Chapter 2: Functions and function attributions

2.1 Introduction

In section 1 of the previous chapter I distinguished three different approaches to a philosophical analysis of function attributions. The different approaches are often seen as rival accounts of the unique meaning the notion of 'biological function' is assumed to have. This attitude is perhaps best illustrated by the fact that all accounts (without any exception) mention the attribution of the function to propagate the blood to the heart or the heartbeat as a typical example of a function attribution that conforms to their approach. In section 2.2 I shall show that biologists use the notion of function in a number of different ways. These different kind of functions have different explanatory roles. As will become clear in the following chapters some of the supposed rival analyses of the notion of 'function' pertain to different kind of function attribution. In section 2.3 I discuss the role of these different kind of function attributions in biological enquiry.

An additional aim of this chapter is to deal with some terminological issues. Unfortunately, among functional biologists as well as among philosophers there is a considerable lack of unity in the use of basic terms. In order not to get lost in a linguistic morass it is important to stick to a number of terminological conventions. I shall introduce these conventions in the course of my argument. At this point it is worth stating that I shall use the term 'item' to refer to any part or substance of an organism (molecules, sub cellular organelles, cells, tissues, organs, organ systems and so on). Examples of items are chlorophyll molecules, chromosomes, the cell nucleus, membranes, white blood cells, hearts, limbs, fingers, the circulatory system and so on. Biologists often use the word 'structure' as a countable noun to refer to parts and substances.[1] This is confusing because that term is also used as an uncountable noun to refer to the way something is built or organized (as in 'the human heart has a four chambered structure'). I shall use the term 'structure' in this latter sense. Another term one often finds in the literature is 'trait'. I shall use the term 'trait' to refer to: (a) the presence or absence of certain items (such as hearts and circulatory systems), behavioural patterns (such as the fanning behaviour of a stickleback) and processes (such as the beating of a heart and the circulation of the blood) of/in individual organisms; and (b) the properties (features / characteristics) of the entities under (a) (such as the structure of the heart and blood-vessels and the rate of the heartbeat) or of the

[1] Other terms used to refer to items: "feature" (Bock & von Wahlert 1965, Bock 1980), "element" (Dullemeijer 1974), "component" (Lauder 1986, Lauder 1990).

organism as a whole (such the size of an elephant). Roughly spoken, the term ‘trait’ refers to the presence or character of an item or behaviour in certain organisms.

2.2 Different kinds of function

I distinguish four kinds of function, namely (1) what an item or behaviour does or is capable of doing (its activities and capacities), (2) the causal role of an item or behaviour in maintaining a complex activity or capacity, (3) the survival value of a certain trait, (4) the advantages of a certain trait for which it was selected in the past. $Function_1$ attributions describe what an item does or is capable of doing, whether or not this is important in the life of the organism. Claims about the second and the third kind of function are concerned with how a certain item or behavioural pattern is important in the life of the organism. Attributions of causal roles ($function_2$) describe how a certain item or behaviour is used, that is how it contributes to a complex activity or capacity (that is to a complex $function_1$), claims about survival value ($function_3$) explain why a certain trait is useful to the organisms that have it. The fourth kind of function attribution is concerned with the past significance of a certain trait. $Function_4$ attributions sum up the effects for which that trait was selected in the past.

2.2.1 Function as activity

Functional biologists often use the term ‘function’ in opposition to ‘form’ or to ‘structure’. Roughly spoken, ‘function’ in this sense refers to what an item does or is capable of doing and ‘form’ to what the item is made of, the way it is built and the way it looks like. For example, the beating of my heart is said to be a function (i.e. an activity it performs), whereas its size, its colour and its four chambered structure are aspects of its form. I shall refer to this use of the term ‘function’ as ‘function as activity’ or ‘$function_1$’. $Function_1$ attributions describe a certain kind of observable and measurable property whether or not these properties causally contribute(d) to some complex capacity, goal, survival, reproduction, selection, evolution or whatever. $Function_1$ attributions may be qualitative (e.g. “the heart beats” or “this gland secretes mucus”) or quantitative (e.g. “the heart rate of normal human beings at rest is about 70 beats per minute, but there is much individual variation” (Keeton & Gould 1993: 850)).

The form and the $function_1$ of an item together with the environment determine what an element is capable of doing in the life of an organism. However, not everything an item does or is capable of doing is important in the life of that organism. For example, the heart’s capacity to produce sounds is of no importance in the life of most non-human organisms. Following a suggestion of Bock & Von Wahlert (1965), I shall call the activities and capacities that are of no importance in the life of an organism ‘unutilized’ and the activities and capacities that are important ‘utilized’ (Bock & Von Wahlert talk of (un)utilized functions). Bock & Von Wahlert emphasize that non-utilized activities and capacities are important in biology for two reasons. One is methodological: “we generally do not know which functions [activities and capacities] are utilized and which are not utilized by the organism” (p. 274). The second is theoretical: the utilization of a yet unutilized activity or capacity is an important mechanism of evolutionary change. An example is the utilization of the capacity of muscles to resist shearing stresses. Muscles become rigid during contraction and will support a load acting at right angles of the muscle fibres. This capacity (which is unutilized in most muscles) becomes important in the tongue flipping mechanism of frogs: in this mechanism the musculus submentalis serves as a pivot about which another muscle (the musculus geniolossus) swings (Gans 1962).

I shall refer to the form and the function_1 of an item together as its ‘character’. I will, occasionally, use the terms ‘functional characteristics’ (without a subscript) to refer to function_1 properties, and ‘structural characteristics’ to refer to form properties. This means that ‘function_1 attribution’ is just another word for ‘description of a functional characteristic’.

2.2.2 Function as causal role

Attributions of causal roles are concerned with the way in which a certain item or activity is important in the life of the organism. They describe how that item or activity contributes to a certain complex activity or capacity. As will become clear, attributions of causal roles are the key to understanding explanation in functional biology. For that reason I will discuss three examples in some detail.

Example 2.1: the causal role of the heart

My first example concerns a classic: William Harvey’s (1628) study of the circulation of the blood. In the beginning of the seventeenth century physiologists thought of the structure and function of the human body in terms of a tripartition. This tripartition was based upon the principal cavities they observed in dissection: the abdomen, the thorax and the head, each with their own central organ: the liver, the heart and the brain. Associated with the body cavities three fluids were distinguished: (1) venous blood containing natural spirit, formed in the liver from nutrients drawn from the stomach and transported to the organs via the veins, was supposed to supply the organs with nutrients and to remove wastes; (2) arterial blood was supposed to bring heat and life (vital spirit) to the organs; (3) animal spirit, formed in the brain and carried to the organs via the nerves, was supposed to serve the functions of movement and sensation. The heart was thought to have a central causal role in the production of heat and life. The left ventricle of the heart is the primary source of heat. Blood from the liver (were it originates) is received in the right ventricle. During contraction blood is driven from the heart to the lungs where it takes up air. Air mixed with blood is sucked back to the heart during expansion. In the left ventricle aired blood from the lungs is mixed with venous blood from the right ventricle.

Motion and heat work on it to produce the vital spirits, essential for life. Heat and life together are transported to the organs via the arteries.

Harvey's study rejects this whole picture. In the first part of *De Motu Cordis* (Chapter I–VII) Harvey improves on previous studies of pulmonary circulation. It was previously held that the active movement is expansion and that this movement originates in the chest and the lungs. Harvey argues that the heart itself is muscular and that contraction rather than dilation is the active phase of heart movement. He observes that there are no pores in the septum separating the two ventricles and draws the conclusion that all the blood must go through the lungs to get from the right to the left ventricle. The most important innovation is in the second part (chapter VII–XIV). In this part Harvey presents the idea of a continuous circulation through the whole body, from the left ventricle of the heart to the arteries, through pores in the tissues to the veins and then to the right atrium of the heart. His main argument is surprisingly simple, namely that the amount of blood pumped out of the heart during an hour greatly exceeds the weight of the organism. Harvey estimated the volume of the left ventricle as about 2 to 3 ounces. If the heart beats 65 times per minute this would amount to 10 pounds of blood in a minute or 600 pounds in an hour. This is more than three times the weight of an average man. It is more than can be supplied by the food consumed and much more than is needed for nutrition.

> It must therefore be concluded that the blood in the animal body moves around in a circle continuously, and that the function of the heart is to accomplish this by pumping. This is the only reason for the motion and the beat of the heart (Harvey 1628: 104).

Harvey's second conclusion ("the function of the heart is to propagate the blood") has become the philosopher's standard example of a function attribution in biology. It is, however, important to be aware that this attribution did not come in isolation. As is often the case in scientific research Harvey accomplished several things at once. His central claim concerns the existence of a certain complex activity (function$_1$): the circulation of the blood. This hypothesis enables him to make sense of a lot of other phenomena, such as the movement of the heart and the presence of valves in the veins. He makes sense of these items or activities by showing how they contribute to the claimed activity: the heart propagates the blood and the valves in the veins maintain the direction of the flow. This contribution to a complex activity is their causal role (function$_2$) in that system.

Example 2.2: the causal role of the thymus

My second example is the discovery of the essential causal role of the thymus in the development of the immune system in the early sixties. This example is also discussed by Canfield (1964) and by Schaffner (1993).

A standard method in discovering the causal role of an organ is to remove that organ from the body and analyze the resulting disabilities. This method had been applied innumerable times to the thymus of adult animals of different classes of Vertebrates, but it produced no results. It appeared that the thymus had no causal role whatsoever and could be removed from the body without any loss. In 1961 Jacques Miller discovered that the extirpation of the thymus in *new-born* mice does lead to serious damage. The animals suffer from atrophy of certain lymphoid organs and a shortage of lymphocytes (a certain kind of white blood cells) and die within 3 or 4 months. This is how Miller summarizes his work:

> In this laboratory, we have been interested in the role of the thymus in leukaemogenesis. During this work it has become increasingly evident that the thymus at an early stage in life plays a very important part in the development of the immunological response (Miller 1961: 748)

This discovery marked the beginning of a completely new view on the development of the immune system. Until then it was thought that all the different kinds of cells involved in the immune response were produced locally in lymphoid organs. Experiments like this one led to the hypothesis of the existence of a relatively rare population of undifferentiated stem cells. Their descendants proliferate and differentiate in the thymus into so-called ‘T-lymphocytes’. The T-lymphocytes released by the thymus colonize certain areas in other lymphoid organs, after which these organs develop and start to produce their own T-lymphocytes. The effect of thymus extirpation in adults is small because a large stock of long living T-lymphocytes has been formed at that age and because after their initial development, shortly after birth, the lymphoid organs are able to maintain themselves independent of the thymus. What the extirpation experiments show is that the thymus causally contributes to the initial differentiation of T-lymphocytes.

Canfield (1964) discusses Burnet’s (1962) overview of the state of the art. In 1962 the interpretation of the experiments was not as clear as it is now. One plausible interpretation is that

> the thymus produces and liberates into the blood the lymphocytes that pass to spleen and lymph nodes and there settle down and mature into the populations of cells that look after the integrity and security of the body (Burnet 1962: 55).

One main problem was the causal role of the lymphocytes produced by the thymus. It was found that when the thymus is removed from a particular strain of mice at birth, they do not reject skin transplants (grafts) from unrelated mice or rats (as they would normally do within 10 days). This suggests that the lymphocytes have a causal role in the recognition and removal of anomalous cells (a function “necessary for the survival and proper functioning of the individual” (p. 57)).

In chickens there appeared to be two organs involved in primary lymphocyte production: the thymus and the bursa of Fabricius. The bursa gives rise to so-called ‘B-lymphocytes’ whose descendants are responsible for antibody production, the thymus liberates those cells whose descendants are involved in the recognition of anomalous cells. Burnet believes that is “highly likely” that in mammals “the thymus also carries out the function performed by the bursa of Fabricius in the chicken” (p. 57). Later research proved this to be wrong. Initial differentiation of B-lymphocytes in mammals is now thought to take place in the bone-marrow.

As in the case of the heart the discovery of the causal role of the thymus is a complex affair. The initial experiments proved that the thymus had some causal role in the maintenance of the organism, but the nature of the activity in which the thymus takes part remained unclear. The central breakthrough came with the hypothesis of differentiating stem cells. Another important clue was the discovery that there are two lineages of differentiating lymphocytes: B-lymphocytes, involved in anti-body production, and T-lymphocytes, involved in the recognition of anomalous cells. Given this insights it is possible to make sense of the thymus by showing how it contributes to the newly discovered activity: it initiates the differentiation of T-lymphocytes.

Example 2.3: the snake’s forked tongue

My third example is a recent one: Kurt Schwenk’s explanation of “Why Snakes Have Forked Tongues” (1994). In the 1920s and ‘30s it became clear that the tongue of squamate reptiles, such as lizards and snakes, is involved in chemoreception. By flicking their tongues these organisms sample environmental chemicals and deliver it to a pair of chemoreceptors in the snout (the so-called ‘vomeronasal organ’). However, it remained unclear why the tongues of snakes (and some lineages of lizards) are forked. Until recently the functional significance of the forking was sought in the delivery phase of the tongue flicking mechanism. The idea was that the two tips are inserted directly into the two openings of the vomeronasal organ. This idea conflicts both with observations of what happens during tongue flicking and with the observation that many reptiles without forked tongues are able to deliver chemicals effectively into the vomeronasal organ.

Schwenk argues that the explanation of the forkedness must be sought in the causal role of the tongue in the sampling phase. The taxa with highly forked tongues use their tongue to follow scent trails of preys and mates. They do so by comparing the stimulus intensities of two sides of the body (a mechanism called ‘chemosensory tropotaxis’). This allows them to detect the edges of a chemical trail and follow it with minimal deviation. The larger part of Schwenk’s paper deals with the evidence for the “ineluctable” (p. 1574) conclusion that the tongue has a causal role in trail-following. This evidence consists of: (1) observations of the behaviour during trail following, (2) experiments showing that removal of the forked portion of the tongue eliminates the ability to follow scent trails, but not the delivery of stimuli to the vomeronasal organ, (3) comparative data showing a rough correlation between depth of tongue bifurcation and ability to follow chemical trails, (4) observations of the nervous system showing circuits suitable for comparing signal strength from each side of the tongue.

Once the causal role of the tongue in trail-following is established this knowledge can be used to explain the forking both at the organismal and at the historical level.

> A trail-following function for forked tongues in squamates is compelling because of its explanatory power at several hierarchical levels (Schwenk 1994: 1576).

At the organismal level the forking of the tongue is explained by observing that it meets a requirement imposed on it by chemosensory tropotaxis. In order to be able to compare stimulus intensities at two points the organism must be able to sample chemicals at two points at the same time. This is made possible by the forking:

> For a snake or a lizard to use chemosensory tropotaxis, it must be able to sense simultaneously the chemical stimulus at two points. This requirement is met admirably by the forked tongue (Schwenk 1994: 1574).

To explain the forking at the historical level Schwenk fits this trait on a phylogenetic tree. This shows that forked tongues have evolved at least twice but possibly four times. He then states (p. 1576) that “the reason for its initial evolution remains obscure”. “Probably [...] it did initially confer a performance advantage in chemical delivery to the vomeronasal organ.” Subsequent selection for increased efficiency in scent trail-following “may have caused” the tongue to become increasingly forked, a trend evident in some clades.

Characteristics of attributions of causal roles

Attributions of causal roles describe how a certain part, organ or behavioural pattern contributes to an activity or capacity of a system of which that item or behavioural pattern is a part.[2] Basically, they have the following form:

> item / behaviour *i* has causal role *f* in maintaining activity / capacity *c* of system *s*.

[2]The term ‘function’ is also used to refer to how a certain organ works. For example, when biologists say that the right ventricle of the heart functions like a bellow and the left one like a pressure pump they are describing the way in which the heart works. This fifth use of term ‘function’ should not be confused with function as causal role.

For example:

(1) Harvey's function attribution (the heart propagates the blood) describes how the heart (*i*) contributes to the organism's (*s*) capacity to circulate the blood (*c*) (namely by propagating it (*f*));

(2) Miller (the thymus produces T-lymphocytes) describes how the thymus (*i*) contributes to the organism's (*s*) capacity to defend the organism against invaders (*c*) (namely by producing T-lymphocytes (*f*)); and

(3) Schwenk (the tongue has a trail-following role) describes how the tongue of a snake (*i*) contributes to the snake's (*s*) capacity to find preys and mates (*c*) (namely by detecting the trails of preys and mates (*f*)).

In these examples the system *s* is the organism as a whole. The system might also be a part of an organism, for example the valves in the veins (*i*) contribute to the capacity of the veins (*s*) to direct the blood back to the heart (*c*) by preventing the blood to flow back (*f*). Attributions of causal roles may simply state that an item contributes to a certain complex activity (e.g. "the heart has a function in circulation", "the thymus plays a part in the development of the immunological response") or describe that causal role in more or less detail (such as in "the heart is the source of energy of the circulatory system", "the thymus initiates the differentiation of T-lymphocytes", "the tongue has a trail-following role"). Sometimes an attribution of a causal role is even more complex and describes the activity (function_1) by means of which the causal role is performed in addition to the causal role itself. An example would be the statement "the heart contributes to circulation by beating".

In the case of the heart, a newly discovered activity (function_1), the circulation of the blood, resulted in a change in the causal role (function_2) attributed to the heart. Insight in the causal role of the thymus came only after the discovery of a yet unknown activity (function_1) to which the thymus contributes: the process of differentiating lymphocytes. In the case of the forked tongue no new activities had to be discovered: it turned out that the tongue has a causal role in a known activity: trail-following.

The distinction between function as activity (function_1) and function as causal role (function_2) is a distinction between statements describing a certain kind of observable properties and statements describing how (the activity of) that item contributes to some complex activity or capacity. If one reports about a certain item without taking into account the effects of that items on its environment (e.g. "the heart beats") one describes the activity of that item. Attributions of causal roles tell us about the effects of (the activity of) certain items in a larger context[3]. It depends, of course, on the environment whether or not the heart beats and how fast it will beat but in saying that the heart beats one does not say much about the influence of the heart on the

[3] And so do attributions of survival value (function_3) (as will become clear in the next section).

organism. However, if one states that “the heart propagates the blood” one takes into account a larger context of the heart’s activity (namely the circulatory system), which makes it appropriate to speak of the causal role of that item (in that larger context). Similarly, if a certain behaviour is described as “swimming” or “walking” or “flying” one does not take into account the influence of that behaviour on the environment, which means that one describes an activity. However, if one says that walking serves to acquire food one details the causal role of that behaviour in a larger context.[4]

2.2.3 Function as survival value

The term ‘function’ is also used to refer to the selective advantages of a certain trait in comparison with another trait. I call this use of the term ‘function’ ‘function as survival value’ (function_3). The study of survival value aims to find out why it is useful that a certain item or behaviour is present or absent and/or why it is useful to certain organisms that a certain item or behaviour has a certain character. Such an account is seldom given in one sentence.

Example 3.1: the survival value of egg shell removal in birds

An example of research into survival value is the study of the egg shell removal behaviour in birds. Many birds remove the empty egg shell after the chick has hatched. In most species, the egg is picked up and dropped at some distance of the nest, but there are several other ways to dispose of an empty egg shell. Tinbergen and his students (1962) performed a series of now classical experiments on this pattern of behaviour in the black-headed gull. Their study concerns the causes of the egg shell removal behaviour (i.e. the stimuli that elicit this behaviour) as well as its survival value. I restrict my account to the latter part of the study.

Tinbergen c.s. list a number of different ways in which the presence of an empty egg shell might be disadvantageous to the brood or to the parents. It might be that the sharp edges of the empty shells would injure the chicks, that the empty shells would interfere in some way or other with brooding, that the empty shells would provide a breeding ground for bacteria and moulds, or that the shells would draw the attention of predators. The egg removal behaviour is not performed by the kittiwake and the sandwich tern. These birds live in conditions were predation is low. This suggest that the main function of the behaviour is the maintenance of the camouflage of the brood (in all other cases there is no reason why the kittiwake and the sandwich tern should lack the response).

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[4] Whether or not a certain kind of movement counts as swimming, walking or flying depends, of course, on the environment, but, in labelling a certain behaviour as walking one does not imply much about the effect of that behaviour on the environment.

The hypothesis that the egg shell removal behaviour serves to maintain the camouflage of the brood presupposes that the brood *is* camouflaged. For that reason, Tinbergen c.s. performed a experiments which test this presupposition. These experiments show that carrion crows, herring gulls and black-headed gulls find eggs that are painted white more easily than normal eggs. It is concluded that

> the natural egg colour of the Black-headed Gull's eggs makes them less vulnerable to attack by predators hunting by sight than they would be if they were white; in other words their colour acts as camouflage (Tinbergen et al. 1962: 80/81).

The second series of experiments shows that predators find normal eggs covered with some straws of grass more easily if those eggs are given an egg shell at 15 cm. distance. It is concluded that

> the near presence of an egg shell helps Carrion Crows and Herring Gulls in finding a more or less concealed, camouflaged prey, and that therefore egg shells would endanger the brood if they were not carried away (Tinbergen et al. 1962: 82).

In a third series of experiments it is shown that this "betrayal effect" decreases rapidly with an increasing distance between eggs and shells. It is concluded the egg shell removal behaviour has survival value because it helps to keep predators away:

> The conclusion of this part of the study must therefore be that the eggs of the Black-headed Gulls are subject to predation; that in tests outside the colony the number of eggs found by Carrion Crows and Herring Gull is lower than it would be if the eggs where white; that the proximity of the egg shell endangers the brood; and that this effect decreases with increasing distance. While it will now be worth investigating the predators' responsiveness to eggs and shells in more detail, the facts reported leave little room for doubt about the survival value of egg shell removal as an antipredator device. Whether or not the response has other functions is of course left undecided (Tinbergen et al. 1962: 85).

In addition, Tinbergen c.s. observe that black-headed gulls wait for an hour or two before removing the empty egg shell, whereas waders such as ringed plovers and oystercatchers remove the empty shell immediately. They point out that this lack of promptness (of the removal action in black-headed gulls) has survival value because it tends to reduce predation by other black-headed gulls. After hatching, it takes the chick a few hours to dry. In any colony of black-headed gulls there are some individuals who prey selectively on nearly hatched eggs and wet chicks. They take the chick when the parents leave the nest to attack other predators or to remove the egg shell. Dry chicks are left alone. Waders don't live in colonies and their bills aren't fit for eating chicks. Tinbergen c.s. draw the following conclusion:

> We feel justified therefore to ascribe the lack of promptness of the response to this tendency of some members of the colony to prey on wet chick (Tinbergen et al. 1962: 110)

In the discussion section of the paper the authors discuss the anti-predator system of black-headed gulls as a whole. They explain among others that the camouflage of the eggs is important because breeding gulls leave the brood at the first sign of danger. This behaviour in turn is related to the suspicious colour of the adult: in species in which the breeding adult itself is camouflaged (such as ducks and pheasants) it usually remains on the nest. Tinbergen c.s. also show that the total system is best explained as a compromise between conflicting demands. An example of such a conflict was mentioned above: removal of the egg shell might help to defend the brood against carrion crows, but it increases the chance that the chick is eaten by a neighbour. A delayed response seems the best compromise between these conflicting demands.

Example 3.2: social foraging by black-headed gulls

Bleak-headed gulls usually fish in groups. Two hypotheses have been advanced concerning the survival value of this behaviour: the parasitism hypothesis and the co-operative hypothesis. According to the parasitism hypothesis (Ward & Zahavi 1973) the flocks consists mainly of birds that have followed another gull ("the leader") who has found a rich fishing place. The behaviour is advantageous to the followers because it enables them to locate food resources they would not have found otherwise. To the leader the following behaviour is neutral or negative (because it depletes the food source found by the leader). A group of Swedish researchers argues for the co-operative hypothesis (Gotmark, Winkler & Anderson 1986). On this hypothesis the flocking behaviour is useful because it enables each gull to catch more fish than it would have done if it fished alone (a fish that tries to escape from one gull might run into the beak of another). The research group put different numbers of gulls in a large aviary with a fishing pool and counted the number of fish the gulls catched. They found that birds in groups catch more fish (per gull) than do solitary birds in the same time and that the number of fish catched per gull increases if the group size increase. They draw the conclusion that flock feeding has survival value because it allows all gulls to catch more fish than they would have done otherwise.

Example 3.3: behavioural differences between two species of gazelles

In an issue of the *Journal of Zoology* K. Habibi, C.R Thouless & N. Lindsay (1993) compare the behaviour of the two species of gazelles that live in Saudi Arabia: the sand gazelle (*Gazella subgutturosa*) and the mountain gazelle (*Gazella gazella*). Their study reveals differences in group size and composition, mating season, territory size, territory marking, sexual and agonistic behaviour. Sand gazelles are seasonal breeders that form large herds of up to 65 individuals. Outside the breeding season, these groups consist of individuals of both sexes. During the breeding season, the males round up the females in harems (consisting of 15–20 individuals). The males hold territories which they defend vigorously, often engaging in prolonged fights. The territories are considerably smaller than those of the mountain gazelle and are marked both by urination marks and by a substance secreted by the preorbital glands. Mountain gazelles reproduce during the whole year. They live alone or in small groups of 2–5 individuals (usually consisting of a female and her offspring). Mountain gazelle males hold territories during the whole year. They exhibit threat displays rather than engaging in actual combat. The territories are about twice as large as those of the sand gazelle and they are marked by dung piles deposited at the border of the territory. Instead of chasing and herding all females that enter his territory (as the male sand gazelles do) a mountain gazelle male approaches a female after she has entered his territory and checks if she is in oestrus. If she is, he will closely guard her, attempting to prevent that she leaves his territory.

In the discussion section of their paper the authors try to relate the differences in terms of survival value. Their account is rather speculative, but it gives a good insight in the way in which appeals to survival value are explanatory.

The authors argue that the differences in territory behaviour (harems / individual territories) and the differences in the duration of the territory holding "may be attributable to" the difference in the timing of reproduction: the survival value of herding females in harems is greater in the case of seasonal breeding whereas the survival value of holding individual territories is greater in the case of reproduction during the whole year. During the rutting season of sand gazelles, a large proportion of adult females will be either sexually receptive or about to become receptive. Therefore, it is worthwhile for a male sand gazelle to round up all females, regardless of their immediate status and keep them in his territory. In contrast, the probability that a particular female mountain gazelle will soon become receptive is fairly low, at any time of year. Therefore, for a male mountain gazelle it is of no use to herd all females that come across his path. Rather, it is worthwhile to keep an individual territory during the whole year as this increases his chances of meeting receptive females.

The differences in the duration of the territory holding in their turn explain the differences in agonistic behaviour (fight / threat): the male mountain is familiar with his territory and with his neighbours which will increase the survival value of threat displays over actual combat (an invader has the disadvantage of fighting on unknown land, neighbours know what the other is worth).

Next, the authors suggest that the difference in territory marking "may be connected with" the difference in territory size: "scent-marks may be less long-lasting, and it would not be possible for a male to replenish them fast enough to be effective in a large territory".

The difference in the timing of reproduction is somewhat puzzling (according to the authors). Seasonal breeding is usually related to seasonal variation in food abundance. Northern populations of both species face this condition, however, only one of the species is a seasonal breeder. Perhaps the difference is related to a difference in "life strategy": sand gazelles live in open country and travel over long distance to find their food; mountain gazelles, on the other hand, live in more broken areas and stay in the same place. “An extended birth season is disadvantageous to a migrating herd as the neonates and lactating females would be under stress when travelling long distances to new feeding grounds”.

The snake’s forked tongue, revisited

The examples above are concerned with ethology. The study of survival value is as important in functional morphology, as it is in ethology. In fact, I have already discussed an example of an account of survival value in functional morphology, namely in example 2.3 (the snake’s forked tongue). As I said there, after having established that the tongues of snakes have a causal role in trail-following, namely to sample chemicals at two points at the same time, Schwenk observes that the tongue is able to perform this causal role if it is forked but not if it is blunt. This means that the forked character of the tongue is useful to the organisms that have it because it enables the tongue to perform its causal role to sample chemicals at two points simultaneously.

The thymus, continued

Note that, the story of the thymus, as I presented it above (example 2.2), ends with the attribution of a causal role, not with a claim about survival value. The research in the early 1960s made plain the causal role of the thymus (namely to initiate the differentiation of T-lymphocytes) but it remained unclear why it is useful to land vertebrates to have a special organ to perform this causal role. It also remained unclear why it is useful to have a complex mechanism in which differentiation is initiated in the thymus and continued in the lymphoid organs.

The first attempts to answer such questions date from the late 1980s. Rodney Langman’s *The Immune System* (1989) is an excellent example of an explanation in terms of survival value. Langman seeks to explain the way in which the immune system is organized. He does so by showing that the way in which the immune system is actually organized is more useful to the organisms that have it than other conceivable ways of organizing this system.

Unfortunately, the explanation is too complex to summarize it adequately in a sentence or two. The main line of explanation is this: in order to avoid self-destruction the immune system of an organism must be able to distinguish between what belongs to the organism (“self”) and what belongs to an invader (“non-self”). The knowledge of which things count as self and which count as non-self might be genetically fixed or it might be learned in the course of ontogenetic development. Langman argues that, in the conditions in which land vertebrates live, the latter mechanisms is to be preferred (if the criterion by which the immune system recognizes self is genetically fixed, invader cells might learn what the criterion is and use this knowledge to present themselves as self).

He also argues that the best mechanism to learn to distinguish self from non-self uses the following distinction between self and non-self: self is what is present during a long period, non-self is what is present during a relative short period. Learning to distinguish between self and non-self is a complex process. It is therefore more efficient to delegate the task to recognize non-self to specialized cells (the T-helper cells) which regulate the other immune cells (this saves the costs of learning all immune cells to distinguish between self and non-self).

Furthermore, as the learning process is complex it is more efficient to locate this process in a specialized organ and transport the ability to distinguish between self and non-self afterwards to the places where this ability is needed than to generate this ability everywhere where this ability might be useful. This organ is the thymus. Initially, young organisms produce many different types of proto-T-lymphocytes, each type is able to recognize another antigen (but it is not yet able to activate other immune cells). What happens in the thymus is that those proto-T-lymphocytes which recognize antigens of parts which are present during a long time are deactivated, whereas the other types of T-lymphocytes acquire the ability to activate other immune cells. The initialized T-lymphocytes are transported to the lymphoid organs were they mature and proliferate.

In sum, Langman’s main point is that in the conditions that apply to land vertebrates it has survival value to have a specialized organ to initiate the differentation of T-lymphocytes because this allows for a more efficient mechanism to distinguish self from non-self than distributed production would do.

Characteristics of claims about survival value

Claims about survival value state why under certain conditions it is more useful for an organism to have a trait it has rather than another one. Such claims have the following basic form:

> trait *t* has survival value in comparison with trait *t'* under conditions *c* because of ... (follows an explication of why an organism in condition *c* would be worse off if it had *t'* instead of *t*).

Examples are:

“if the eggs are subject to predation by carrion crows and herring gulls (*c*) it is more useful to remove the empty shell after the chick has hatched (*t*) than to leave it near the nest (*t'*) because the empty egg shells would break the camouflage of the remaining eggs”,

“flock-feeding (*t*) is more advantageous to gulls than solitary feeding (*t'*) because it enables them to locate food resources they would not have found otherwise“,

“flock feeding (*t*) has survival value (in comparison to solitary feeding (*t'*)) to gulls because it allows all individuals in the flock to catch more fish than they would have done otherwise”, "if the territory is large (*c*) dung piles (*t*) are better territory markers than scent-marks (*t′*), because the latter are more volatile and it would not be possible to replenish them fast enough",

"a forked tongue (*t*) is more useful than a blunt one (*t′*) to organisms that use their tongue in chemosensory tropotaxis (*c*) because a forked tongue enables them to sample chemicals simultaneously at two places, which would not be possible with a blunt one".

The explication might be quite a complex piece of reasoning, as we have seen in the case of territory behaviour and also in the case of the immune system.

Claims about survival value are essentially comparative: the presence of a certain item or behavioural pattern or the character of such an item or behaviour has survival value in comparison to another trait. Typically the comparison is counterfactual: an organism with a certain trait *t* is compared to a hypothetical organism that is similar to the real organism except that *t* is lacking or replaced by another trait *t′*. Arguments concerning survival value make ample use of a kind of counterfactual which I shall call 'functional counterfactual'. Functional counterfactuals state that an organisms would have certain disadvantages if a trait it has would be replaced by another one (or if they would lack that trait). Examples can be found in the examples above: "the natural colour of the eggs makes them less vulnerable to attack than they would be if they were white", "the eggs shells would endanger the brood if they were not carried away", 'flock feeding enables gulls to locate food resources they would not have found otherwise', 'flock feeding enables each gull to catch more fish than it would have done if it fished alone', 'it would not be possible for a male to replenish scent marks fast enough to be effective in a large territory', 'neonates and lactating females would be under stress when travelling long distances to new feeding grounds'.

The conditions in which the trait in question (*t*) is more useful than the alternative trait (*t′*) can be properties of the organisms to which the attribution applies (internal conditions) and / or characteristics of the environment in which those organisms live (external conditions). Quite often the conditions are not completely specified. In the case of flock feeding for example, the conditions remain vague. It is, however, clear that the behaviour of the prey (fish) is one on the conditions that makes flock-feeding useful. It is one of the aims of research in functional biology to identify the relevant conditions accurately.[5] It is important not to confuse the conditions that trigger a certain reaction in an organism and the conditions in which this response is useful. For example, the shadow of a bird of prey may cause a hiding response in a hare, but this behaviour is useful only if there really is a bird of prey. So, the shadow is a condition which

[5] In attributions of survival value names of taxa (such as gulls, gazelles, snakes) or pseudo-taxa (such as fishes) usually refer to all individuals that satisfy a vague set of properties rather than to lineages of individuals.

triggers the behaviour and the presence of a bird of prey is the condition in which this behaviour is useful. Only the latter kind of conditions occur in attributions of survival value.[6]

The survival value of the presence or character of an item or behavioural pattern is typically assessed in relation to the causal role of that item or behaviour pattern in the maintenance of the organisms in study. For example, the survival value of feeding in flocks (rather than on your own) is that the causal role of that behaviour (feeding) is performed better (more fish are caught) in the case of flock feeding than in the case of solitary feeding; the survival value of dropping dung piles rather than scent marks is that in large territories dropping dung piles performs its causal role (territory marking) better than leaving scent marks; the survival value of the tongue being forked is that it enables the tongue to perform its sampling role and so on. This means that attributions of survival value ($function_3$) typically depend on a preceding attribution of a causal role ($function_2$).

The ultimate criterion for determining which trait is better is the fitness of the organisms that have those traits. 'Fitness' is a technical term of evolutionary theory. It is best interpreted as the propensity to survive and reproduce in a particular environment (Mills & Beaty 1979). More specifically the fitness of an organism in a specified type of environment is defined as the expected number of offspring of that organism in that type of environment. Because of its dispositional nature fitness can not be measured directly. Evidence for judgements about fitness differences comes from two sources. First, judgements about fitness differences might be based on measurements of the actual number of offspring. If in a certain environment individuals with a certain trait t have on average more offspring than individuals with an alternate trait t' this is evidence that in that environment individuals having t are fitter than individuals having t'. Second, judgements about fitness differences might be based on an examination of physical design. For example, if eggs are subject to predation, it is plausible to assume that the fitness of the parents increases if the eggs are better camouflaged. To determine fitness on the basis of physical design several criteria are used (such as the number of fish catched in a certain time, the number of females fertilized, the efficiency with which a territory is hold). These criteria usually come down to the efficiency with which a certain causal role is performed. It is assumed that these criteria correlate with fitness but the exact relation between the criteria and fitness is often left unspecified. Attributions of survival value typically state that under certain conditions (e.g. large territories) a certain task (e.g. territory marking) is performed more efficiently in one way (e.g. by means of dung piles) than in another (e.g. by means of scent marks). It is assumed that individuals that perform territory marking more efficiently have a

[6] Biologists often use the terms "proximate cause" or "immediate cause" for the conditions that trigger a certain response and "ultimate cause" for the conditions in which a certain response is useful. This terminology is misleading because the so-called "ultimate causes" are not causes at all: they do not bring about the response.

higher fitness than individuals that perform territory marking less efficiently but the exact connection between fitness and efficient performance is left open.

Because causal roles and survival value are so often confused I will give an elaborate account of the differences in section 6.2. For the moment it suffices to mention the main differences. Causal roles are attributed to items or behavioural patterns, whereas claims about survival value concern traits, that is they concern the presence or character of an item or behavioural pattern. For example, one speaks of the causal role of the tongue and of the survival value of the tongue being forked (rather than blunt). An important difference between function as causal role ($function_2$) and function as survival value ($function_3$) is the kind of context which is taken into account. Both attributions of causal roles ($function_2$) and attributions of survival value ($function_3$) are concerned with how a certain item or behavioural pattern is important in the life of an organism. Attributions of causal roles take into account how an item is used to achieve some complex activity or capacity. Attributions of survival value take into account how the presence or character or activity of an item or behaviour influences the life chances of an organism and/or its descendants. One may speak of the causal role of an item or behaviour *in* a certain organism and of the survival value of that item or behaviour having a certain character *for* an organism in a certain environment. Another important difference is this: attributions of survival value are comparative and relative to a certain environment; attributions of causal role are not comparative and independent of the environment.

2.2.4 Function as selected effect

Evolutionary biologists sometimes use the term 'function' in a historical sense to refer to the effects for which a certain trait was selected in the past. I shall call this use of the term 'function' 'function as selected effect' or '$function_4$'. Functions in this sense are singled out by their role in the evolutionary history of the trait to which the function is attributed. Selected effects are past effects that help to explain the trait's current presence and/or frequency in the population.

Example 4.1: the function of inquilinism

A clear example of this use of the term 'function' can be found in the following quote from George Williams's classic on "Adaptation and Natural Selection" (1966) (this passage is also quoted by Wright 1973: 92/3):

> I remember a particularly relevant oral discussion of the function of inquilinism among pearlfishes. These slender-bodied fishes live in the respiratory systems of sea cucumbers. They apparently emerge at night to forage, and return at dawn to their hosts. They are largely without pigment, and there is some evidence that they are harmed by exposure to daylight. The question arose: Do these fishes enter the sea cucumber

> to avoid light, or do they do so to avoid predators? The feeling of the group seemed to be that if the behavior fulfills both needs, it must be regarded as having a dual function. This is a physiological valid conclusion, but teleonomically naïve. The two needs are surely not historically coordinate. All fish are under pressure to avoid predators, but very few are damaged by exposure to light. This must have been the condition of the ancestors of pearlfishes. The habit of entering holothurians developed as a defense against predators, and the fish became extremely specialized in behavior and physiology for exploiting the advantages of inquilinism. This required or permitted the degeneration of a number of adaptations: the caudal fin disappeared; the eyes were reduced; an the integumentary pigments and other defenses against light were reduced in effectiveness. In this way inquilinism became a necessary part of the defense against physiological damage by light. It was not, however, as a defense against radiation that the behavior originated (Williams 1966: 266/7).

In this quote Williams makes a distinction between the needs a trait satisfies and the functions it has: the behaviour of inhabiting sea cucumbers (holothurians) during the day satisfies both the need to avoid light and the need to avoid predators, but only the latter effect counts as a function of that behaviour. To count as a function the effect must not merely satisfy a need but the behaviour that satisfies the need must have *evolved as a means* to do so. The habit to live in sea cucumbers evolved as a means to avoid predators and so its function is to avoid predators. Once this habit had evolved the pearlfishes became dependent on living in sea cucumbers not only to avoid predators but also to avoid light. Hence, the behaviour satisfies the need to avoid light. However, the behaviour did not evolve as a means to avoid light and, according to Williams, avoiding light should, therefore, not count as a function of the behaviour. Williams calls the effects of a certain trait on which the organisms having the trait became dependent after the initial evolution, of that trait "secondary needs".

Characteristics of attributions of selected effects

Williams does not expound on what it means to say that the habit of entering sea cucumbers "developed as a against defense predators". The idea of 'a trait having evolved as a means to some effect' can be unpacked with help of a schematic account of the evolution of that trait. Suppose the habit of entering sea cucumbers emerged in the following way. Imagine an ancestral population of proto-pearlfishes that have not yet evolved the habit of entering sea cucumbers. In this population a mutant pearlfish developed the habit of entering sea cucumbers. As a result of this habit mutant pearlfishes were less easily catched by predators than were the original variants. As a result mutant pearlfishes produced more offspring than did the original variants. This in turn effected a rapid spread of the mutation, up to the point that only inquilinistic pearlfishes remained. According to this scenario, the habit of entering sea cucumbers evolved because it enabled its bearers in an ancestral population to avoid predators more effectively than its rivals that did not perform this behaviour. This might be abbreviated by saying that the habit of entering sea cucumbers evolved ‘as a means to’ avoid predators or by saying that the trait evolved ‘as the result of selection for’ avoiding predators. More generally, a trait evolved ‘as a means to’ a certain effect or ‘as the result of selection for’ that effect if the trait evolved because that effect conferred a greater relative fitness to its bearers in an ancestral population. This effect is its function as selected effect (function_4). Hence, a function as selected effect (function_4) is an advantage a certain trait conferred to its bearers in an ancestral populations that gave rise to the subsequent evolution of that trait (that is of the increase of organism having that trait).

To avoid misunderstandings it should be noted that the selected effects of a certain trait are not necessarily a subset of the effects of that trait that have survival value. Functions as selected effects concern past effects that need not occur in the current organisms having that trait. For example, if pearlfishes and sea cucumbers are kept in an aquarium without predators the inquilinistic behaviour does not have avoiding predators as survival value but that effect is still the effect for which the behaviour evolved. Hence, a clear distinction should be made between claims about survival value (function_3) and attributions of selected effects (function_4). Functions as selected effect are singled out by their role in the evolutionary history of the trait that has that function; functions as survival value are singled out by their value for the organisms that have that trait. An attribution of survival value is a claim about the importance of a certain trait for the survival, reproduction and/or fitness of the organisms that have that trait. An attribution of a selected effect is a claim about the evolutionary history of that trait. Claims about survival value tell you how a trait *could be* important for the *organisms* that have it, attributions of selected effects tell you what *has been* important in the evolution of the *trait* to which the function is attributed.

2.3 The role of function attributions in biological enquiry

2.3.1 Introduction

In the preceding section I distinguished four kinds of function attributions in connection with four kinds of function. In this section I discuss the role of these different kinds of function attributions in biological enquiry. I restrict myself mainly to the parts of biology that are called ‘functional animal morphology’ and ‘ethology’ (because these are the disciplines with which I am best acquainted). In order to specify the role of the different kinds of function attributions I distinguish seven types of questions that guide research in both these disciplines. I detail the role of the different kind of function attributions by stating how those different kind of function attributions are used in posing and answering the seven different types of questions. These questions concern: (1) the character of an item or behaviour, (2) its causal roles, (3) the causes and underlying mechanisms, (4a) the survival value of performing certain tasks, (4b) the survival value of having a certain character, (5) ontogeny, and (6) evolution. The different types of questions and the types of answers produced to these questions are summarized in table 2.1. In section 2.3.2 I present the different types of questions and answers in general. In section 2.3.3 and 2.3.4 I show by means of examples that this frame work of questions applies to functional morphology respectively ethology. My examples concern the heart of mammals and the singing behaviour of birds. In section 2.3.5 I specify the role of the different kinds of function attributions by relating these attributions to the framework.

Table 2.1: Different issues concerning the form and function of a certain item or behaviour

Problem area	**Typical questions**	**Type of answer**
(1) character	what does it look like? how is it built? what is its structure?	description of the form of an item or behaviour
	what does it do? what is it capable of doing?	description of the function$_1$ (activity) characteristics of an item or behaviour
(2) causal role	how is it used?	attribution of one or more causal roles
(3) causes and underlying mechanisms	how does it work?	physiological explanation
(4a) survival value of performing certain tasks	why does the organism have an item / behaviour that performs this role?	design explanation (of the need to perform a certain causal role)
(4b) survival value of having a certain character	why is it built the way it is? why does it work the way it does?	design explanation (of the character of an item or behaviour)
(5) ontogeny	how did it develop in the course of the ontogeny?	developmental explanation
(6) evolution	how and why did it evolve?	evolutionary explanation

2.3.2 Seven types of questions and their answers

Introduction

When functional morphologists and ethologists study a certain item or behaviour they typically ask seven types of questions. These questions concern:

1) the character of the item or behaviour in question,
2) the causal roles of the item or behaviour in question,
3) the causes and underlying mechanisms resulting in the realization of those causal roles,
4a) the survival value of performing the causal roles the item or behaviour in question performs,
4b) the survival value of having the character that the item or behaviour in question has,
5) the development of the item or behaviour in question in the course of the ontogeny,
6) the development of the item or behaviour in question in the course of evolution.

Functional morphologist ask these questions typically about an item under study (such as the heart), ethologists ask these questions typically about a behaviour (such as a bird's song).

The first type of questions concerns the character (form and $function_1$) of the item or behaviour under study. What does the item look like? How is the item built? What does it do? What is the structure of the behaviour? An example of a question of this kind in morphology is the question 'how is the heart built?'; an example from ethology is 'what is the structure of a bird's song?'. Research into this kind of question aims for accurate descriptions of the item or behaviour under study.

The second type of questions concerns the way in which the item or behaviour under study is used by the organism. Examples of questions of this type are 'what is the causal role of the heart?' and 'what functions does a bird's song have?'. These questions are answered by means of one or more attributions of a causal role ($function_2$ attributions). Examples are the attribution of the causal role to pump the blood around to the heart and of the causal role to claim a territory to bird's songs. Note, that causal roles are attributed to items or behaviours, not to their character.

Questions of the third type ask 'how does the item or behaviour in question work?'. That is, how is that item or behaviour able to perform the causal roles attributed to it in answer to a type (2) question? Examples are 'how is the heart able to pump blood?' and 'how are bird's songs produced?'. These questions concern the causes and underlying mechanisms of the activity of an item or of the behaviour of an organism. An answer to such a question is usually called a 'causal explanation' by biologists. As I use the term 'causal explanation' in a broader sense, I shall use the term 'physiological explanation' to refer to explanations in this area of research. Physiological explanations come in (at least) two different kinds. The first kind of physiological explanation explains certain changes in the state of an organism (such as changes in the frequency of the heartbeat, or changes in a bird's readiness to sing) as the effect of preceding changes in the organism or its environment. For example, changes in the frequency of the heartbeat are explained by changes in the activity of the nerves that innervate the heart, which in turn are explained by, say, the fact that the organism hears the alarming call of another organism. The second kind of physiological explanation explains the properties of an organism (including its capacities) as the result of underlying structures and mechanisms. An example would be an explanation of skin colour in terms of cellular pigments and their arrangement. An important subtype of the second kind of physiological explanation are the kind of explanations which I shall call ‘capacity explanations’. A capacity explanation explains a capacity of an item of an organism (or of the organism as a whole) by appeal to the capacities of the parts of that item (or of the organism as a whole) to perform a series of tasks which add up to the capacity to be explained. For example an explanation of an organism’s capacity to circulate oxygen would point out that oxygen circulation is brought about by a system of vessels which contain blood. The blood carries the oxygen and is pumped around by a heart. The two kinds of physiological explanations are related in the following way: explanations of the second type are concerned with the mechanisms that connect the causes and effects mentioned in explanations of the first type. For example, an explanation of the second type might concern the mechanism that bring about changes in the frequency of the heartbeat in response to changes in the activity of the nerves that innervate the heart..

The next two types of questions are both concerned with survival value. For that reason I have labelled them (4a) and (4b). Research into these questions aims for an explanation of the way in which an organism is built and the way in which it behaves in terms of the utility of that design in the environment in which that organism lives. Such explanations are usually called ‘functional explanations’ by those who engage in them. Because many philosophers use the term ‘functional explanation’ in a different sense I shall use the term ‘design explanation’ to refer to this kind of explanation. Design explanations are used both (in answer to type (4b) questions) to explain why it is useful to certain organisms that a certain item or behaviour has a certain character (for example why it is useful to snakes that their tongues are forked), and (in answer to (4a) questions) to explain why it is useful to certain organisms to have an item which performs a certain causal role (for example why it is useful to vertebrates to have a system which circulates oxygen). This utility is related to the other traits of those organisms and the state of the environment in which they live. A design explanation is a claim about the survival value of performing a certain role or of having a certain character.

Questions of type (4a) ask ‘why is it useful to the organism to have an item or behaviour that performs the causal roles attributed to the item or behaviour under study?’. Examples of such questions are ‘why is it useful to circulate the blood?’ and ‘why is it useful to defend a territory?’. Design explanations that answer such questions identify a need that is satisfied by the performance of the role in question and relate that need to the other traits of the organism and to state of the environment in which it lives. An example is the explanation of the presence of a circulatory system in vertebrates by pointing out that because of their size these organisms need to transport oxygen actively rather than passively (that is by mere diffusion). It is a law of physical chemistry that the rate of diffusion decreases proportionally to the distance over which diffusion takes place. In large organism the distance between the inner organs and the outside is such that the rate of diffusion is too slow to get enough oxygen to the organs. This problem is solved by transporting oxygen actively from the outside to the organs. I discuss this example in more detail in section 4.2.3.

Questions of type (4b) ask ‘why it is useful that the item or behaviour under study has the character it has?’. Examples of such questions are ‘why is it useful that the heart of mammals consists of four chambers?’ and ‘why is it useful to defend a territory by singing (rather than by attacking intruders)?’. Design explanations that answer such questions proceed by showing that (in the conditions applying to the organisms concerned) the causal role in question is better performed by an item or behaviour with the character to be explained than by items or behaviours with some plausible alternative character. An example is the explanation of the forkedness of the snake’s tongue (example 2.2 of section 2.2.2) by pointing out that this form meets a requirement imposed on it by the trail-following role of the tongue, namely the requirement to sense simultaneously the chemical stimuli at two points.

The next kind of questions (5) consists of questions that concern the ontogenetic development of the item or behaviour under study. How did this item or behaviour develop in the course of the ontogeny and how is this development controlled? Examples of such questions are ‘how does the heart develop and how is this development regulated?’, ‘how do bird songs develop?’, ‘is the song pattern innate or learned from parents?. The explanations proposed in answer to questions of this kind are usually called ‘developmental explanations’. Developmental explanations explain how a certain trait arises in the course of the ontogeny. In the example of the circulatory system, a developmental explanation would (among other things) point out that the initial differentiation of blood vessels is probably caused by a process of induction (see for example Balinsky 1975: 410). The first blood vessels develop before circulation starts. If the heart rudiment is removed before it starts to beat the large blood vessels continue to develop for some time. Further development depends on the direction and amount of the blood flow through these vessels. Developmental explanations and physiological explanations shade into each other. The main difference is that developmental explanations are concerned with transitions that usually occur only once in the lifetime of an organisms and physiological explanations with transitions that may occur repeatedly.

The part of biology that is concerned with individual development is called ‘developmental biology’. Developmental biology is not limited to type (5) questions about the traits of the adult or larva. Indeed, developmental biology addresses questions of all seven types, but they are asked in regard to development rather than in regard to the adult individual. For example, most textbooks on developmental biology address the following type (4b) question: ‘why does the heart starts to beat early in development (much earlier than all other organs start to perform their causal role)?’. The answer to this question (the embryo at this stage already needs a system to transport oxygen) is a design explanation. Another example concern the items, activities or structures which develop in an embryo and which are not precursors of the organs etc. of the adult or larva but have a causal role in the maintenance of the embryo. Examples are organs which store and utilize yolk (the yolk sac and vitelline blood-vessels), organs which store wastes (such as the allantois) and organs which protect the embryo from desiccation (such as the amnion, the chorion and the cavity between them). About such organs all seven questions are asked. I will not pay much attention to developmental biology in the remainder of this book.

The last kind of questions (6) consists of questions concerning the evolution of the item or behaviour under study. How and why did this item or behaviour evolve and how and why did it acquire the character it has? Examples of such questions are ‘how did the heart became four chambered?’ and ‘how did bird songs became complex?’. Explanations that answer questions of this kind are called ‘evolutionary explanations’. Evolutionary explanations explain how a certain trait developed in the course of the history of the lineage. There are several processes that may explain how form, function$_1$ and behaviour changed in the course of the history. Not all these processes are evolutionary processes. For example, humans are larger now than in the past. This change is a direct effect of better nutrition and medicine and does not involve genetic change. For that reason, this historical change is not evolutionary. Evolutionary processes include mutation, gene flow, recombination, selection and genetic drift. I shall call evolutionary explanations that focus on evolution by natural selection ‘evolutionary selection explanations’.[7] Evolutionary selection explanations explain the presence or character of a certain item or behaviour by telling how and why natural selection modified that item or behaviour in the course of the history.

The part of biology that is concerned with evolution is called ‘evolutionary biology’. Evolutionary biology is broadly defined as the study of the history and mechanisms of evolution. The two main kinds of evolutionary phenomena are branching and character change. Branching is the splitting of lineages of populations into separate branches. Character change is the change of frequencies of characters of individuals in a population over generations.

In the remainder of this section I will give some examples of the application of these types of questions in functional morphology and ethology.

[7] In chapter 7 I distinguish a second kind of selection explanation, namely equilibrium selection explanation.

Functional morphology

Functional morphology is usually broadly defined as the study of the relations between form and function.[8] Its main concerns are:

1) to describe the forms and the functions_1 (activities) of the parts and organs of the body (and of the body as a whole);
2) to find out what the causal role is of those items in the maintenance of the organism;
3) to explain the character and capacities of those items and the changes in their state in terms of underlying structures and mechanisms;
4a) to explain why it useful to perform the causal roles those items perform in the context of the organism as a whole and the environment in which it lives;
4b) to explain the character and capacities of those items in terms of their utility in the context of the organism as a whole and the environment in which it lives;
5) to explain how those items (their form, activity and causal role) have developed in the course of the ontogeny;
6) to explain how those items (their form, activity and causal role) have evolved in the course of history.

Consider, for example, how these questions apply to the heart. The discussion of "the structure and function of the heart" in an arbitrary text on functional morphology (for example Johansen 1977: 387-389) starts with a description of the structure and activity (function_1) of the mammalian heart (question 1). This knowledge is typically conveyed by means of diagrams and tables. I restrict myself to a few typical characteristics of the structure of mammalian hearts. The heart is a hollow muscle containing two separate cavities (a left one and a right one), each consisting of two compartments: an atrium and a ventricle. The left channel contains oxygenated blood, which flows from the lungs to the organs; the right channel contains deoxygenated blood, which flows from the organs to the lungs. Inside each channel the blood moves from the atrium to the ventricle. The atrium and the ventricle are separated by valves. There are also valves at the end of the ventricles. The left and the right ventricle differ markedly in their structural characteristics. The cavity of the right ventricle is narrow space enclosed between two large surfaces; its wall is of moderate thickness. The cavity of the left ventricle has a cylindrical shape with a conical end, it is enclosed in a heavy layer of muscular tissue.

The causal role of the heart in the maintenance of the organism (question 2 – how is the heart used?) is well known to philosophers: the heart contributes to the organism's capacity to circu-

[8] Note that functional morphology if it is defined in this broad sense is not a subdiscipline of morphology if morphology is defined as the study of form.

late blood by pumping the blood around. Note that this answer is part of a capacity explanation of a capacity of a system of which the heart is a part, namely the capacity of the circulatory system (consisting of heart, blood and blood-vessels) to circulate blood.

Subsequently it is asked how the heart works: how is it able to pump blood, how is the flow directed and how is the heart's activity regulated (question 3)? Note that these questions come down to the question 'how is the heart able to perform the causal role it has?' Hearts are, in essence, two-stroke pumps with a filling phase and an emptying phase. The blood is pushed forward by contracting the muscular tissue in the walls of the chambers. The right ventricle works like a bellows (the walls are pulled together and a moderate force is generated which works over a relative large distance), the left one like a pressure pump (the chamber is fiercely constricted). The valves assure unidirectional flow of the blood within the heart and work passively. Note that this capacity explanation attributes causal roles to the parts of the heart. For example it attributes the causal role to generate force to the muscular walls and the causal role to prevent blood from flowing in the wrong direction to the valves.

The answer to the type (4a) question concerning the utility of having (rather than lacking) the ability to pump blood seems trivial: if the circulatory system did not have a pump it would not be able to circulate blood.[9] Note that this answer refers to the causal role of the encompassing system.

Numerous type (4b) questions can be asked about the way in which the pumping role is implemented. For example, 'why is the causal role to pump blood implemented by means of special organ rather than by contracting the arteries?', 'why are there two pumps (a left one and a right one)?', 'why are the two pumps implemented in one organ?'. Other type (4b) questions concern the specific characteristics of the pump. Why does each pump consist of two parts (an atrium and a ventricle)? How to explain the structural and functional differences between the left and the right ventricle? Why does it beat with the frequency with which it beats (this frequency varies between species)? Why does it have the volume it has? Why is it important that the blood flows in only one direction? And so on ....

Type (4b) questions are answered by means of a design explanation of the character of the item or behaviour in question. Consider, for example, the answer to the question why birds and mammals have a double circulation (the blood passes the heart twice) rather than a single circulation (in which the blood would pass the heart only once). When the blood passes the capillaries of the lungs, the blood pressure drops to a level too low to get the blood through the capillaries of the body. A single circulatory system in which the heart pumps the blood directly from

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[9] Because the answer is obvious, the question is often omitted in text books. However, the question can be made more interesting by introducing more interesting alternatives for pumping (more interesting than simply lacking a pump): why for instance is the blood circulated by means of a pump rather than by means of cilia?

the lungs to the organs would need a pump that generates much more pressure than the hearts of birds and mammals do. Such a pump would create several problems. One problem is that the capillaries of the lungs would be blown up because of the high pressure of the blood they contain. Other problems concern the design of such a pump. A double circulatory system in which the blood is routed back to the heart after it has passed the capillaries of the lungs solves the problem created by the drop in blood pressure when passing the lungs without creating the problems a much stronger pump would do. This is a typical design explanation pointing out that given the structure of the lungs the role performed by the system of heart and blood vessels is performed better if that system contains two pumps than if it contains one.

Next, consider the question why both pumps have two compartments. This is because otherwise the blood would flow not fast enough (the two chamber structure reduces the time needed to fill the pump because one part is filled while the other pumps).

Especially interesting is the design explanation of the differences between the structural and functional characteristics of the right and the left ventricle. The right ventricle pumps the blood through the pulmonary circuit (i.e. via the pulmonary artery to the capillaries of the lungs and via the pulmonary veins back to the left atrium). The left ventricle pumps the blood through the systemic circuit (i.e. via the aorta to the capillaries of the organs and back to the right atrium via the veins). The different characteristics reflect the different demands posed upon the pump by these different circuits. The pressure gradient in the systemic circuit is many times that of the pulmonary circuit. This means that the pump of the systemic circuit (the left ventricle) must generate much more pressure than the pump of the pulmonary circuit (the right ventricle). However, as the two circuits are connected in series the pulmonary circuit must transport the same volume of blood per unit of time as the systemic circuit. In order to transport the same amount of blood in the same time with less force the blood must be moved over a greater area in that time. This explains why the left ventricle works as a pressure pump and of the right one as a volume pump. It also explains the form of the cavities and the walls (a volume pump needs a larger surface to volume ratio than a pressure pump and in order to generate high pressures one needs a thick layer of muscle).

Type (5) questions concern the development of the heart in the course of the ontogeny. Heart development starts early in the ontogeny when the embryo is not yet separated from the yolk sac. The heart starts as a paired organ in the mesodermal germ layer. At each side of the body a longitudinal tube develops. As the embryo separates from the yolk sac in the pharyngeal region these two tubes fuse into each other to form a single cavity, in front of and behind this region the tubes remain separate. At the same time the tube elongates and twists resulting in four chambers in series: sinus venosus, atrium, ventricle and conus arteriosus (in the direction in which the blood flows). This resembles the structure of the adult heart in typical fish (except for the absence of valves). Further development includes: subdivision of both the atrium and the ventricle in two parts, absorption of the sinus venosus in the right atrium, separation of the pulmonary veins from the sinus venosus so that they open in the left atrium, and subdivision of the conus arteriosus into the pulmonary trunk originating from the right ventricle and the aorta originating from the left ventricle. The heart is the first organ which starts to perform its causal role. Beating begins even before the two tubes are fused. The heart's development is dependent on its own activity. If there is no blood flow, development stops shortly after the fusion of the tubes. The size of the heart causally depends on the volume of blood passing through it.

Type (6) questions concern the evolution of the heart. The vascular system of the ancestral vertebrates is assumed to resemble that of amphioxus (a non-vertebrate chordate).[10] This system is sketched in fig. 2.1.[11]

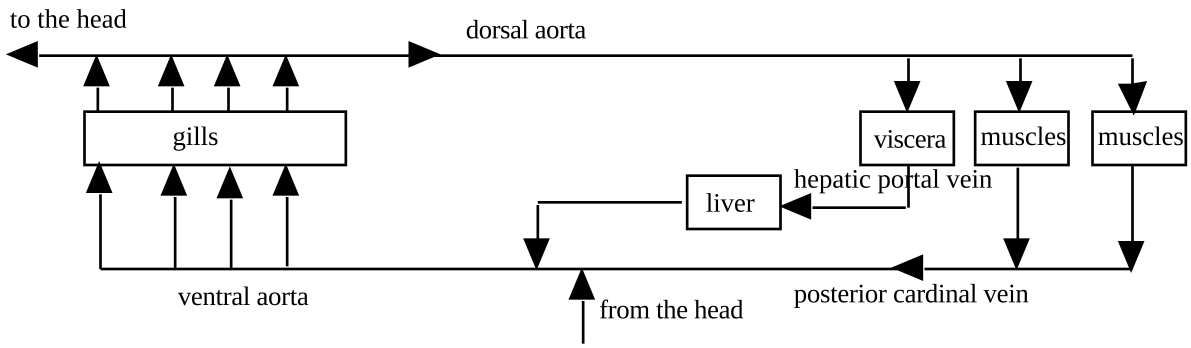

Fig 2.1: blood circulation in amphioxus

Amphioxus does not have a separate heart; its blood is propelled by peristaltic contraction of some large blood vessels in the pharyngeal region, the main one is the ventral aorta. About fifty branchial vessels branch off from the ventral aorta, pass through the gills[12] and reunite into a large longitudinal blood-vessel the dorsal aorta. The branchial vessels are enlarged at their base and these enlargements contract, thus contributing to the propulsion of the blood. From the dorsal aorta blood is routed to the vessels of the segmental muscles and to the vessels of the intestine. Blood from the segmental muscles returns via the cardinal veins to the ventral aorta. Blood from the intestine is routed back via the liver to the ventral aorta. It is supposed that the vertebrate heart developed somewhere in the ventral aorta of an ancestor which an amphioxus like vascular system, resulting in the fish-like circulation outlined in fig 2.2.

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[10] The phylum Chordata consists of three subunits with the rank of subphylum: the Tunicata, the Cephalochordata (of which amphioxus is a species) and the Vertebrata (of which the mammals are a class).

[11] Note that the figures are highly schematized. Important things which are not represented in these schemes include the structure of the heart, the blood vessels to and from the head and the renal portal system.

[12] The gills in amphioxus and, presumably, in vertebrate ancestors have a nutritional rather than a respiratory role. Respiration in amphioxus occurs through the skin.

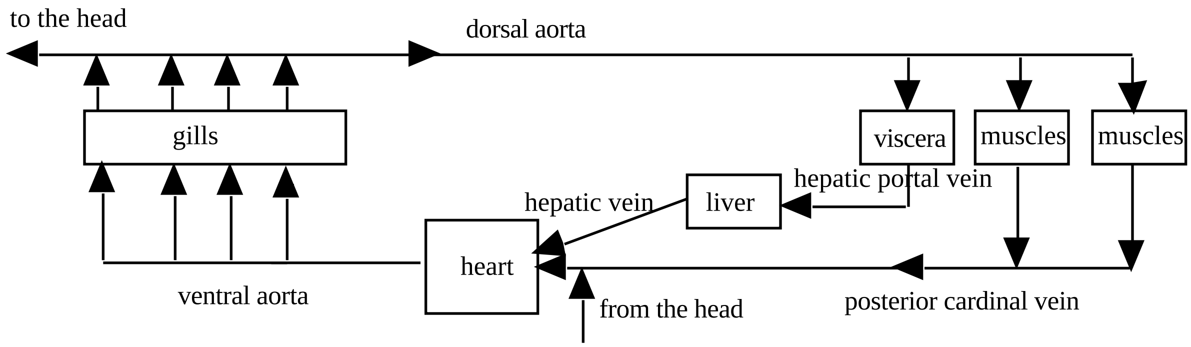

Fig 2.2: blood flow in a fish-like ancestor with a single circulation

The double circulatory system of birds and mammals evolved from such a single circulation in fish-like ancestors. The evolutionary explanation of this transition (see, for example, Johansen 1977: 374-377) points out that birds and mammals evolved from ancestors that changed their respiration from the gills to the lungs. The evolution of a double circulation in modern birds and mammals from a supposed single circulation in their fish-like ancestors started some 350 million years ago. The climate conditions of the time brought about very low oxygen concentrations in large tropical fresh-water basins. As a result many species of fresh-water fish developed a special organ for air breathing in addition to their gills.[13] These species relied on their lungs for oxygen absorption, but retained their gills for the elimination of oxygen and osmoregulation. Such a bimodal (lungs & gills) mode of respiration favoured rearrangements in the vascular system that increased the effectiveness of the new organ for gas exchange. The heart of this ancestral organism probably consisted of four chambers in series: sinus venosus, atrium, ventricle and conus arteriosus (this is the same structure as that in typical fish). The arrangement of the main blood vessels of the ancestral organism is outlined in fig. 2.2. The blood is supposed to flow from the heart via the ventral aorta to the gills and then to the dorsal aorta. The dorsal aorta is a large blood vessel which runs over the entire length of the body. From the dorsal aorta many main arteries branch off which transport the blood to the viscera (intestine) and the muscles. Blood from the viscera returns to the sinus venosus of the heart via the liver and the hepatic vein, blood from the muscles returns to the sinus venosus via the cardinal vein.

The lung evolved as a diverticulum of the foregut. This resulted in the vascular arrangement sketched in fig. 2.3. Blood is routed from the heart to the gills and then to the organs, among which the lung. Blood which is oxygenated in the lungs flows via the hepatic vein to the sinus venosus of the heart.

[13] Modern teleost fish too are supposedly derived from an ancestor having a lung. This lung developed into a swim bladder.

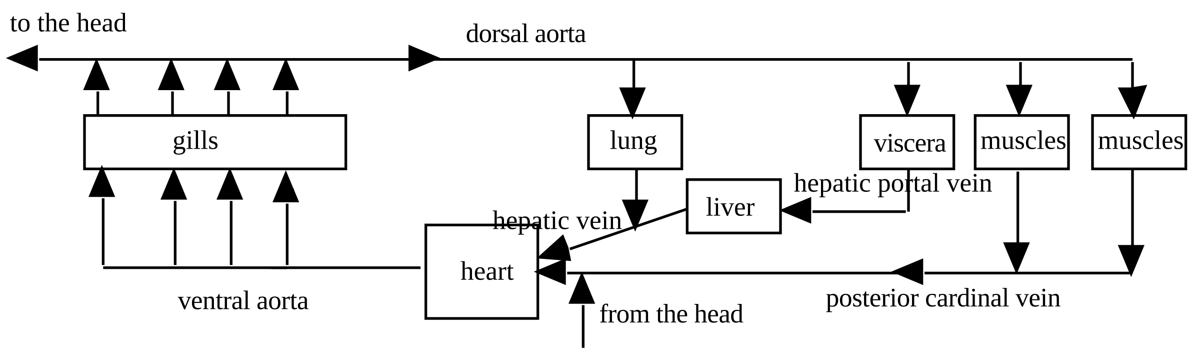

Fig 2.3: development of the lungs

Note that already at this stage oxygenated blood does not flow directly from the main respiratory organ (the lung) to the organs that need the oxygen, as is the case in a single circulation. Instead it flows from the lungs back to the heart and then to the other organs (this is a consequence of the fact that the lung evolved as a an organ in an organism in which the blood flowed in the manner sketched in fig. 2.2). As a result oxygen rich blood from the lungs mixes with oxygen poor blood from the organs. This arrangement favours structural changes in which oxygenated and deoxygenated blood are kept separate. An arrangement in which oxygenated and deoxygenated blood are separated is more efficient because in this situation the concentration gradient in the lungs as well as in the oxygen consuming organs is greater, which speeds up the diffusion process at these sites. The first step in the direction of more efficient air breathing was the development of a separate blood-vessel (the so-called ‘pulmonary vein’), routing blood from the aerial gas exchange organ (the ‘lung’) directly back to the atrium of the heart (fig. 2.4).

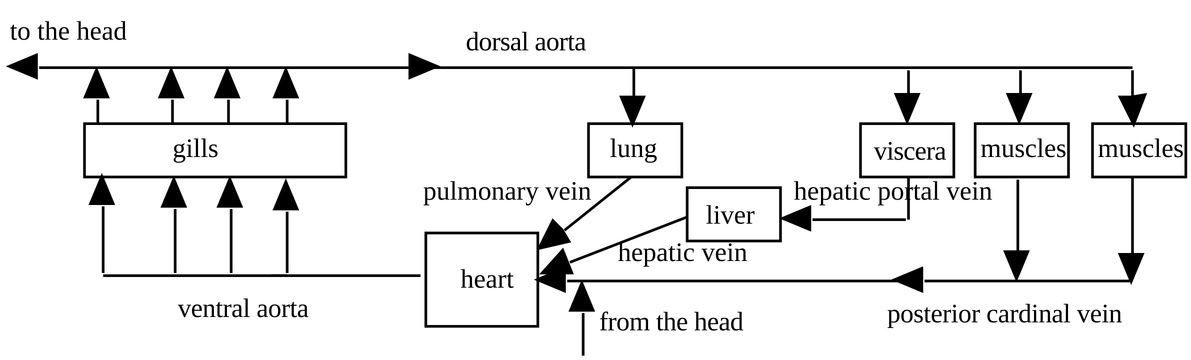

Fig 2.3: emergence of a pulmonary vein

Thus, the pulmonary vein emerged as a means to minimize the mixing of oxygenated and deoxygenated blood in an aquatic ancestor with a bimodal mode of respiration. In air breathing fish the surface area of the gills became reduced as air breathing became more important. The reduction of the gills is correlated with changes in the aortic arches. The first change was the development of a pulmonary artery (fig. 2.5).

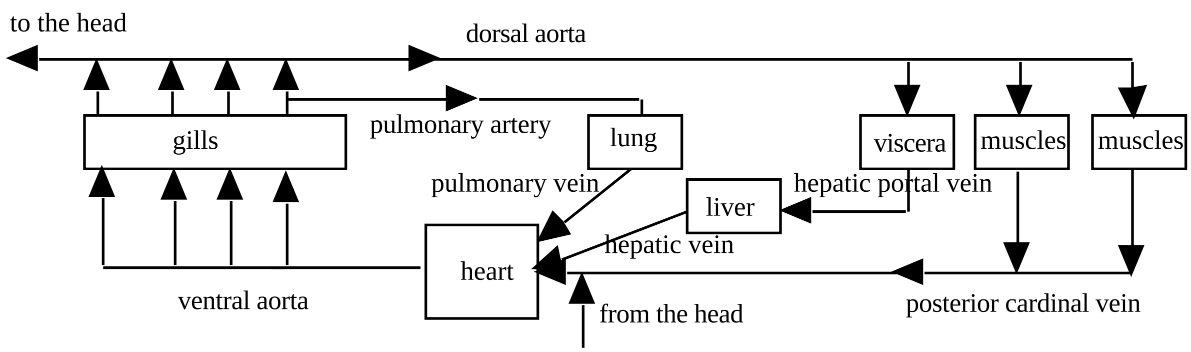

Fig 2.5: emergence of pulmonary artery

The development of specialized blood vessels routing the blood from the heart to the lung and back from the lung to the heart was accompanied by structural changes in the heart. In the stage sketched in fig 2.3 the pulmonary vein (containing oxygen rich blood from the lungs) enters the heart in the left part of the atrium, whereas the hepatic and cardinal veins (containing oxygen poor blood from the organs) enter the heart in the sinus venosus. The left and the right part of the atrium are partially separated by means of a septum. The left part receives oxygenated blood from the pulmonary vein, the right part receives deoxygenated blood from the sinus venosus. In the ventricle two partial septa develop (from opposite sites) which separate the left and the right part of the ventricle. The conus arteriosus modifies such that deoxygenated blood from the right part of the ventricle is shuttled to the branch of the aorta from which the pulmonary artery departs and oxygen rich blood from the left part of the ventricle is shuttled to the other branches. In the subsequent history the sinus venosus is gradually incorporated into the right atrium, the septum in the atrium becomes complete, the two ventricular septa fuse, and the conus arteriosus reduces. This results in the four chambered heart found in birds and mammals. In the circulatory system of these organisms oxygen rich blood and oxygen poor blood are completely separated (fig. 2.6).

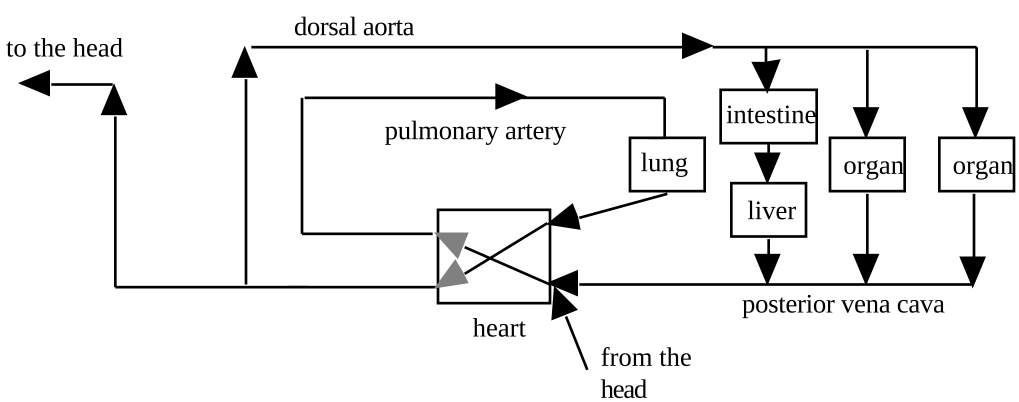

Fig. 2.6: double circulation in birds and mammals

Ethology

Ethology is often broadly defined as “the biological study of animal behaviour”. It’s main concerns are:

1) the description of behavioural patterns,
2) the causal role of those behavioural patterns in the maintenance of the organism,
3) the causation of occurrences of behavioural patterns and the mechanisms by which behaviour is produced,
4a) the survival value of performing certain causal roles,
4b) the survival value of the different forms of behaviour,
5) the ontogenetic development of behaviour,
6) the evolution of behaviour.

I shall discuss these questions with an emphasize on the singing behaviour of birds.

The empirical foundation of ethology consists of accurate descriptions of the behaviour of the organisms under study (the so-called ‘ethograms’). These descriptions may concern both the structural aspects of behaviour (such as the order in which certain activities are performed) as the functional ($function_1$) aspects (how fast does a leopard run? how many fish does a gull catch within an hour?). Beginning students are warned not to make hypotheses about the causal role of the behaviour when they describe behaviour. Singing is a typical example of a behaviour that is characterized in terms of its structure. Bird sounds are traditionally divided into calls and songs. One of the main distinctions between these two is that songs are much more complex in structure than calls.

The second kind of problems (type (2) questions) concerns the causal role of the described behavioural patterns in the maintenance of the organism. After the behaviour is described one may hypothesize about the causal role of that behaviour in some larger context. For example: the horse’s habit to pile up their faeces and the fox’s habit to urinate at certain places have a causal role in keeping a territory; the gull’s habit to catch fishes has a causal role in feeding and so on. According to Catchpole (1979: 31-37) the two main causal roles of singing in birds are attracting females and repelling rivals (other possible causal roles are synchronizing the reproductive behaviour of a pair and maintaining the strength of the pair-bond). In saying that the singing attracts females one describes how the singing contributes to the capacity to reproduce, in saying that the singing repels rivals one describes how the singing contributes to the capacity to maintain a territory. The song acts as a first line of defence. If singing does not work (e.g. because the birds are muted by an experimenter) invaders are expelled by visual display and actual attack. There appears to be an interesting difference between the causal roles of singing in reed warblers and in sedge warblers: in reed warblers singing has both a sexual and a territorial role, whereas in sedge warblers it has only a sexual role.

Type (3) questions are concerned with the generation of behaviour: the external causes (stimuli), the internal causes (motivation), the mechanisms that link sensory information to behaviour and the way in which the behaviour is organized. The explanations is this areas of research are usually called ‘causal explanations’ by ethologists. An example is the explanation of why a certain male chaffinch starts to sing in the spring by pointing to the increasing length of the day. These explanations are of the same kind as ‘physiological explanations’ in functional morphology, and I will use that latter term to avoid confusion with other uses of the term ‘causal explanation’.

The next two kinds of problems (type 4a and type 4b questions) concern the survival value of behaviour. Explanations that appeal to survival value are usually called ‘functional explanations’ or ‘ecological explanations’ by ethologists. I shall use the term ‘design explanations’. Design explanations in ethology explain why a certain behaviour is performed in the way it is performed in terms of the utility of performing this behaviour to the organism that perform it. This utility is related to the other traits of the organism and the state of the environment in which they live.

Type (4a) questions concern the utility of performing the roles performed by the behaviour under study. After having concluded that singing has a causal role in reproduction and in maintaining a territory one continue and ask ‘why is it useful to reproduce?’ and ‘why is it useful to defend a territory (rather than occupy an undefended living space)?’. The answer to the first questions is obvious and trivial.[14] The answer to the second questions is an important subject of research.

Type (4b) questions concern the way in which those roles are implemented. An example is Catchpole’s (1979: 31-37) explanation of why in reed warblers singing has both a sexual and a territorial role, whereas in sedge warblers it has only a sexual role. This difference is explained by means of a design explanation by pointing to the different environmental conditions:

> Reed warblers inhabit dense, impenetrable reed beds where vision is poor, and have small territories which need to be constantly defended by vocal means. In contrast, sedge warblers are more scattered throughout open, terrestrial habitats, where vision is good and less premium placed upon focal defense (Catchpole 1979: 33)

In other words: given the environmental conditions in which reed warblers live they need to defend their territory by singing, whereas given the environmental conditions in which sedge warblers live, they can do without.

[14] However, the answer to the question why reproduction in e.g. birds takes the form of sexual reproduction (a type (4b) question) is not obvious and far from trivial.

Type (5) questions ask for an explanation of the behaviour under study as the result of the interaction between genetic and environmental influences. It was Thorpe who started the study of song development in the late fifties (Thorpe 1958). If a young chaffinch is reared without ever hearing a singing chaffinch it will never be able to sing the full song. This shows that the young chaffinch must *learn* the song from its father. Thorpe shows that the juvenile learns the song in the first few months of its life, long before it is able to produce that song itself. The period during which the young is able to learn the song is called the 'critical period'. The young chaffinch does not learn any song it hears in its youth. It picks up only the songs of the chaffinch and songs that are very much like those of the chaffinch, such as that of the willow warbler and the tree pipit. Hence, there must be an *innate* component that enables the juvenile to recognize the song of its father as one that it should learn. Marler (1975: 24-29) explains this pattern of development, that is manifested by the chaffinch and many other birds, by hypothesizing the existence of an inherited, but modifiable, auditorial template. During the critical period this template is improved in view of the adult model. The template itself determines which songs are accepted as a model. The improved template specifies which dialect the bird has learned. When the young starts to sing it first produces the so-called 'subsong', which differs from the full song in a number of ways. It is more quiet, has a much wider range of frequencies and has little or no structure. The vocal output is gradually matched to the dialect specified by the improved template until the bird manifests its full song.

Not much is known of the evolutionary history of bird songs (type 6 questions). An intriguing question in this area is the question why songs have become so complex during evolution. Bird sounds are traditionally divided into calls and songs. One of the main distinctions between these two is that songs are much more complex in structure than calls. Yet, simple calls are quite capable of carrying the information that is conveyed via songs. Indeed, only songbirds have evolved complex songs and all other birds manage to keep a territory and find a mate without singing. Several hypotheses have been suggested to explain the evolution of complex songs, the main ones are based on the mechanism of sexual selection. Suppose that due to some cause or another female birds prefer vocalizations that are more complex than average. As a result, mutant males with more elaborate songs will produce more offspring and the complexity of the song will gradually increase. The female preference might be just a quirk of brain chemistry (this is the so-called "runaway theory of sexual selection"). Another hypothesis is that the preference of females results from natural selection. On this hypothesis male birds that are able to sing elaborately in the morning show that they have enough energy resources left after a night of fasting. Hence, female birds who choose a male that sings elaborately choose a male that is fitter in terms of his ability to look after offspring and will, therefore, produce more offspring (Hutchinson, McNamara & Cuthill 1993).

Conclusion

I have argued that functional biologists ask seven types of questions in relation to the item or behaviour in which they are interested. These questions concern: (1) the character of the item or behaviour under study, (2) their causal roles, (3) the causes and underlying mechanisms resulting in the realization of those causal roles, (4a) the survival value of performing those, (4b) the survival value of the character of the item or behaviour under study, (5) the way in which the item or behaviour under study develops in the course of the ontogeny, (6) the way in which the item or behaviour under study developed in the course of evolution. These questions may be phrased as follows:

(1) what is the character of the item or behaviour under study?
(2) what are its causal roles?
(3) how does it perform those causal roles?
(4a) why is it useful to the organism that it has an item that performs those causal roles?
(4b) why is it useful to the organism that the item or behaviour in question has the character it has?
(5) how did that item or behaviour develop in the course of the ontogeny?
(6) how did that item or behaviour develop in the course of the evolutionary history?

Note, that the type of question is determined by the kind of problem it addresses, not by the words used to phrase that question. In the overview above I have phrased these questions in such way that they best represent the issues at stake. Of course biologists may use and do (often) use other words to phrase these questions. Biologists typically use the phrase ‘what is the function of [item] ....?’ (for example ‘what is the function of the thymus?’) to phrase a type (2) question. The phrase ‘why do .... organisms have [item] ...?’ (for example ‘why do vertebrates have a circulatory system?’) is often used to phrase a type (4a) question, and the phrase ‘why does [item / behaviour] .... of .... organisms have [character] ....?’ (for example ‘why do snakes have a forked tongue?’) is often used to phrase a type (4b) question. The why-questions as they are phrased by biologists are notoriously ambiguous. For example, biologists use the phrase ‘why do .... organisms have [trait] .....?’ not only to ask for design explanations but also to ask for physiological or evolutionary explanations.

In order to avoid confusion it would be best to phrase the questions in the manner in which I have phrased them in the overview above. However, I will sometimes use the ‘why do .... organisms have [trait] .....?’ mode in order to connect the things I say to things others have said. In this case I will use subscripts to distinguish the several types of why-questions. I distinguish:

1) questions that ask for causes at the level of an individual organism (why$_1$-questions)

2) questions that ask for the utility of a certain trait to the organisms that have it (why_2-questions)

3) questions that ask for evolutionary causes (why_3-questions)

Why_1-questions ask for physiological and/or developmental explanations, why_2-questions ask for design explanations and why_3-questions ask for selection explanations.

2.3.3 The role of the different kinds of function statements

Descriptions of (potential) activity ($function_1$)

$Function_1$ attributions (description of functional characteristics) have the same role in biological research as descriptions of structural characteristics.

The structural (form) and functional (activity) characteristics of an organism, its parts and behaviours are to be explained by means of four kinds of explanations:

– physiological explanations (explain how a certain activity or behaviour is brought about in certain organisms, that is they answer type (3) questions);

– design explanations (explain why it is useful to the organism that the item or behaviour in question has the functional and structural characteristics it has—answer type (4a) and (4b) questions);

– developmental explanations (explain how the functional and structural characteristics of an item or behaviour are brought about in the ontogeny—answer type (5) questions);

– evolutionary explanations (explain how the functional and structural characteristics of an item or behaviour are brought about in the evolutionary history—answer type (6) questions).

These four ways of explaining an item or behaviour are complementary. In most cases a complete explanation of an item or behaviour of an organism would include all four kinds of explanations. There are, however, exceptions. For example, if an item does not have a causal role (think of the human veriform appendix) or if a certain character does not have survival value (think of the colour of vertebrate bones) there is no need for a design explanation.

Furthermore, functional and structural characteristics are used to explain the utility of other functional and structural characteristics (of the same organism) in a design explanation of those latter functional and structural characteristics.

Attributions of causal roles ($function_2$)

It will be clear from the discussion in the preceding sections that the notion of function as causal role ($function_2$) is central to functional biology. It is the handle by means of which functional biologists get a grip on their subject matter:

(i) Attributions of causal role tell us which tasks a certain item or behaviour has. They answer a type (2) question (how is that item used?). The tasks of an item or behaviour are to be explained by means of a capacity explanation (in answer to a type (3) question – how is that item or behaviour able to perform those tasks?) and a design explanation (in answer to a type (4a) question – why is it useful to the organism to have an item or behaviour which performs those tasks?).

(ii) Attributions of causal role serve to explain how an item or behaviour is able to perform the tasks it has by means of capacity explanations (in answer to a type (3) question). Capacity explanation work by attributing causal roles to the components of the item or behaviour the capacity of which is to be explained.

(iii) Attributions of causal role serve to asses survival value as part of design explanations of the character or presence of an item or behaviour (in answer to type (4b) questions). Such design explanations explain why an organism is built the way it is, why it works the way it works, or why it behaves the way it does, by appeal to the utility of those items and behaviours to the organisms that have it. They typically proceed by showing (1) that the item or behaviour in question has some causal role in the maintenance of the organism; (2) that given the way in which the organism is built, the way it behaves and the state of the environment in which it lives, that role is better performed by an item or behaviour with the character in question than by other conceivable forms.

(iv) Attributions of causal role serve to explain the evolution of an item or behaviour by showing that that item or behaviour evolved because some variant appeared in which that item or behaviour performed its causal role better (in answer to type (6) questions).

Function as survival value –design explanation (function$_3$)

Claims about survival value are an essential part of design explanations. Design explanations answer type (4a) and type (4b) questions. They explain why the character or presence of the item or behaviour under study is useful to the organisms that have it. Design explanation is one of the four complementary ways in which biologists explain items and behaviours. Design explanations of the character or presence of an item or behaviour of a certain organism compare real organisms with hypothetical organism in which that item or behaviour has another structure, or in which that item or behaviour is absent or replaced by another item or behaviour.

Function as selected effect–selection explanation (function$_4$)

Functional biologists seldom or never use the term ‘function’ in the sense of function as selected effect.[15] I have nevertheless included this notion in my list because it is important to

[15] Please note that I argue for this claim in chapter 7.

distinguish this notion clearly from the other notions of function. This is important because (1) the notion of function as selected effect seems to be the notion of function with which philosophers who favour an etiological account are concerned, and (2) there is at least one evolutionary biologist (Williams) who maintains that function should be defined in historical terms.

Analyses of biological function in historical terms have added nothing but confusion: such analyses suggest that they are concerned with the clarification of an existing use of the term ‘function’, whereas in fact they give an existing term a meaning it never had before. In other words such analyses introduce a new meaning for a term which was already highly ambiguous. This is a bad way of doing philosophy.

Of course, when I say that analyses of function in historical terms add nothing but confusion I do not mean to say that biologists do not or should not study function in an evolutionary context. On the contrary, as I will show, appeals to functions are an important part of explanations which explain why and how a certain item evolved. Furthermore, change of function in the course of evolution is an important mechanism of evolutionary change. My point is rather that when biologists use the term ‘function’ in the context of an evolutionary study they use that term in a non-historical sense. They aim to refer to the causal role ($function_2$) of an item or behaviour or to the survival value of a certain trait but not to function in some fancy historical sense. Definitions of function in historical terms obscure this fact.

2.4 Summary and conclusion

In this chapter I sketched the practice of functional biology. I showed that the term ‘function’ is used in at least four different ways. It may refer to (1) the activity of an item or behaviour ($function_1$), (2) the causal role of an item or behaviour ($function_2$), (3) the survival value of having a certain character or performing a certain role ($function_3$), (4) the effects for which a certain trait was selected in the past ($function_4$). To understand how these notions are used in functional biology, I discussed the aims of research in functional biology.

I showed that functional biologists try to answer seven different types of questions about the form (structure), $function_1$ (activity characteristics) and behaviour of organisms and their parts. These questions concern: (1) the character of those items and behaviours, (2) their causal roles in the maintenance of the organism; (3) the mechanisms by means of which these causal roles are performed, (4a) the survival value of performing these causal roles, (4b) the survival value of having a certain character, (5) the development of those items and behaviours in the course of the ontogeny, (6) the evolutionary history of those items and behaviours.

Let me review these questions with respect to their relevance to explanation (after all, my main concern is the role of appeal to function in explanation in functional biology). Functional biologists aim to explain the form, $function_1$ and behaviour of organisms and their parts. They do so in four different and complementary ways: by means of physiological explanations, design explanations, developmental explanations and evolutionary explanations. Physiological explanations answer questions of type (3). They explain how a certain item or behaviour works, that is how it performs the tasks it has. A special kind of physiological explanation is capacity explanation. A capacity explanation is a physiological explanation that explains the capacity of an item or behaviour to perform a complex task by attributing to the parts of that item or behaviour the ability to perform a series of less complex tasks that add up to the capacity to be explained. Design explanations answer questions of type (4a) and (4b). They explain why it is useful that a certain item or behaviour has a certain character or why it is useful that a certain role is performed by relating this trait to the other traits of the organisms that have that trait and to the state of the environment in which they live. Developmental explanations answer questions of type (5). They explain how a certain item or behaviour develops in the course of the individual's history. Evolutionary explanations answer questions of type (6). They explain how a certain item or behaviour evolved in the course of the history of the lineage. A special kind of evolutionary explanation is evolutionary selection explanation. An evolutionary selection explanation is an evolutionary explanation that focuses on natural selection.

In order to explain the form, $function_1$ and behaviour of a certain type of organism one needs to know what the form, $function_1$ and behaviour are. One reason why type (1) questions are relevant to explanation is that the phenomena described in answer to type (1) questions are to be explained by means of physiological, design, developmental and evolutionary explanations. Of course, form, $function_1$ and behaviour are not only important in posing questions about mechanisms, design, development and evolution, but also in answering them. This is another reason why type (1) questions are important to explanations.

Questions of type (2) are relevant to explanation because attributions of causal roles have a key role in the strategies of explanation in functional biology. The causal role of an item or behaviour is important in at least three kinds of explanation: physiological explanation, design explanation and evolutionary explanation. Attributions of causal role give biologists a handle that enables them to get a grip on these explanations and to connect them. Attributions of causal roles specify the tasks a certain item or behaviour fulfils. These task define what is to be explained by means of physiological explanations (how does an organisms perform a certain task?). Design explanations are concerned with the question why these tasks are performed and why they are performed in the way they are performed. Evolutionary selection explanation explain character change by pointing out that somewhere in the past a new variant emerged which performed a certain task better than the old variant (in the conditions in which those organisms lived).