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Thyroid hormone

There are two thyroid hormones produced and secreted by the thyroid gland, these being thyroxine (T_4) and triiodothyronine (T_3). Thyroxine and triiodothyronine are produced from tyrosine, having either four (T_4) or three (T_3) iodine atoms on the thyronine ring. Low dietary intake of iodine will lower the production of these two hormones.

The production and secretion of these hormones are initiated by the **hypothalamus**, which secretes thyrotropin-releasing hormone (TRH), which enters the hypophyseal portal system to reach the anterior **pituitary gland** to bind to membrane receptors on thyrotrophs – cells in the anterior pituitary that produce thyroid-stimulating hormone (TSH); the anterior pituitary gland then produces and secretes TSH. Upon thyroid stimulation, thyroglobulin – which is the storage form of T_3 and T_4 – is transported from the lumen of the follicle, by pinocytosis, into the follicular cells of the thyroid gland. In these cells the large protein, thyroglobulin, is hydrolyzed into T_3 and T_4 and secreted into the peripheral circulation. The majority of thyroid hormone produced and in circulation is T_4. The majority of T_3 and T_4 concentrations are then bound by thyroxine-binding globulin, while the remaining 30% is bound to albumin or thyroxin-binding pre-albumin. Only a fraction of 1% remains unbound in the peripheral circulation. The large percentage of bound hormone supplies the body with a large pool from which to draw and prevents its degradation until it reaches its target tissue.

Of the two thyroid hormones it is T_3 that is considered the biologically active hormone, although T_4 to a lesser extent can bind to thyroid receptors. After entering the peripheral circulation, T_4 is converted into T_3 in organs such as the anterior pituitary gland, the kidney and the liver. Most tissues in the body have nuclear receptors for thyroid hormone, and by activating these receptors thyroid hormones set the basal rate of heat production and oxygen consumption for an animal. Thyroid hormones also influence the rate of lipid, protein and carbohydrate metabolism, increasing these rates when thyroid hormone concentrations are elevated and decreasing them when thyroid concentrations are low.

Overall secretion of thyroid hormone is regulated by a negative **feedback** system, in which high concentrations of circulating hormone cause the anterior pituitary gland to decrease production of TSH and thus decrease the production of thyroid hormone. Thyroid hormone is particularly important in the processes of physical and behavioural maturation, as well as in cognitive development (**see: Cognition**), and differences in thyroid hormone effects have been suggested as one of the factors controlling neoteny. (DCL)

Further reading

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Thyrotropin-releasing hormone

Also known as either TRH, thyrotropin-releasing factor or TRF, this is a peptide hormone produced by the **hypothalamus** that stimulates the **pituitary gland** to produce the peptide thyroid-stimulating hormone (TSH, or thyrotropin), which itself regulates the production of thyroid hormones. Its action is antagonized by growth hormone-inhibiting hormone. The relationship between TRH and welfare is complex and depends on the specific **stressor** and species concerned. TRH can also stimulate **prolactin** production. (DSM)

Further reading

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Tid-bitting

Tid-bitting is a behaviour performed during courtship displays in many species of galliformes, in which the male pecks repeatedly at the ground to attract females. During this the cock may also scratch and give food calls. The behaviour may also be performed as a threat during **competition** between males. Tid-bitting is also performed by female birds, which will peck at a food source to attract their chicks to it. (RJNM)

Time budget

Time budgets measure the amount of time animals spend performing various behaviour patterns, and are often measured over 24 h periods. Some behaviours may occupy a large amount of an animal's available time while others may take very little time to perform, but this does not necessarily reflect their relative importance. Time can be thought of as a commodity, as only a finite number of activities are possible during a set period of time. Thus an animal may modify the amount of time spent performing different behaviour patterns depending on the time and behaviours available. For example, when the milk supply of deer fawns was reduced, their time

spent **nursing** also decreased but their time spent **grazing** increased to compensate for the change in nutrition.

The way animals behave throughout a period of time can be viewed as the result of a series of **preferences** or choices between different behavioural options. In **wild animals**, the daily time budgets followed can be seen as strategies for **coping** with environmental changes, such as increases or decreases in food availability or variations in temperature. Allocating the appropriate amount of time to different behaviours and performing these behaviours at appropriate times of day will affect an animal's ability to survive and reproduce. Factors that affect the amount of time spent on different behaviour patterns include food reserves, risk of **predation**, time available to perform the behaviour and the results of behaviours performed earlier.

Time budget measurement can be used as a tool to assess animal behaviour and evaluate **welfare**. Resources or environments can be manipulated and the effects on different behaviour patterns can be recorded (**see: Economics of behaviour**). Time budgets of wild and captive animals can also be compared to determine the potential effects **captivity** may have on behaviour (Veasey *et al.*, 1996). As measuring time budgets requires only recording of the start and stop times of certain behaviour patterns, it is an easy technique to implement. It can be done through live observation or through video-recording and measuring time budgets from tapes. Thus, it does not require any expensive or elaborate equipment.

However, there are problems with using only time budget measurements. While measuring time budgets can determine how behaviour is affected by different factors, a difference in the amount of time spent performing a behaviour pattern does not necessarily indicate deprivation or **suffering**. The behaviour may be strongly dependent on external cues and is not shown in situations where the cue is not present. For example, anti-predator behaviour is commonly found in wild species and is important to survival and **reproduction**. However, in captive environments, where predators are not present, anti-predator behaviour is not important and thus rarely shown. In addition, some behaviour patterns may be performed when possible but the animal does not suffer if the behaviour is prevented, i.e. the animal *wants* to perform the behaviour but does not *need* to perform the behaviour.

One way around these constraints has been devised by placing costs on the performance of certain behaviour patterns and measuring what happens as the costs increase. In other words, the animal's **motivation** to perform certain behaviour patterns is measured. These methods have been adapted from human economics and are generally referred to as consumer demand experiments. As part of these experiments, the time devoted to performing certain behaviour patterns can be measured as it becomes harder and harder to perform the behaviour. If the amount of time devoted to a behaviour pattern decreases as costs increase, the behaviour is thought to be less important to the animal. However, if the time devoted to performing a behaviour pattern remains fairly constant as the cost increases, the behaviour is thought to be important to the animal. Alternatively, the amount of time available to perform a range of behaviours can be decreased (cost) and the animals will reschedule their behaviour patterns to allow more time to be spent on the more important behaviours.

Consumer demand techniques are not without their own problems (**see: Preference test**). Thus, care should be taken when designing these types of experiments to avoid or compensate for as many problems as possible. (LMD)

Further reading

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Tinbergen, Nikolaas (Niko)

Niko Tinbergen (1907–1988) was born in The Hague, Netherlands, on 15 April 1907 and studied at the University of Leiden, where he was awarded his PhD in 1932. Together with **Konrad Lorenz** and **Karl von Frisch**, he was awarded the Nobel Prize for Physiology or Medicine in 1973. He first met Lorenz in 1936 when he was invited to lecture at Leiden, and the two soon became close friends and colleagues, with Lorenz traditionally being seen as the scientific speculator and Tinbergen the more analytical scientist.

The two became separated by World War II and Tinbergen, like Lorenz, was held hostage during some of this time. After the war he was invited to set up a behaviour research group at Oxford, UK, and this ultimately led to his reunion with Lorenz. Perhaps his most enduring legacy is what has become known as **Tinbergen's Four Questions**, which outline four approaches to the study of animal behaviour relating to proximate and ultimate factors: namely its physical mechanism, lifetime development, **evolution** and **adaptive** function. Tinbergen was notoriously modest about his abilities and, in addition to being a formidable scientist, was also an accomplished illustrator. (DSM)

Further reading

Nikolaas Tinbergen autobiography, available at: http://nobelprize.org/nobel_prizes/medicine/laureates/1973/tinbergen-autobio.html (accessed 24 November 2009).

Tinbergen's Four Questions

In 1963, **Niko Tinbergen** wrote 'On the aims and methods of ethology', and proposed what are now referred to as Tinbergen's Four Questions. These questions, based in part on previous suggestions by Ernst Mayr, have helped guide behavioural research for the past four decades. These four logically distinctive and mutually exclusive types of questions about causation, development, **adaptive** utility and evolutionary history can be profitably applied to any bio-behavioural phenomenon. Importantly, by asking questions at multiple levels of analysis, our knowledge about behaviour is enriched. Broadly, a bio-behavioural question could focus on how something works, or why it is as it is.

Proximate questions are those employed to explain how something works or how it develops. For instance, studies of functional morphology tell us how behaviour is patterned and its structural basis. Studies of behavioural genetics identify the degree to which genes are responsible for behaviour, and the field of genomics identifies those genes. Studies of behavioural endocrinology tell us about the hormonal control or regulation of behaviour. These three examples illustrate causal questions. By answering them, we learn about how behaviour functions. A logically distinct type of proximate question focuses on the development (or **ontogeny**) of behaviour. Ontogenetic questions might ask about the degree to which a particular behaviour requires specific experiences to be properly performed, and address the time course of development.

Ultimate questions are those employed to explain why we see the diversity of behaviour. For instance, studies that focus on the **evolution** of behaviour tell us how or when a particular behaviour evolved. They might also tell us how many times a behaviour evolved. To do so, evolutionary biologists construct phylogenetic trees (hypotheses about the relationships between species) and then 'optimize' (i.e. map) behavioural traits on these trees. A logically distinct type of ultimate question focuses on the current adaptive utility of a trait. Only traits that increase the **fitness** of individuals who possess them will evolve or be maintained by natural **selection**. For instance, if long legs aid in escaping predators, we will expect natural selection for leg length and running speed to evolve.

Importantly, these four types of questions (or levels of analysis) produce questions that are mutually exclusive only within a level. Consider birdsong: we can ask about the evolutionary history of song learning. Song learning has evolved in parrots, hummingbirds and passerine birds. Among passerines, it is seen in a broad group called the oscine birds. These are questions about the evolutionary history of birdsong. We can also ask about the current adaptive utility, or function, of birdsong. Male birds may sing to attract females or to defend their **territory** from other males. In some species, males that sing more songs have more mates and therefore have higher fitness. It would be illogical to use evidence that, because male birds sing to defend territories, song learning has evolved only once. Questions within a level of analysis are mutually exclusive only with other questions within that level.

We can ask proximate questions about birdsong as well. For instance, recent work on the genetics of song has discovered that humans and birds both express the *FoxP1* and *FoxP2* genes. In birds, these genes are specifically expressed during song learning. A set of **neuron(e)s**, called the higher vocal centre (HVC), seems to be responsible for the neural control of song learning. In some species, the size of the HVC is correlated with the number of songs they produce, while in other species the size of the HVC changes seasonally and becomes largest when song learning is required. Finding evidence that the HVC does not change seasonally has no direct bearing on whether or not *Fox* genes are expressed during song learning; nor does it directly bear on hypotheses about the evolution of song-learning abilities, or about whether or not males that exhibit larger repertoires have higher fitness. Again, these questions are mutually exclusive.

By taking a Tinbergenian approach to studying behaviour, it forces us to examine qualitatively different sorts of questions. By doing so, we generate considerable knowledge about the diversity of behaviour. Recognizing that these are qualitatively different questions is essential, as well as ensuring that arguments about explanation are contrasting different hypotheses at the same level of analysis.

A fifth question to help extend the scope of behavioural research might also be proposed: What is the applied value of a trait or phenomenon? Formal recognition of a fifth question has several benefits and no real costs. Virtually all questions can be applied in some way and, by recognizing the applied value of a phenomenon, we expand the scope of inquisition. Much, but not all, applied research asks proximate questions, but these questions are targeted to address a larger question. For instance, researchers who study animal **welfare**, **conservation** biology and **comparative psychology** routinely apply the results of their studies to non-humans or to humans to increase welfare, manage wild or captive populations or to understand the biological basis of human behaviour. In many cases, the applied benefits of a study are the central question.

Not all researchers will desire to apply behavioural knowledge, just as not all evolutionary biologists are interested in studying proximate questions about causation. This, in itself, is no reason not to recognize the study of applied behaviour as a formal, logically distinct field of enquiry. It is essential to value high-quality research at whatever level of analysis it is conducted and not to dismiss the importance of focused studies operating only at a single level. By formally testing hypotheses about application, we can clearly identify applied benefits and this may help 'market' behavioural research to the public. Formal acknowledgement of the applied value of behaviour should make the future of bio-behavioural study even richer. (DTB)

Reference and further reading

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T-maze

A T-maze is an apparatus employed to examine spatial memory in animals. The animal is placed at the bottom of the T-shaped apparatus in a start box, is required to move along the apparatus and then to turn either left or right to reach a reward. After that the animal is taken back to the start box, where it is retained for a period of time (termed the retention interval). At the end of the retention interval the animal is released and allowed to search for the reward. There are several types of tests. For example, in a match-to-sample procedure, the animal has to choose the same arm that it visited recently in order to receive a reward. In a non-match-to-sample procedure, the animal has to choose the alternative arm to the one last visited.

Knowledge of animals' spatial **memory** abilities is necessary in many species and, in particular, for farm animals in extensive production systems, since such animals would need to locate and exploit distant resources. For example, laying hens in large systems are not always in sight of resources such as food, water, litter and nestboxes, and may need to remember the location of these resources, as well as to navigate to them. Clearly, a failure to find resources would severely compromise the **welfare** of animals in production systems.

Research involving T-mazes, and also other apparatuses such as radial-arm mazes, has proved invaluable in investigating

spatial memory in animals, and hence identifying potential cognitive deficits which would impinge on welfare (**see: Cognition**). For example, Mendl *et al.* (1997) investigated the effects of rearing pigs in both a substrate-enriched and a substrate-impoverished environment on their performance in a T-maze, and concluded that substrate-impoverished environments provide inadequate stimulation for the expression of their natural behaviour. (RF)

Reference

Mendl, M., Erhard, H.W., Haskell, M., Wemelsfelder, F. and Lawrence, A.B. (1997) Experience in substrate-enriched and substrate-impoverished environments affects behaviour of pigs in a T-Maze task. *Behaviour* 134, 643–659.

Tongue rolling

Although it occurs rarely, the most common stereotypy among adult **cattle** is tongue rolling; it is also found in many other captive species, notably **horses** and **pigs**, when they are subject to marked **confinement**. The behaviour involves repetitive, circular movements of the tongue inside or outside of the mouth. Among adult dairy cows, tongue rolling occurs more frequently when the animals are tethered, rather than being loose housed, but the method of feeding is more important than the way cows are housed.

Tongue rolling in cows occurs most when they are fed a small amount of food. Adding straw to cows' diets reduces tongue rolling, even though the energy content of the diet is not significantly altered. By transferring ruminal content between cows (using ruminal fistulas), researchers have shown that tongue rolling in cows occurs most when they can eat only a small amount of feed, during a short period of time and have low ruminal content after the meal. Tongue rolling occurs also in young calves and fattening bulls. Providing calves with more water or increased fibre, or with objects that they can suck or chew, such as a piece of rubber tyre or a chain, reduces tongue rolling. There has been little scientific investigation of tongue rolling in horses, but it may be that its occurrence relates to similar factors.

There are large differences between animals in the extent to which they show tongue rolling; most individuals show little or no tongue rolling, while a small number perform the behaviour frequently. Little is known about the individual differences that underlie this. There are few clear relations between the occurrence of tongue rolling and signs of **stress** or production levels in farm animals, and the relation between tongue rolling and animal **welfare** is uncertain. (JRu)

See also: Bar biting; Feedlot

Further reading

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Tonic immobility

Tonic immobility is an unlearned response to a brief period of physical **restraint** and is characterized by a reduced-reactivity, 'catatonic-like' state (Jones, 1986). Tonic immobility can also refer to the seemingly immobile state, or 'freezing', response to the presence of a predator or other dangerous stimuli. It was initially characterized in 1636 by Daniel Schwenter, and has since been referred to by several different names including **death** feigning, animal hypnosis, catalepsy and fright paralysis. Tonic immobility response has been characterized in many invertebrate and vertebrate species. It is most commonly used and best defined in bird species, including domestic fowl. Although there is no loss of **consciousness**, animals in a state of tonic immobility appear to be in a hypnotic state, remaining virtually immobile with suppressed respiration and body temperature. Altered **heart rates**, decreased movement and **vocalization**, and muscle rigidity are also common. The animal is not entirely immobile, however, because tonic immobility is also marked by muscle tremors in the extremities, spontaneous eye movements and jerking or bobbing movements of the head and neck.

There are two well-accepted definitions of tonic immobility: the first includes two stages of tonic immobility (Jones and Faure, 1981) and the second defines this phenomenon as having three levels (Rovee and Luciano, 1973). The two-stage definition includes the initial stage that lasts from the induction of tonic immobility until the first vigilant movement of the head. This first stage is marked by severe suppression of alert activity; however, it may include muscle tremors or jerking movements of the extremities and spontaneous movement of the eyes and head. The second stage continues from the first attentive head movement until the animal rights itself. This stage is marked by vigilant head movements and may consist of increasing frequency of leg movements and vocalizations.

The three-level definition describes tonic immobility by the level or degree of immobility or awareness. An animal in level one of tonic immobility has open eyes and generally makes loud vocalizations. This level is reached immediately at the onset of immobility and again just before its cessation. At level two, vocalizations are reduced and the eyelids flutter open and shut. The third level is marked by cessation of all vocalizations and movements, with the exception of jerking movements of the body and extremities and characteristic head bobbing. An animal in level three of tonic immobility also maintains closed eyelids.

In a clinical setting, tonic immobility is generally induced with brief physical restraint, often lasting only between 10 and 30 s, being applied to the animal in order to induce tonic immobility. The protocol for physical restraint varies within and across species. In avian research, the bird is typically laid upside down in a U- or V-shaped cradle and restrained by light pressure on the sternum for a brief period (approximately 15 s). Piglets are also often laid upside down in a U- or V-shaped cradle while the experimenter places a cloth bag filled with sand on the piglet's chin, to stretch its head back, and the piglet's legs are stretched gently back to induce the immobility response. However, animals may also be laid on a flat surface with or without cushioning, or in an induction box, and may be laid laterally, ventrally or dorsally. After this initial restraint, the animal voluntarily remains in the characteristic catatonic-like state for a varied period of time afterward.

Measures taken generally include: (i) number of inductions required to achieve the immobile state; (ii) time to first