Do ideas about function help in the study of causation?

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Abstract—One of Tinbergen's most lasting contributions to the study of behaviour was the distinction he drew between causal, functional, developmental, and evolutionary questions about behaviour. More recently, behavioural ecologists have claimed that understanding the function of behaviour is an important step towards understanding its causes. This claim has, in turn, been criticised for confusing the fundamental distinction that Tinbergen defined. The study of behaviour, however, usually begins by identifying units of behaviour functionally and only then proceeds to causal analysis. Research carried out on four phenomena — disassortative mating by MHC loci, memory for cache sites in food-storing birds, auditory localisation of prey by barn owls, and magnetic orientation — illustrates the contributions made to causal research through understanding the function of behaviour. Understanding function, and sometimes simply a hypothesis about function, defines the causal questions that are asked, identifies novel questions for causal investigation, and sets the criteria that causal explanations must satisfy.

In his 1963 paper on the aims and methods of ethology, Tinbergen gave credit to Julian Huxley for identifying 'causation', 'survival value', and 'evolution' as the three major problems in biology. To this list of three, Tinbergen added the problem of ontogeny. The distinction that Tinbergen described between causal, functional, developmental, and evolutionary questions about behaviour is one of the most enduring legacies of ethology. The idea that each of these questions can be asked of any behaviour, and that each requires its own distinctive answer, continues to shape the way we think about behaviour. Tinbergen did not believe these questions stood in isolation and never interacted. He pointed out, for example, that we can ask about the cause, function and evolution of development (Tinbergen, 1963). Contemporary behavioural ecologists often make the point that the cause of behaviour is easier to analyse and understand if its function is known (Stephens and Krebs, 1986; Krebs and Davies, 1997). This idea has been criticised, however, for confusing

the essential difference between causal and functional explanations of behaviour (Bolhuis and Macphail, 2001; Macphail and Bolhuis, 2001; Bolhuis, 2005).

The reasons for drawing a distinction between causal and functional explanations of behaviour are so clear and so familiar that it is surprising the two are sometimes confused by students and, occasionally, by professional researchers. The difference between causal and functional explanations can be illustrated with a non-behavioural example. The function of a hammer is to drive nails. Indeed, it is function that makes an object a hammer, to use a favourite illustration of the philosopher, Martin Heidegger (1996). The causes of a hammer have nothing to do with driving nails but instead involve shaping a piece of wood to make a handle, forming stone or metal into a hammer head, and fastening the two pieces firmly together. No matter how important the function of a hammer may be, it cannot cause a hammer to come into being. In addition, a function performed in the future, like driving nails, cannot act at an earlier point in time to bring a hammer into existence. Nevertheless, we have all read student essays and even papers in the scientific literature with statements like, "Better over-winter survival in the tropics causes migratory birds to leave the breeding grounds early in autumn". Why does this confusion exist?

There are at least two reasons why otherwise sensible people confuse causal and functional explanations of animal behaviour. The first is that we, as humans, can consciously anticipate the future function of our behaviour, and planning for the future can be a cause of behaviour. Because I can foresee needing a hammer tomorrow I can make one today, or at least go out and buy one. This is not a case of a function propagating backwards in time to cause behaviour but, instead, the outcome of learning and past experience acting as a cause. As humans we are used to foreseeing functions and acting accordingly, and this way of thinking is sometimes applied — surely without giving the matter much thought — to animal behaviour. As far as we are aware, animals cannot do this. There may be some instances, such as chimps and other primates carrying rocks to places where they will later use them to break open nuts (Boesch and Boesch, 1984; Mercader et al., 2002; Cleveland et al., 2004), and it is possible, although not proven (Jalles-Filho et al., 2001), that foresight is something human and non-human primate cognition have in common. For the most part, however, we have little evidence that anticipation of future function serves as a cause of behaviour in animals.

The second reason for confusion about the cause and function of animal behaviour is the theory of natural selection. A statement such as "Selection for over-winter survival causes birds to migrate early in autumn" is an example. Sometimes this is genuine confusion, sometimes it is the fault of sloppy writing (or sloppy thinking), but it is not always completely illogical. Sometimes it is simply shorthand for, "Natural selection, in the form of differential over-winter survival, acts on heritable variation in the timing of autumn migration. The result is greater frequency in the population of those causal mechanisms that lead to early autumn migration". Such shorthand is widely used and understood in behavioural ecology (Cuthill, 2005).

Tinbergen was, of course, aware of the fallacy of mistaking functional explanations for causal explanations, and was also aware of some more subtle pitfalls for the unwary concerning cause and function (Tinbergen, 1963; see also other papers in this issue). We identify behaviour for scientific investigation by its function. We study mate choice, foraging, migration, flight, parental care, anti-predator behaviour, communication and similar functional categories. Research that specifically addresses broad causal mechanisms, such as learning, often does so in a narrower context that is functionally defined, such as avoidance learning, spatial learning, imprinting, or song learning. The behaviour that seizes our interest is usually not behaviour that is defined descriptively, topographically, or because it shares causes with other behaviour, but instead behaviour that serves some readily identifiable function in the life of the animal. Tinbergen (1963) felt that one of the greatest contributions ethology made to the life sciences was: ". . .to consider behaviour patterns (and by implication the mechanisms underlying them) as organs, attributes with special functions to which they were intricately adapted. This again facilitated causal analysis without interference by subjectivism or teleology" (p. 413). "The treatment of behaviour patterns as organs has not merely removed obstacles to analysis, it also positively facilitated causal analysis. . ." (p. 414).

There are hazards in this functional approach though, and one that Tinbergen pointed out is that although we usually identify and label behaviour by its function, it is not true that behaviour serving the same function in different species necessarily shares the same causes (Tinbergen, 1963). This may seem an obvious point, but there is an ever-present temptation to suppose that behaviour we identify as 'communication', 'parental care' or 'food hoarding' in different animals has common neural, hormonal or energetic causes in these animals. This need not be the case, even in closely-related animals. Recognition of mating calls in the treefrogs *Hyla cinerea* and *H. gratiosa*, for example, is based on quite different auditory features (Gerhardt, 1981, 2001). Female preferences and selectivity in their response to male calls can be investigated experimentally by observing the phonotactic responses of females to the playback of recorded male calls and synthetic calls. Although the mating calls of males of both species have an abrupt pulsed onset, female *H. cinerea* do not discriminate between calls that have this pulse and calls that do not, while female *H. gratiosa* do. *Hyla gratiosa* females are selective for the low frequency component of a call while *H. cinerea* females are not. Female *H. cinerea* discriminate against male calls with added mid-frequency components while female *H. gratiosa* do not (Gerhardt, 2001). The function of the male call is identical in both species and the treefrogs share all but their most recent evolutionary history, but the acoustic features used for call recognition are quite different.

A second, more subtle, hazard noted by Tinbergen is that behaviour we identify as a discrete functional unit may be not be organised as a discrete unit causally. As observers we see smoothly integrated functional units of behaviour, but that does not mean that the nervous system organises things in such a way. Recognising an object and reaching out to grasp it seems a simple integrated unit of behaviour but

is, in humans at least, brought about by two separate visual processing streams, one serving perception and another serving the reaching and grasping action (Goodale and Westwood, 2004).

I will to argue that, on balance, understanding the function of behaviour, or even having a plausible hypothesis about the function of behaviour, facilitates causal analysis. It can do this in at least three different ways. As described above, function defines the categories of behaviour about which we ask causal questions. In addition, discoveries about the function of behaviour raise novel questions for causal analysis. These are the 'clues' about causation described by Bolhuis (2005). Finally, functional considerations set the criteria that causal explanations of behaviour must satisfy.

Is it possible to synthesise the study of cause and function? Reading some of the historical literature in ethology to prepare for this symposium, I could find only one ethologist who was rash enough to suppose it might be possible to synthesise the study of cause and function into one seamless enterprise, but this radical ethologist was unique in many ways; more about him later.

NOVEL CAUSAL QUESTIONS

The major histocompatibility complex

Discoveries about function can raise new questions for causal investigation. The idea that kinship and relatedness play a significant role in animal social behaviour revolutionised the study of behaviour from the 1960s onward (Hamilton, 1964; Trivers, 1972). Inclusive fitness provided a powerful new theoretical framework for the study of animal social organisation and directed attention to behaviour, such as cooperative care of the young, that was previously noted primarily for its novelty rather than its theoretical importance. There was also a revival of interest in inter-sexual or 'epigamic' sexual selection, mate choice, and the possibility that animals may choose mates of the basis of 'good genes' (Andersson, 1994; Neff and Pitcher, 2005). But these phenomena immediately raise a host of causal questions. How do animals recognise kin? How do animals determine whether a potential mate possesses genes that will increase offspring reproductive success? There are many ways, both simple and complex, that animals can distinguish kin from non-kin (Holmes and Sherman, 1983; Holmes, 2004; Sherman et al., 1997) and assess the suitability of a mate. One of the most unexpected causal mechanisms, however, is the discovery that animals can discriminate by odour among individuals differing only at loci of the major histocompatibility complex (Singer et al., 1997; Penn and Potts, 1999).

The major histocompatibility complex in mammals is a set of about 50 highly variable, linked genetic loci that play a central role in the immune response and self/non-self recognition. MHC Class I genes code for cell surface proteins in most cells, while MHC Class II genes code for cell surface proteins of antigen-presenting cells such as macrophages. The proteins coded for by these genes bind

to peptide antigens which are then presented at the cell surface for immune system surveillance. Helper T-cells recognise the MHC plus antigen complex and initiate an immune response to the antigen. Most Class I and Class II MHC loci, called the H-2 loci in mice and the HLA loci in humans, are highly polymorphic with hundreds of alleles at some loci. The particular combination of alleles occupying the linked MHC loci on a chromosome is called the MHC haplotype. The extreme allelic diversity that occurs at the MHC loci produces differences in MHC haplotype among all but the most closely-related individuals (and is the reason that unrelated individuals are rarely suitable as organ donors).

Research by Yamazaki and his colleagues (Yamazaki et al., 1976) first showed that inbred strains of mice have disassortative mating preferences for MHC haplotype. Mice of some strains, but not all, prefer to mate with individuals which differ from them at MHC loci. In the initial experiments of Yamazaki et al. (1976), male mice were caged with pairs of oestrous females that were genetically identical to the males except at MHC loci. In these tests, one female shared all or part of her MHC haplotype with the male and one female did not. Males mated preferentially with the female that differed from them in MHC haplotype. Subsequent research has shown that female mice, too, discriminate among potential male mates that differ only at MHC loci. When offered a choice, females prefer to mate with MHC-dissimilar males. Cross-fostering studies show that MHC preferences are learned during a period of association with parents and siblings in the nest (Penn and Potts, 1998). Mice prefer to mate with individuals that are MHC-dissimilar to the animals with which they were raised, and that can mean, for experimentally cross-fostered mice, that they prefer to mate with individuals of their own MHC haplotype.

Disassortative mating preference for MHC genotype has a number of consequences for mice, including avoidance of inbreeding, and promotion of pathogen resistance in offspring both through MHC heterozygosity itself and by creating a moving target for pathogens by maintaining very high levels of MHC variation (Penn, 2002).

In addition to disassortative mating preferences, there are circumstances in which animals prefer to associate with individuals that are similar to themselves at MHC loci. Female mice, which will nest and nurse pups communally, prefer to nest with other females of similar MHC haplotype (Manning et al., 1992) and there is mutual attraction between MHC-similar mothers and pups (Yamazaki et al., 2000). Attraction to individuals of the same MHC genotype in communal nesting and parental care by female mice is a form of kin recognition (Penn, 2002).

Mice detect and respond to the MHC identity of other mice using odour cues that are affected by the MHC loci (Singer et al., 1997). Mice can discriminate, by odour, inbred mice that differ only at the MHC loci, and can also discriminate the volatile components of the urine of these individuals. Chromatographic analyses show that it is not unique volatile components of urine that distinguish MHC haplotypes but instead the relative proportions of the many volatile components of urine (Singer et al., 1997). How MHC genotype influences the odour of mouse urine is not entirely

clear. MHC molecules may bind protein fragments of odorous molecules and in this way influence their relative proportions in urine. It is has been suggested that gut microflora are the source of some of the molecules bound by MHC molecules.

All of the research on the MHC loci described so far concerns inbred strains of mice, selected to be genetically uniform at all loci apart from the MHC loci of interest. This confers experimental control over MHC similarity, but at the cost of realism. It is therefore reassuring that discrimination among individuals and mating preferences based on MHC loci have also been described in other animals, such as three-spined sticklebacks *Gasterosteus aculeatus* (Milinski et al., 2005).

In research on the MHC loci, functional ideas about mating preferences and kin recognition raised new questions about causal mechanisms. Functional considerations gave a context and significance to the discovery that mice of the same MHC haplotype preferred not to mate. The discovery that mice and other animals can discriminate among even very closely-related individuals on the basis of MHC loci provided an answer to questions that had been identified in functional analyses of behaviour.

Memory in food-storing birds

Most species in the passerine families Corvidae (the crows and jays), Sittidae (the nuthatches) and Paridae (the chickadees and tits) store food. They place some thousands of food items in widely-dispersed cache sites and later retrieve these caches by remembering where they hid them (Sherry et al., 1981; Shettleworth and Krebs, 1982; Vander Wall, 1982; Kamil and Balda, 1985). The discovery that these birds can remember many scattered spatial locations, in some cases for many months, has led to a great deal of research on the properties of memory for cache sites and on how memory is implemented neurally in food-storing birds (Smulders and DeVoogd, 2000; Shettleworth, 2003).

Memory for cache sites, like mate choice and kin recognition, is a functionally defined category of behaviour. The discovery that animals can perform the feat of remembering large numbers of dispersed cache sites in the wild raises a host of new causal questions about behaviour. How is memory for cache sites organised, and how are cache site memories encoded, stored, and retrieved? What is remembered about a cache site, how is its spatial location specified, how is it represented neurally, and what parts of the brain are involved? Recent research on three causal aspects of memory for cache sites shows how a novel function, namely memory for cache sites, has led to novel lines of causal inquiry.

An early discovery in work with food-storing birds was that the hippocampus plays an essential role in accurate memory for food caches and in memory for other kinds of spatial information. Removal of the hippocampus severely impairs the birds' ability to find caches and perform other kinds of spatial tasks (Hampton and Shettleworth, 1996; Sherry and Vaccarino, 1989). Cache retrieval is hippocampus-dependent. In addition, it was discovered that the hippocampus is considerably larger in food-storing birds than in non-storing species (Krebs et al., 1989; Sherry

et al., 1989). These initial findings have stimulated extensive research on the avian hippocampus and its relation to memory, including descriptions of the distribution of neurotransmitters and neuropeptides in the avian hippocampus (Erichsen et al., 1991; Krebs et al., 1991), studies of seasonal change in the size of the hippocampus (Krebs et al., 1995; Shettleworth et al., 1995; Smulders et al., 1995; Smulders et al., 2000; MacDougall-Shackleton et al., 2003), and research on seasonal patterns in hippocampal neurogenesis (Barnea and Nottebohm, 1994, 1996; Hoshooley and Sherry, 2004). Long-term potentiation, the effect of stress hormones, hippocampal development, sex differences, and species differences in the hippocampus have all been examined in an effort to understand how memory is implemented by the avian hippocampus (Smulders and DeVoogd, 2000).

Hippocampal size.   The first descriptions of species differences in hippocampal size showed that food-storing birds have a larger hippocampus, relative to the rest of the forebrain, than non-food-storing species (Krebs et al., 1989; Sherry et al., 1989). These studies compared members of the corvid, sittid, and parid families with a variety of non-food-storing birds in other passerine families. Over a wide range of forebrain size, food-storing birds had a consistently larger hippocampus.

Not all members of the corvid and parid families store food, and even among those that do, there is variation in how much storing occurs. A number of studies have examined the relation between size of the hippocampus and food storing behaviour within the corvid and parid families and found that relative hippocampal size is greater in species that store more (Hampton and Sherry, 1992; Hampton et al., 1995; Healy et al., 1994; Healy and Krebs, 1992). Brodin and Lundborg (2003) performed a meta-analysis of these data along with new data of their own and concluded, however, that there was no relation between the level of food storing and hippocampal size among species within either the corvid family or the parid family. This finding raises a number of questions about the actual relation between food storing and the hippocampus. It is possible, of course, that the large differences between food-storing and non-food-storing passerine families described by Krebs et al. (1989) and Sherry et al. (1989) simply do not occur within food-storing families. All members of the corvid family are more closely related to each other than they are to members of other passerine families in which food storing does not occur, and the same is true for all members of the parid family. Perhaps there has not been the kind of divergence within food-storing families that is seen between food-storing and non-food-storing passerine families. It is also possible that the assignment of corvid and parid species to categories of food-storing intensity in the studies re-analysed by Brodin and Lundborg (2003) was not accurate. A further re-analysis, however, has produced a remarkable and unexpected finding (Lucas et al., 2004).

Lucas et al. (2004) noticed what they called an obvious but inexplicable trend in the available data: hippocampal size is consistently greater in Eurasian corvids and parids than in North American members of these families. When 'continent' is

included as a factor in the statistical analysis, there is a significant continent effect, and the hippocampus is significantly larger in species that store more food both within corvids and within parids.

It is indeed unexpected that Eurasian species of food-storing birds have larger hippocampuses than North American species. The effect of this, however, is that the relation between hippocampal size and food-storing behaviour that can be seen in North American birds and Eurasian birds in both the corvid and the parid families is masked when birds of different continents are pooled as Brodin and Lundborg (2003) did. Lucas et al. (2004) tested for possible confounding variables that might produce this continent effect, such as the time birds were held in captivity before sacrifice, or differences among laboratories in processing brains and estimating hippocampal size, and found little evidence that these factors were the causes of the continent effect. Instead they proposed that ecological differences between Eurasia and North America, and phylogenetic differences between Eurasian and North American food-storing birds, may account for the continent effect. In North America, for example, there are no non-food-storing parids, while in Eurasia there are two. Differences between North America and Eurasia in the history of human impact on ecosystems and species diversity may have had effects on the food-storing species present in the two continents and their degree of reliance on stored food. In addition, the 'continent' effect matches quite closely with a phylogenetic difference between North American and Eurasian corvids. This is not the case for parids. It is possible that this phylogenetic difference is responsible for differences in the relation between food-storing and hippocampal size between Eurasian and North American corvids. Whatever the eventual explanation for the continent effect, it is clear that in Brodin and Lundborg's (2003) meta-analysis it masked the relationship between food-storing behaviour and hippocampal size described in previous studies that made comparisons among birds from the same continent (Hampton and Sherry, 1992; Healy and Krebs, 1992; Healy et al., 1994; Hampton et al., 1995; Basil et al., 1996).

Hippocampal neurogenesis. Until very recently the prevailing view was that neurogenesis was rare or non-existent in the adult brain. Although evidence for adult neurogenesis in rats had been available as early as the 1960s (Altman and Das, 1965), it was research on neurogenesis in the adult songbird brain that stimulated the current intense interest in adult neurogenesis (Goldman and Nottebohm, 1983). New neurons are added not only to some song control nuclei but are found throughout the forebrain, including the hippocampus, of adult songbirds. In the food-storing black-capped chickadee, there is a seasonal pattern of recruitment of new neurons into the hippocampus that peaks in autumn at about the time the annual food-storing cycle is beginning (Barnea and Nottebohm, 1994, 1996). Recruitment in this context refers to the presence of neurons labelled with a cell-division marker injected 6 weeks previously. The occurrence of a cell division marker, such as tritiated thymidine or bromodeoxyuridine (BrdU), in the nuclei of these cells indicates that they were

dividing when the marker was injected, have differentiated and migrated from the ventricular zone where they originated, and have survived for 6 weeks.

The seasonal pattern in recruitment described by Barnea and Nottebohm (1994) could occur for a number of reasons. One possibility is that more cells are born in early autumn than at other times of year and, allowing 6 weeks for migration and differentiation, there are therefore more new neurons in the hippocampus in the autumn. Another possibility is that cells are born at the same rate all year round but differential survival in different seasons leads to the autumn peak in recruitment. Hoshooley and Sherry (2004) showed that the rate of cell birth did not change with season, making it more likely that differential attrition is responsible for the seasonal pattern in recruitment. This finding answers one question but raises many more. Given that the production of cells is relatively constant all year round, what seasonally varying process causes the observed seasonal variation in recruitment? Recruitment and attrition may be under photoperiodic control, leading to the seasonal profile observed by Barnea and Nottebohm (2003). It is also possible that use and disuse influence the number of new neurons that are incorporated into hippocampal circuits and that the seasonal onset of food storing directly influences hippocampal activity and, hence, neuronal recruitment. The behaviour of food-storing birds may thus provide clues to the control of adult neurogenesis that not only answer questions about the natural history of food storing but also have implications for the therapeutic use of neuronal stem cells in humans (Nottebohm, 2002).

CRITERIA FOR CAUSAL EXPLANATIONS

When the function of behaviour is known, and even when there is a plausible hypothesis about function, the details of any proposed causal hypothesis are constrained. Causal explanations must meet design criteria that are set by the function of behaviour.

Auditory localisation in barn owls

Barns owls can capture prey in complete darkness using only sound to determine the prey's location. The faint sounds produced by a mouse walking over the ground are sufficient for barn owls to establish during flight where the mouse is, capture it, and carry it off. To understand how barn owls are able to do this, Konishi and his colleagues established first what functional problems the owl auditory system had to solve, then searched in the barn owl auditory system for circuits that could extract the information required to establish the spatial coordinates of a rustling mouse (Konishi, 1995).

A point sound source that is not perfectly aligned with the front of a listener's head, whether barn owl or human, will be detected slightly differently by the two ears. As the sound source is displaced laterally with respect to the sagittal plane

through the listener, the sound will reach one ear before it reaches the other and the sound waves will arrive at the two ears out of phase. The degree to which they are out of phase provides a cue to whether the displacement is to the left or right and by how much. As the sound source is displaced vertically relative to the horizontal plane through the listener's ears, differences in the structure of the external ear result in an intensity difference that provides cues to elevation. In the barn owl, the external ears are asymmetric and modified to increase this intensity difference. The right ear is located slightly below the left ear and directed upward while the left ear is directed downward. Sounds originating above the horizontal plane are loudest in the right ear, and sounds below the horizontal plane are loudest in the left ear.

By placing miniature microphones in the ears of barn owls, researchers were able to verify these asymmetries in sound reception (Moiseff and Konishi, 1981). Barn owls will turn their head to orient to a sound source, and by placing miniature speakers in the ears of barn owls, researchers could make the owls orient to phantom sound sources by varying the time and intensity differences between sounds presented to the two ears (Moiseff and Konishi, 1981).

This research has led to a detailed characterisation of the auditory processing streams involved in sound localisation in barn owls. Phase-sensitive auditory neurons extract information about the arrival time of sound at the cochlea of each ear. Neurons in the nucleus magnocellularis encode the phase of the sound signal from each ear. Axonal 'delay lines' projecting from the nucleus magnocellularis bring the phase of the two signals into register in the nucleus laminaris where 'coincidence detector' neurons fire maximally only when signals from the two ears are in phase. The subset of coincidence detectors that fires corresponds to the phase difference between the two ears and hence encodes the lateral displacement of the sound with respect to the head (Moiseff and Konishi, 1983; Carr and Konishi, 1990; Peña et al., 2001).

Intensity differences between the two ears are handled by a different auditory processing stream. The intensity of the auditory signal at each ear is relayed by neurons in the cochlear nuclei to the nucleus ventralis lemnisci lateralis pars posterior (VLVp) in the pons. Neurons in this nucleus receive an excitatory signal corresponding to loudness in the contralateral ear and an inhibitory signal corresponding to loudness in the ipsilateral ear. VLVp neurons are selective for particular loudness differences and thus code for displacement of the sound source above or below the horizontal plane. Finally, timing differences and intensity difference signals are combined in the inferior colliculus to yield a representation of the horizontal and vertical location of the sound source (Konishi, 1993, 1995).

Konishi (1995) is particularly clear that functional ideas about sound localisation by barn owls guided the search for causal mechanisms. ". . .had the researchers not known the perceptual problems the animals must solve, they would not have looked for neurons selective for these natural stimuli" (p. 270).

Orientation to the magnetic field of the Earth

Birds, mammals, reptiles, amphibians, fish, and a variety of insects can derive orientation cues from the Earth's magnetic field. Hatchling sea turtles, for example, maintain a bearing with respect to the earth's magnetic field to leave their natal beach and head out to sea. Migratory birds and homing pigeons orient with respect to the magnetic field, and calibrate their magnetic bearing against a bearing derived from sun compass information. Surprisingly, it is not the polarity of the Earth's magnetic field that animals use to maintain a bearing but the inclination of the magnetic field.

The magnetic field of the Earth has a north pole, a south pole, and a field of magnetic force that connects the two. At the poles the magnetic field lines are oriented perpendicular to the surface of the earth, while at the magnetic equator these field lines are parallel to the Earth's surface. Between the equator and the pole, magnetic field lines have intermediate inclinations to the surface of the earth that correspond roughly to latitude. The magnetic compasses of birds and sea turtles respond not to the polarity of the Earth's magnetic field, but instead to the inclination of magnetic field lines. Sensitivity to the inclination of the field allows animals to distinguish pole-ward from equator-ward. Migratory birds that cross the magnetic equator (flying in an equator-ward direction to get there) must therefore change their bearing to pole-ward in order to continue on their migratory path (Wiltschko and Wiltschko, 2002).

A variety of mechanisms have been proposed by which animals might detect magnetic fields, including magnetic induction, chemical magnetoreception, and the use of biogenic magnetite. There is no clear answer to how animals detect and orient to magnetic fields, but functional considerations dictate that whatever the mechanism may be, it must be sensitive to the inclination of the magnetic field (Lohmann and Johnsen, 2000). Behavioural experiments have set further functional criteria that the magnetic receptor must satisfy, such as sensitivity in the range of 10-50 nT (Walker et al., 2002), against the background of the earth's magnetic field that ranges from 20,000-50,000 nT.

Kramer (1953) introduced the idea that oriented movement toward a goal has two distinct components, which he called the "map" and "compass". The map component refers to determining the relation of the animal's current position to the goal, while the compass component consists of orienting in the correct direction to reach the goal. For animals to extract both map and compass information from the magnetic field of the earth requires sensitivity to different components of the magnetic field. This is because inclination is correlated with latitude and makes it possible for a migratory bird, as described above, to discriminate the pole-ward direction from the equator-ward direction (Wiltschko and Wiltschko, 2002). Obtaining positional information, however, requires discriminating the properties of the magnetic field at different locations (Walker et al., 2002).

Among current proposals for magnetic sensory receptors are photopigment arrays in the retina of birds (Wiltschko and Wiltschko, 2002), and chains of membrane-

enclosed magnetite crystals attached by microtubules to mechanically gated ion channels that open and close with oscillations of the magnetite chain (Walker et al., 2002). Recently, magnetite chains have been described in the trigeminal afferents of the pigeon with properties that correspond well to those predicted by theoretical models (Fleissner et al., 2003).

Although the exact nature of the magnetic sense and magnetic receptors remains tantalisingly unknown, many of its design features have been identified on the basis of known functions that this system is capable of performing. These functional specifications come from an understanding of the geophysical properties of the magnetic field of the earth and extensive behavioural research with homing pigeons, migratory birds, sea turtles, fish and other animals showing how they respond to experimental alterations of the local magnetic field.

THE SYNTHESIS OF CAUSE AND FUNCTION

Although research on the cause and function of behaviour are two different enterprises, with different aims and different practical methodologies, I have tried to show that ideas derived from considering the function of behaviour have a number of important implications for the study of causation. Function defines the categories of behaviour about which we ask causal questions, it can raise novel causal questions for examination, and it sets the criteria that satisfactory causal explanations must meet. The distinction between cause and function is, nevertheless, a crucial one and failing to distinguish the two can lead to confusion, faulty explanations of behaviour, and fruitless debate (Hogan, 1994). I have been able find only one ethologist who made the radical suggestion that it might be possible to synthesise the study of cause and function into one seamless enterprise. He wrote:

"The fact that we tend to distinguish so sharply between the study of causes and the study of effects is due to what we could call an accident of human perception. We happen to observe behaviour more readily than survival, and that is why we start at what is really an arbitrary point in the flow of events. If we would agree to take survival as the starting point of our inquiry, our problem would just be that of causation; we would ask: "How does the animal — an unstable 'improbable' system — manage to survive?" Both fields would fuse into one: the study of the causation of survival. Indeed, logically, survival should be the starting point of our studies. However, since we cannot ignore the fact that behaviour rather than survival is the thing we observe directly, we have, for practical reasons, to start there. But this being so, we have to study both causation and effects."

It is a remarkable passage, and as the reader may have guessed, it comes from Tinbergen himself in his 'Aims and Methods' paper. By 'effects' he means what we would today call 'function'. In Tinbergen's view, there is a straightforward sequence of causal steps that ultimately affects survival, selection, and the evolution of behaviour. For practical reasons, however, we have to dichotomise this sequence into the functional consequences of the behaviour we observe and its causal

antecedents. Because the goal of causal analysis, in his view, is to understand survival and the function of behaviour, he would not find it surprising that function defines the categories of behaviour we investigate, raises new causal questions, and ultimately sets the criteria that causal explanations must satisfy.

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