable. The price paid for their convenience is altogether too high when proximate causes are in question. Their convenience is a pitfall trap. Convenience aside, their role is only to confuse ultimate with proximate causes. Referring as they do to ultimate rather than proximate causes, they are devoid of physiological meaning.

The worst effect of the false dichotomy between reflex action and "higher" modes of behaviour is that it has deprived ethologists of the help they could have had from real reflex physiology. It thus keeps wide open what Roeder called "the gap between what nerve cells do and how animals behave". Hopes were high in the 1950's that this great gap would be closed in the foreseeable future. But current textbooks agree that there has been disappointingly little progress towards closing it. To do that required, first of all, a meeting of minds across the gap, but mentalist language obstructs that for it is fundamentally alien to physiologists. Neuroethologists have been working hard on their side of the gap, but discouraged ethologists have found it more profitable to abandon bridge building and go over to abstract modelling, ultimate causation (now labelled "Behavioural Ecology"), and human behaviour, where mentalist language has a still free rein. It is a vicious circle.

Subconsciousness

What Dethier said of psychologists applies equally to zoologists who borrow their language:

> "physiological psychologists ... have not purged their subconsciousness of human subjective and philosophical underpinnings." (Dethier 1981)

"*Sub*consciousness" is the operative word. The effect of these "underpinnings" and overtones is insidious because so often we are not aware of it, as in Keeton's case.

Now Tinbergen was well aware that the subjective language of Ethology was a serious impedement. He warned repeatedly over the years against what he called, prophetically, the "tenacious hold" of subjectivist teleology. He also said:

> "A tendency to answer the causal question by merely pointing to the goal, end, or purpose of behaviour ... is seriously hampering the progress of ethology". (Tinbergen 1951)

and "Our habit of giving names to systems characterized by an achievement, has made thinking along consistent analytical lines much more difficult than it would have been if we could have applied a more neutral terminology." (Tinbergen 1963)

All the same, he found such "neutral" (meaning objective) terminology too "dry" and "non-committal"; so all he could suggest was "to accept any frankly functional term, as long as this is done consciously." But to ask people to do that consistently was asking too much. His warnings were ineffective: twenty years later Dethier still finds "enormous resistance" to abandoning the concept of motivation.

The warnings were ineffective because Tinbergen did not allow for the subconscious, *unintended* anthropomorphism carried by such terminology.

Dethier did recognize this key point and, most importantly, he demonstrated a way to deal with the problem of subconscious anthropomorphism, when he carefully translated the mentalist terms used to define motivation into their "dry", objective equivalents. This is the only way I know that users of mentalist terms for animal behaviour (I am one, of course!) can make sure they have not overlooked some of the actual inputs and outputs and central nervous interactions governing a given behaviour, as in the case of displacement activities discussed above.

Dethier's warning against anthropomorphism may actually carry more weight than Tinbergen's because, unlike Tinbergen, he started out content with motivation and other mentalist terms and distinctly hostile to the anti-anthropomorphists, and then hunted experimentally for a separate motivating process, failed to find it, and eventually reached the conclusion that such mentalist concepts positively hinder understanding.

Liberation?

Dethier is thus making a bid to liberate the proximately causal analysis of animal behaviour from the false dichotomy between reflex and motivated behaviours, leaving us with a single, coherent system to deal with. It is a system that uses similar unit mechanisms throughout but generates emergent properties through its hierarchical organization as C.R. Gallistel in particular has described.

Certainly the liberation movement does face stubborn resistance and may fail. Yet the tide might be turning, given the currents in Psychology flowing in much the same direction. There is the return to build anew on the neglected achievements of Sherrington, Pavlov and other pioneer behavioural physiologists. While psychologists have recently demonstrated astonishing cerebral "map-making" capacities in animals (long anticipated by G.P. Baerends in a Digger Wasp), they have at the same time widened the "cognitive" gap between ourselves and even our nearest relative the chimpanzee in the matter of language. Cognition is another subjective term and it has not been shown that what is called cognition in animals is conscious. The imputation of a conscious mind and motives to any animal now seems less plausible than ever.

There is admittedly one important respect in which motivation and reflex integration do fall into quite separate classes, although only in ourselves. It is simply the kind of evidence that we have about them. Evidence of motivation, etc. can only be introspective, while evidence of causal mechsnisms can only be exteroceptive. We still have virtually no idea of how to relate the two pictures that we get from these two profoundly different viewpoints. One day no doubt that mystery will be cleared up too. Ethologists will bring essential aid to physiologist and psychologists in that task by abandoning the misleading concept of motivation in animals. At present, motivation is a problem with no agreed bounds. There is no telling how far it might extend down the phylogenetic scale, even perhaps to animals that have no nervous systems. The problem can hardly be tackled so long as it seems boundless. Just possibly, that liberating step of abandoning the notion of animal motivation may now be on the agenda, reviving hope of closing the great gap between what nerve cells do and how animals behave.

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