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Adaptation

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Abstract

The term adaptation is used in biology in three different ways. It may refer to changes which occur at the cell and organ level, or at the individual level, or at the level of gene action and evolutionary processes. Adaptation by cells, especially nerve cells helps in: communication within the body, the distinguishing of stimuli, the avoidance of overload and the conservation of energy. The time course and complexity of these mechanisms varies. Adaptive characters of organisms, including adaptive behaviours, increase fitness so this adaptation is evolutionary.

The major part of this paper concerns adaptation by individuals and its relationships to welfare. In complex animals, feedforward control is widely used. Individuals predict problems and adapt by acting before the environmental effect is substantial. Much of adaptation involves brain control and animals have a set of needs, located in the brain and acting largely via motivational mechanisms, to regulate life. Needs may be for resources but are also for actions and stimuli which are part of the mechanism which has evolved to obtain the resources. Hence pigs do not just need food but need to be able to carry out actions like rooting in earth or manipulating materials which are part of foraging behaviour.

The welfare of an individual is its state as regards its attempts to cope with its environment. This state includes various adaptive mechanisms including feelings and those which cope with disease. The part of welfare which is concerned with coping with pathology is health. Disease, which implies some significant effect of pathology, always results in poor welfare. Welfare varies over a range from very good, when adaptation is effective and there are feelings of pleasure or contentment, to very poor.

A key point concerning the concept of individual adaptation in relation to welfare is that welfare may be good or poor while adaptation is occurring. Some adaptation is very easy and energetically cheap and welfare can be very good when it is occurring. Other adaptation is difficult and may involve lower or higher level emergency physiological responses or abnormal behaviour, often with bad feelings such as pain or fear. In that case, welfare is poor or very poor even if complete adaptation eventually occurs and there is no long-term threat to the life

of the individual. In some circumstances, adaptation may be unsuccessful, the individual is not able to cope, stress occurs and welfare is ultimately very poor.

Anpassung

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Zusammenfassung

Der Begriff Anpassung wird in der Biologie in drei unterschiedlichen Zusammenhängen genutzt. Er bezieht sich entweder auf Änderungen auf Ebene von Zellen oder Organen, auf Ebene eines Individuums oder auf genetischer Ebene bzw. auf evolutionäre Prozesse. Anpassung von Zellen, insbesondere von Nervenzellen, unterstützt die Kommunikation innerhalb des Körpers durch Unterscheidung einzelner Stimuli, die Vermeidung von Überreizungen sowie einen sinnvollen Energiehaushalt. Die zeitlichen Abläufe und die Komplexizität dieser Mechanismen variieren stark. Adaptive Eigenschaften von Organismen, auch im Verhalten, erhöhen die Fitness, hier handelt es sich also um eine evolutionäre Anpassung.

Dieses Manuskript befasst sich größtenteils mit der Anpassung von Individuen und deren Bezug zum Tierschutz. In komplexen tierischen Organismen wird häufig die „feedforward control“angewendet. Individuen sehen Probleme voraus und passen sich bereits an, bevor der Umweltreiz ein substantielles Ausmaß erreicht hat. Ein Großteil der Anpassung wird über das Großhirn vermittelt, denn Tiere haben bestimmte Ansprüche, die durch Motivation entstehen und zentral gesteuert werden, wodurch der Tagesablauf gesteuert wird. Bedürfnisse liegen vor für Nährstoffe, aber auch für Aktionen und Stimuli, die Teil jener Mechanismen sind, die sich aufgrund der Bedürfnisse nach Nährstoffen entwickelt haben. So benötigen Schweine z.B. nicht nur Nahrung, sondern sie müssen ebenfalls in der Lage sein bestimmte Tätigkeiten auszuführen, wie etwa das Wühlen im Erdboden oder die Bearbeitung von Materialien, die Teil ihres furagieren Verhaltens sind.

Das Wohlbefinden eines Tieres ist der Zustand, in dem es in der Lage ist, mit seiner Umwelt artgerecht umgehen zu können. Dieser Zustand beinhaltet verschiedenste adaptive Mechanismen, wie z.B. Gefühle oder Auseiander-setzung mit Krankheiten. Jener Anteil, der sich mit pathologischen Vorgängen befasst, ist die Krankheit. Da Krankheit natürlicherweise pathologische Zustände beinhaltet, resultiert sie zwangsläufig in Unwohlsein. Hingegen variiert der Zustand des Wohlbefindens stark, von sehr gut im Falle einer gelungenen Anpassung mit Gefühlen wie Freude oder Zufriedenheit bis hin zu sehr schlecht.

Eine zentrale Annahme des Konzepts der individuellen Anpassung im Rahmen des Tierschutzes ist jenes, dass das Wohlbefinden durch den Anpassungs-prozess direkt positiv beeinflusst wird. Manche Formen der Anpassung sind ohne nennenswerten Aufwand und sehr einfach, und führen trotzdem zu einem

ausgesprochen großen Wohlbefinden. Andere Anpassungen sind schwierig, beinhalten mehr oder weniger starke physiologische Notfallsituationen oder abnormes Verhalten, das oft auch mit Unannehmlichkeiten wie Schmerz oder Angst verbunden ist. Solche Zustände führen zu Stress, auch wenn die Anpassung schließlich gelingt und auch kein langfristiger lebensbedrohender Zustand vorliegt. In anderen Situationen wiederum bleibt die Anpassung erfolglos, das Individuum kommt mit der Situation nicht zurecht. Dann überwiegt Stress, und das Wohlbefinden ist ultimativ sehr schwach.

1. Introduction

In order to use animals in a human-orientated environment, and in order to ensure that the welfare of those animals is good, we need to know about the ability of animals to adapt. Indeed, the process of domestication depends upon the efficiency of adaptation by the animals concerned. However, "adaptation" has several biological meanings (Broom and Johnson 1993, Broom 2001a). At the cell and organ level, *adaptation is the waning of a physiological response to a particular condition, for example the decline over time in the rate of firing of a nerve cell.* At the individual level, *adaptation is the use of regulatory systems, with their behavioural and physiological components, to help an individual to cope with its environmental conditions.* In evolutionary biology, *adaptation is the evolutionary process involving natural selection and leading to the formation of a successful trait.* Hence, adaptive behaviour in an individual could help the individual without increasing fitness but if adaptive behaviour in a species is mentioned this would imply increased fitness. *An adaptation is a structure, physiological process or behavioural feature which makes an organism better able to survive and to reproduce than other members of the same species.* The major topic of this paper is adaptation at the individual level but the other two meanings of the term will be considered briefly in sections 2 and 8.

2. Adaptation at the cell and organ level.

Neural mechanisms which sense the environment often decline in their response as they are exposed to continuing or repeated stimulation (Guyton 1991). For example most sensory receptors show more of a phasic than a tonic response to continuing stimulation in that the rate of firing in the axon from a sensory neuron reduces over time (Broom 1981). Such changes in receptors may result in reduced imposition of the environment on the animal, information gain without energy wastage, efficient use of information channels, possibilities to distinguish stimuli, and avoidance of information overload. Sensory receptors adapt at different rates, for example vibration receptors in less than a second, touch receptors in a few seconds, temperature receptors in minutes, and blood pressure receptors over a number of days. Pain receptors adapt little and if there is adaptation, it is slow (Broom 2001b). The adaptation in receptors often occurs in single cells or in a combination of receptor cell and sensory neuron. However, a change in the frequency or intensity of responses of animals to repeated stimulation is often a much more complex matter (Broom and Johnson 1993). The response might increase, in which case it is sensitisation, or decrease, in which case it is habituation. Habituation involves complex processing and is not the result of simple adaptation of receptors or of fatigue in muscles (Broom 1991). It is often very specific (Sokolov 1960, Broom 1968) so those brain processes must be as elaborate as those which occur during conditioning

When a stimulus signalling the need for action is perceived, the delay before the maximal response, whether physiological such as a heart-rate change or behavioural, varies according to the sensory modality and the context. Some of this variation is a consequence of the functioning of receptor cells and sensory neurons but sophisticated brain processing, including inhibitory effects on sensory cell functioning usually plays a major part. The neural response to a peal of thunder reaches a peak in no more than a few seconds and behavioural changes are usually also brief. Orientation reactions are rapid and startle responses (Broom 1981, Broom and Johnson 1993) range from absent to substantial depending on sound level and degree of familiarity with thunder. Responses to painful or other noxious stimuli will also depend on magnitude of input and perceived risk of further problems, both those indicated by that stimulus and others which might occur at that time. The peak response may be reached in seconds or may be delayed according to which other emergency physiological and behavioural processes are initiated. Once the peak response is passed, adaptation is occurring but may not be complete for some minutes or hours as explained below.

3. Types of control used in individual adaptation.

There are two principal types of control mechanism which allow individuals to adapt to environmental impacts on them. Negative feedback control involves detecting a displacement of body state from the tolerable range and responding so as to counteract that displacement and return to within the range. For example, an individual may have incurred a carbohydrate deficiency which is detected by blood glucose level receptors. The response to that information from the receptors is that the individual commences eating appropriate food and continues eating until the glucose levels return to the tolerable range or another input inhibits eating. In feedforward control, a future deviation from a tolerable range of body state, or from a desirable position, is predicted and action is taken to keep within the tolerable range or at the desirable position. An example is the ad lib fed cow (Metz 1975) which predicts an overnight period when feeding will be difficult and eats enough to provide for her nutrient needs during that period. Metz found that the size of meals taken by the cows was proportional to the interval to the next time of feeding, rather than to the interval since the last meal, as would occur if the control was by negative feedback. A further example of feedforward control in relation to nutrient intake, on a different time scale, is the migrating bird which eats and stores enough food prior to migration to provide for its energy needs during a migration flight which may be at night and may be over water or desert where feeding is not possible. Many other examples of feedforward control involve taking action to avoid potential danger before the danger source is detected. Feedforward control, which is widespread in many vertebrate and some invertebrate animals, requires considerable cognitive ability to be effective.

4. Systems of needs in relation to control and adaptation

In order to control interactions with the environment of the individual, brain mechanisms including motivational systems have evolved. Motivational systems enable individuals to ascribe priorities to certain actions, as well as to determine the timing of actions. Natural selection has acted so that genes which promoted effective decision making and appropriate means of determining importance of actions, have spread in the population.

A need is a requirement, which is part of the basic biology of an animal, to obtain a particular resource or respond to a particular environmental or bodily stimulus (Broom 2001b). The need itself is in the brain of the animal and is a prerequisite for effective control of functioning. Needs can be identified by behavioural studies which indicate strength of motivation, by some physiological measurements and by assessing the welfare of individuals whose needs are not satisfied (Hughes and Duncan 1988a, b; Dawkins 1990; Broom and Johnson 1993). Some needs are for particular resources, such as water or heat, whilst others are to carry out actions whose function is to attain an objective (Toates and Jensen 1991, Broom 1996, 1997). The action is a biological mechanism for achieving an objective but that action has itself become an objective. For example, pigs often find food by rooting in soil or manipulating litter but will work for the opportunity to root even in the presence of food (Hutson 1989) and show behavioural abnormalities if unable to root. Hens use dust-bathing to keep their feathers clean and are greatly disturbed if unable to carry out the behaviour (Vestergaard 1980). Both pigs and hens are highly motivated to build a nest before giving birth (Arey 1992) or laying eggs (Brantas 1980). Many animals will continue to work for food even in the presence of food so it seems that they need to carry out the work itself. It is clear from such studies that a hen finds it difficult to adapt to its environment unless dust-bathing is possible, or at the time when egg-laying is imminent, unless nest-building is possible. The sow attempting to find and manipulate nest material prior to parturition will not die if she cannot gain access to such material but she will show behavioural and physiological responses which indicate poor welfare and may not show normal maternal behaviour to the piglets. The need is a Bedürfniss, i.e. emphasising what the animal wants but perhaps should also be considered to be a Bedarf, i.e. concerning what it has to have.

Since the need is a construction in the brain, even if it has might be triggered by or have consequences for peripheral cells and tissues, it is not itself physiological or behavioural. If an individual becomes hypothermic, physiological changes ensue and these affect the brain via monitoring systems or direct effects. The need mechanism exists in the brain and is changed by inputs reflecting environmental events. It is the fulfilment of needs which requires physiological change or a certain behaviour to be shown. Hence it not precise to qualify the word ‘need’ with ‘physiological’ or ‘behavioural’. It is sufficient to just refer to ‘needs’ or, as in Council of Europe Recommendations, to refer to ‘biological

needs'. If the fulfilment of the need involves some behaviour, this can be explained by referring to 'needs, such as those to show certain behaviours,'.

5. Limits to adaptation

An individual which is in the process of adapting to some perturbation of its state, which might for example be caused by an extreme external temperature, or a pathogen, or the loss of a partner, may succeed in coping with the problem or may fail to do so. Coping means having control of mental and bodily stability (Fraser and Broom 1990). Where there is no true coping, there may temporarily be tolerance of displacement of state from the optimal range. If coping is not possible and the individual is not able to adapt to the new circumstance, the ultimate result will be death. Prior to death there may be pathological effects on the individual. Health refers to what is happening in body systems, including those in the brain, which combat pathogens, tissue damage or physiological disorder and may be defined as an individual's state as regards its attempts to cope with pathology (Broom and Kirkden 2004). Disease is described by Canon (1935) as "a fight to maintain the homeostatic balance of our tissues". With this kind of challenge, as well as with others, difficult or inadequate adaptation results in poor welfare.

As explained by Broom and Johnson (1993 p.35) "Failure to adapt sometimes arises because events occur rapidly, for example, if there is a sudden predator attack or rock fall". With more long-lasting problems, failure to adapt may occur because of the magnitude of the effect or because there are repeated effects or multiple effects of different kinds. Two potentially noxious stimuli may have additive or multiplicative effects on an individual. When a wild animal is brought into captivity, for example it is transported in a cage, or sold as a pet so that it is confined and has frequent close contact with humans, or is confined in a cage in a zoo or in a laboratory, it will be subject to several difficult environmental changes. Confinement, contact with animals perceived to be dangerous predators such as humans, changes in diet, and general difficulties in controlling life will often have the overall effect that the animal dies. Adaptation may well be impossible in captivity for some animals. Wild caught birds, cetaceans and wild reptiles such as tortoises are amongst the types of animals which have much reduced life expectancy in zoos or when kept as pets. Where more than 5% of such wild animals are unable to survive at all in captivity or are not able to live in captivity without very poor welfare, is it not immoral to keep in captivity any wild animals of the species?

6.Rates of adaptation

Individual differences in responses to disturbance by humans are well established (Lazarus and Folkman 1984). There may be differences in adaptability because of the previous experience of the individual or because of

variation in biological rhythms such as the ovarian cycle. There might also be apparent differences in response because of the rapid changes during the time course of adaptive responses. A disturbed individual may commence its response with a brief orientation reaction followed quickly by a freezing response. However this response might then change to an active escape response (Broom 1969) so an observation before or after the transition to active response would show large differences in response at a particular time. If all individuals went through the three phases of response described above, they might appear to be responding differently.

When the response to a perceived problem involves the hypothalamic - pituitary - adrenal cortex axis (HPA), the energy-liberating adrenal cortex response, producing elevated cortisol or corticosterone in the blood, will take one and a half to two minutes to commence. Within one minute of this commencement time the glucocorticoid starts to diffuse into the saliva. The concentration in the saliva rapidly comes to be proportional to the concentration in plasma of glucocorticoid which is not bound to protein so salivary glucocorticoid measurements can be useful as welfare indicators. Peak glucocorticoid concentration may occur within five minutes or could be delayed, especially if the causal stimulus is large.

The development of regulatory ability varies greatly amongst animal species. Precocial animals such as lambs, foals or domestic chicks can adapt to more kinds of demanding situations at an early age than can species such as humans, rats or blackbirds, which are altricial, or kangaroos which are even more altricial. The progress of experience during the neonatal period, and the consequent development of the animal, can have a profound influence on the animal's success in adapting to conditions in later life (Wiepkema 1987). The strategies which individual mammals use when attempting to cope with their complex environment can be affected by conditions in utero and these may be modified by the experience of the mother (Bateson et al 2004).

7. Adaptation, stress and welfare

Coping with adversity might occur easily, might be successful but only with difficulty, or might not occur at all, in that there is damage to the individual, other pathology, impaired reproduction or death earlier than would otherwise have occurred. It is in this last situation, where adaptation is not possible without harm, where the effect is stressful (Broom 2001a). For most people, stress implies the effects of a challenge to the individual that disrupts homeostasis resulting in adverse effects rather than just a stimulus which activates energetically cheap control mechanisms. Stimuli whose effects are beneficial and some of the great diversity of situations which have the effect of activating the hypothalamic - pituitary - adrenal cortical axis, but whose effects are useful to the individual, would not be called stressors by most people. I consider that stress is an environmental effect on an individual which overtaxes

control systems and results in adverse consequences, eventually reduced fitness (modified after Broom 1983, Broom and Johnson 1993).

If stress occurs, welfare will be poor but welfare is also poor in individuals which have difficulty in adapting. If an environmental effect results in pain, fear, abnormalities of behaviour or substantial emergency physiological responses, welfare will be poor even though the individual survives without any significant long term effect. The welfare of an individual is its state as regards its attempts to cope with its environment (Broom 1986). Welfare ranges from very good, in which case adaptation has been effective and easy and there are positive, pleasurable consequences, to very poor. Good welfare often involves good feelings and poor welfare involves bad feelings. Indeed feelings are biological mechanisms which are an important part of coping methods. Pain, fear, achievement pleasure, sexual pleasure, etc are adaptive and have evolved as a result of natural selection like other biological mechanisms (Broom 1998). Coping with pathology is an important part of biological mechanisms so health is also a part of welfare. Poor health is a major component of poor welfare. As Fraser (1993) points out, health, like welfare can vary from good to poor. If individuals are diseased, i.e. they are affected by pathogens to the extent that they are harmed or have difficulty in coping, then their health is poor. By definition, their welfare will also be poor (Broom and Kirkden 2004). The individual which is diseased is having some difficulty in adapting to pathogens and disease is always associated with at least some degree of poor welfare. However, there are many situations with which individuals have to try to cope which do not involve pathology. These include situations where there are extreme ambient temperatures, or where psychological stability is threatened, or where detrimental effects on physical stability are compensated for by management practices such as antibiotic use, or where there is pain but no significant tissue damage. In each case no pathology occurs but coping is not easy.

Poor welfare is often associated with lack of control over interactions with the environment of the individual, i.e. with difficulty in adapting. Hence welfare depends greatly on the nature and efficacy of control systems. In an individual whose control systems are organised so as to receive frequent input, lack of sensory input can be a problem. For man, and for other species with complex brains, barren environments with lack of stimulation pose problems. This is in part because specific, important stimuli are missing and in part because the total level of input to the sensory mechanisms of the animal is too low. Adaptation is also difficult when there is an overload of stimulation or when aspects of a normally predictable environment become unpredictable. Specific, noxious stimuli also pose adaptation problems. Some of these noxious stimuli are simple, for example a chemical which causes tissue damage or a loud noise which could cause failure of sensory receptor function. Others are complex and require sophisticated brain processing in order that they can be recognised. The difference between a potential rival conspecific who is advertising potential

fighting quality and an individual who is about to attack and injure may be very subtle but the consequences of failure to distinguish between the two and respond appropriately may be very serious. In animals with complex brains, many of the circumstances in which adaptation is necessary demand a considerable degree of cognitive ability. Coping implies carrying out both simple and complex adaptive responses.

When individuals are trying to adapt to environmental impositions, they may show various physiological and behavioural responses. These responses have precursors and consequences in brain changes (Broom and Zanella 2004). The problem may be long-term or short-term and different responses are used for each. Welfare indicators show the extent of difficulty in adapting and of adverse effects on the individual. Major progress has been made in recent years in formulating methodologies for welfare assessment (Broom and Johnson 1993) including assessment of pain (Broom 2001b, Flecknell 1994). In studies of welfare, measures of the severity of effect are used and the overall effect on the animal is a function of duration and severity (Broom 2001b).

A key point concerning the concept of individual adaptation in relation to welfare is that welfare may vary from very good to very poor while adaptation is occurring. Some adaptation is very easy and energetically cheap and welfare can be good while it occurs. Other adaptation is difficult and may involve lower or higher level emergency physiological responses or abnormal behaviour, often with bad feelings such as pain or fear. In that case, welfare is poor or very poor even if complete adaptation eventually occurs and there is no long-term threat to the life of the individual. In some circumstances, adaptation may be unsuccessful, the individual is not able to cope and stress occurs: welfare is then ultimately very poor.

8. Adapting in relation to evolutionary processes

When the responses of an individual are described as being part of its adaptation, the benefit of the effective action is assumed to accrue to the individual itself. However, there might also be a benefit in terms of the reproductive output of the individual so the adaptation might have consequences for the next generations. When responses are described as adaptive, there is usually an implication that an evolutionary advantage is conferred by the response. It is assumed that genes which promote such a response will be more likely to spread in the population as a consequence of that response. As explained in Section 1 above, adaptive behaviour in a species means behaviour which increases fitness

Many animals have adapted to humans in various ways. Some exploit humans by being parasites on them. Others utilise resources which humans collect, as

does the house mouse (*Mus musculus*), or benefit from human waste products, for example the herring gull (*Larus argentatus*). It is probably over 12000 years since the wolf *Canis lupus / Canis familiaris* domesticated humans. Wolves / dogs could benefit from humans because the humans could kill prey which the wolf / dog could catch so it was useful to associate with humans. Since the humans also benefited from this commercial relationship, they soon learned to rear and care for wolves / dogs and to protect them as well as giving them some of their food. Some humans who describe these adaptations on the part of both species assume that the initiative was entirely human but this seems unlikely to me.

Another species which has adapted to new human environments and has benefited greatly from this is the chicken *Gallus gallus domesticus.* This relatively rare species from South East Asia has become the commonest bird in the world as a consequence of its ability to adapt to human contact and to continue to grow and reproduce in human-designed environments. The fact that chickens, and several other species, have adapted, during the course of domestication, does not necessarily mean that the level of adaptation is such that their welfare is good. Incomplete adaptation can be associated with very poor welfare.

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