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Auditory awareness

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Abstract

This paper reviews seven lines of auditory research which bear upon the issue of awareness in animals. First, comparative studies of auditory sensitivity have found important differences in the hearing abilities of animals such that sounds easily audible to one species may be inaudible to others. Second, studies of auditory attention indicate that when an animal is presented with a complex stimulus, such as a sound that varies in both quality and location, it may attend to one feature and not the other depending on the particular situation. Third, studies of relational concepts have indicated that animals can respond to relations between sounds, for example, indicating whether two sounds are the same or different. Fourth, memory studies have begun to examine the ability of animals to remember sounds. Fifth, studies of auditory perception have demonstrated that animals can classify sounds into natural categories such as dog sounds vs. other sounds. Sixth, studies of primate alarm calls indicate the degree to which animals can use vocal communication within a species. Seventh, studies of an African grey parrot have demonstrated that this animal can communicate with us using human speech sounds. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Audition; Birds; Cattle; Dogs; Hearing; Primates

1. Introduction

The study of animal awareness, and related topics such as animal intelligence and cognition, have had a long and controversial history dating back at least to Charles Darwin (Blumberg and Wasserman, 1995; Masterton, 1998; Wasserman, 1993). Major problems in this field have resulted from the use of anecdotal data as evidence as well as the failure to devise objective definitions of the phenomena being studied. Indeed, definitions of awareness often use ill-defined terms such as ‘mental images’ and

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'conscious intention', leaving one writer to comment that "... the still befuddled state of definitions and descriptions of human awareness ... should give us pause about resolving terminology regarding animals!" (Burghardt, 1985).

Although the minds of animals, not to mention those of humans, are completely unobservable, the view taken here is that the topic of awareness in animals is one that can be productively studied. Indeed, a major source of information regarding animal awareness has been the animal behaviourists who, contrary to the popular notion of the radical behaviourist who rejects the study of animal minds, have indicated that animals often show an unexpected degree of awareness (e.g., Epstein, 1996; Wasserman, 1993). This paper will not attempt a comprehensive review, but will illustrate both the types of studies that can be conducted as well as what is generally known about auditory awareness in animals. Reference is made where possible to studies of domesticated animals, with other species mentioned when necessary in order to illustrate major points.

2. Auditory awareness

That there are different levels of auditory awareness is demonstrated by brain-damage in humans that results in an inability to recognize sounds, i.e., auditory agnosia (e.g., Bauer, 1993). In this disorder, a patient is able to hear a sound, but is unable to identify the object that made it. For example, the sound of a violin or of a finger being run across the teeth of a comb is meaningless noise to the patient. This demonstrates that not only may such a person be aware of a sound without being aware of the sound's source, but that there are separate neurological mechanisms for sound detection and sound recognition.

The example of auditory agnosia also illustrates the distinction between sensation and perception. Sensation can be defined as the ability to respond to the physical characteristics of the stimulus. Thus, the ability to detect sound and to discriminate between sounds on the basis of frequency, intensity, or temporal characteristics are all examples of responding to sounds *per se*. Perception, on the other hand, is the ability to respond to the biological characteristics of the sound source. An example of auditory perception is the ability to respond differentially to a sound depending on whether it was produced by a predator, prey, or member of one's own species. Thus, there are two conspicuous levels of auditory awareness: the awareness of sounds and awareness of the sound sources.

In addition to the distinction between sensation and perception, auditory awareness can be investigated in terms of the ability of an animal to attend to sound, to form auditory concepts, to remember sounds, and to use sounds for communication. These are described in the following sections.

2.1. Auditory sensitivity

It would seem obvious that an animal cannot be aware of a sound (or the object that made the sound) if it cannot hear it. However, it is often assumed that any sound audible to humans is equally audible to other animals and there is a small but significant number

of studies in the literature that attempted to train animals to respond to sounds they could barely hear. The fact that the auditory sensitivity of animals varies is illustrated in Table 1, which lists the hearing ranges and sensitivities of various domestic animals with humans shown for comparison.

There are three points that can be made regarding the hearing parameters shown in Table 1. First, high-frequency hearing among this sample varies from 6000 Hz in the mallard duck to 79,000 Hz in the laboratory mouse, a range of over four octaves. In mammals, high-frequency hearing evolved as a means of localizing sound and the smaller the animal (or, more precisely, the smaller its head), the higher it must hear in order to use high-frequency locus cues (Heffner and Heffner, 1992b). Thus, most mammals hear high-frequency sounds that are inaudible to humans because most mammals have smaller heads than humans (the Indian elephant, on the other hand, with its large head has a high-frequency limit of 10,500 Hz, almost an octave less than the human high-frequency limit of 17,600 Hz). However, birds do not make the same use of high frequencies for sound localization as do mammals and no bird comes close to equaling even human high-frequency hearing.

A second source of variation is low-frequency hearing, which varies from 23 Hz in domestic cattle to 900 Hz in the laboratory mouse, a range of more than five octaves.

Table 1
The hearing range and sensitivity of domestic birds and mammals compared with that of humans

Animal	Low-frequency limit (Hz)	High-frequency limit (Hz)	Best sensitivity (dB)	Best frequency (Hz)
Laboratory mouse	900	79,000	5	15,000
Cat	55	79,000	-10	8000
Laboratory rat	530	70,500	0	8000
Rabbit	96	49,000	4	4000
Guinea pig	47	49,000	-6	8000
Dog	67	44,000	-1	8000
Sheep	125	42,000	-6	10,000
Pig	42	40,500	9	8000
Goat	78	37,000	-11	2000
Cattle	23	37,000	-11	8000
Horse	55	33,500	7	2000
Chinchilla	50	33,000	1	1000
Human	31	17,600	-10	4000
Canary	250	10,000	8	2800
Budgerigar	125	8000	2	2800
Zebra finch	< 250	7000	21	4000
Turkey	< 250	7000	17	1000
Pigeon	< 125	6600	10	3000
Mallard duck	< 300	6000	15	2000

Species are listed in descending order of high-frequency hearing and then low-frequency hearing. Low- and high-frequency limits are the lowest and highest frequencies audible at a level of 60 dB (re 20 $\mu\text{N}/\text{m}^2$). Best sensitivity is a species' lowest threshold and best frequency is the frequency at which it occurs. For individual data, see the works of Fay (1988) and Heffner and Heffner (1992a).

Here, humans, along with cattle, excel and low-frequency sounds easily audible to us may be less audible to other animals. Low-frequency hearing in birds is less well studied and there is some indication that pigeons may be sensitive to very low-frequency sounds (Kreithen and Quine, 1979).

Finally, animals vary in their absolute sensitivity to sound. As shown in Table 1, mammals, especially humans, cattle and goats, tend to be extremely sensitive at their frequency of best hearing whereas birds are usually less sensitive (see the works of Fay, 1988; Heffner and Heffner, 1992a). Just why this variation in best sensitivity occurs is currently unknown.

A knowledge of the auditory sensitivity of domestic animals is of obvious use in determining what sounds animals might find annoying. Indeed, recent studies have found that loud sounds are often annoying as animals tend to avoid them (e.g., MacKenzie et al., 1993; McAdie et al., 1993). However, it should be noted that loud sounds may not necessarily be annoying as animals are quite adaptable—witness the lack of proof regarding the effectiveness of ultrasonic pest repellents. Therefore, whether an animal prefers a quiet or noisy environment will depend on its history, a factor that has not been systematically investigated. Thus, an animal reared in a quiet environment may prefer quiet to noise, but an animal raised in a noisy environment may well prefer that environment due to its association with food and shelter. The ultimate measure of the adequacy of an environment is whether it allows the animal to ‘thrive’, that is, to maintain its health and gain weight.

2.2. *Attending to sound*

When an animal is simultaneously presented with two stimuli in a learning situation, it will often attend to one stimulus and ignore the other. For example, when both light and sound cues were simultaneously presented as signals of impending shock, cats learned to avoid the shock by attending to the sound, but not the light (Jane et al., 1965). Thus, of the two stimuli, the auditory stimulus was more salient than the light (although it should be noted that a different task or species may give a different result).

Similarly, certain properties of a sound are more easily associated with certain types of responses. In particular, it has been demonstrated that animals generally attend to the *locus* of a sound when required to make a spatial response and to the *quality* of the sound when making a non-spatial response (Dobrzecka et al., 1966). For example, when presented with two sounds that differ in both location and quality (e.g., a metronome placed in front of the animal and a buzzer placed behind) dogs predominately used the locus of the sound as a cue when they had to respond by either going left or right. However, when they were required to make a response to one sound, but not to the other (a go/no-go task), the dogs tended to use the quality difference as a cue. This finding, that animals more easily learn to make a spatial response to a spatial stimulus and a nonspatial response to a nonspatial stimulus, has been replicated in a number of situations and in animals as diverse as dogs, rats, and opossums (Heffner, 1978; Neill and Harrison, 1987; Stasiak and Masterton, 1996).

However, there are exceptions to this rule as other factors can also determine the aspect of a sound to which an animal attends—two factors being adjacency of the

stimulus to the response and the novelty of the stimulus. For example, rats rapidly learned to discriminate location using a go/no-go procedure when they were required to press a lever located next to one of the sound sources (Neill and Harrison, 1987). Similarly, horses easily learned to discriminate location using a go/no-go procedure when they were first habituated to sound coming from one location and then trained to respond when the sound occasionally shifted to another location (Heffner and Heffner, 1984).

The major conclusion to be drawn from these studies is that animals have natural propensities to attend to stimuli and often attend to only one feature of a complex stimulus. Just what feature they attend to can depend on the task. As a general rule, animals will attend to the location of a sound when making a spatial response, especially if the response is directed towards the sound source. However, they can easily learn to make a nonspatial response to a spatial cue if the response is to be directed towards (or away) from the source of one of the sounds (adjacency) or if the task involves detecting a change in locus (novelty). The quality of a sound, on the other hand, is more readily attended to in a non-spatial task (e.g., go/no-go) and it is difficult, although not impossible, for an animal to learn to attend to quality in a spatial task (e.g., go left to one type of sound and go right to another; Heffner, 1978).

2.3. Relational concepts

Not only can animals be trained to detect and discriminate stimuli, they can also learn to respond to relations between the stimuli themselves, thereby demonstrating their ability to form 'relational' concepts (e.g., Thompson, 1995). Tests of relational concepts include 'oddity', in which an animal must choose the one of three or more stimuli that differs from the others; 'same/different', in which an animal makes one response if two stimuli are identical and a different response if they are not; 'matching-to-sample', in which an animal is briefly presented with a stimulus and required to select it from two subsequent samples; and 'repetition', in which an animal indicates whether a stimulus has previously been presented. Such tasks have been successfully performed by monkeys, pigeons, and rats using visual stimuli, with various degrees of success (e.g., Herrnstein, 1985; Thompson, 1995). However, it has been much more difficult to train animals to respond to relational concepts among auditory stimuli.

An example of an auditory same/different task is provided by a study in which monkeys were trained to discriminate environmental and animal sounds, ranging from door buzzers to monkey calls (Wright et al., 1990). In this study, two sounds were presented in succession and the monkeys were rewarded for pressing a lever on their right if the sounds were the same and for pressing a lever on their left if they were different. Not only were the animals able to learn to respond correctly to the original training sounds, they were also able to respond correctly when new sounds were presented. The success of this study was attributed in part to the fact that the animals were required to touch the loudspeaker from which the initial sound was presented, a 'ready' response which indicated that they were attending to the sound and were ready to hear the second sound.

Not all studies have been so successful. Researchers using an auditory same/different task involving tones were able to train only four of eight monkeys (D'Amato and Colombo, 1985). Similarly, it was reported that it took budgerigars months to learn a same/different task involving four different sounds (Downing et al., 1988). (Although these two studies stated that they used a matching task, strictly speaking, it was a same/different task.)

Overall, it has proven difficult to demonstrate auditory relational concepts in animals, although there are several factors which may facilitate training on relational tasks (Wright et al., 1990). These include requiring the animal to approach the sound source, employing a large sample of different sounds, and using 'natural' sounds—that is, sounds produced by other animals as opposed to pure tones and noise bursts.

2.4. Auditory memory

The ability of animals to remember a previously presented sound has been tested using a variety of same/different and matching tests. Most of these tests have been performed with monkeys for the purpose of studying the neurology of auditory memory and the results may be specific to the particular test. However, the types of tests which have been devised are of some interest.

An auditory-visual task was used to test auditory discrimination and recall in monkeys (Dewson and Burlingame, 1975). The monkeys were presented with a sequence of two sounds, either of which could be a noise burst or a 1000-Hz tone, and were rewarded for pressing a red panel if the two sounds were the same (i.e., noise-noise or tone-tone) and for pressing a green panel if they were different (i.e., tone-noise or noise-tone). An animal's recall ability was determined by increasing the delay between the two sounds. The monkeys learned to perform well on this task, taking about 18 weeks to do so, but their ability to respond correctly usually fell to chance when the delay was greater than 5 s.

Another auditory recall task used a go-left/go-right procedure that rewarded monkeys for pressing a left panel when a tone was presented and for pressing a right panel when a noise was presented (Cowey and Dewson, 1972). The animals were then presented with a sequence of two sounds and were rewarded for pressing the left and right panels in the same sequence as the sounds (e.g., press left-right following tone-noise). The monkeys' auditory recall was tested by delaying the time between the two sounds and it was found that their performance generally fell to chance when the delay exceeded 10 s. However, a later study indicated that monkeys could successfully perform this type of task with a 32-s delay between sounds (Colombo et al., 1996).

Finally, auditory short-term memory has been studied in the budgerigar using a go/no-go task in which the birds were rewarded for pecking a key when two sequential sounds were different, but not when they were the same (Downing et al., 1988). Again, the task was difficult to learn and performance fell to chance when the delay between the two sounds was more than 1 s.

Although several studies have successfully trained animals in auditory memory tasks, the animals learned these tasks with difficulty and could perform successfully only when

the time span was very short. Either the auditory memories of animals are quite limited or else more appropriate tests need to be devised.

2.5. *Auditory perception*

Sounds are most useful when they provide information about the object that made the sound, i.e., the sound source. The perception of sound sources can be studied in the laboratory by training animals to classify sounds into natural categories. For example, dogs were trained to classify sounds into two categories (Heffner, 1975): sounds produced by dogs (barks, whines, whimpers, growls, and pants) and 'non-dog' sounds (various mechanical sounds as well as the sounds of other animals). The dogs were trained to touch one panel when a dog sound was presented and a different panel when a non-dog sound was presented. After learning 32 different sounds (half dog and half non-dog), the animals were tested with 96 new sounds (again, half dog and half non-dog). All eight dogs tested responded correctly on the first presentation of the new sounds at levels well above chance, indicating that they had acquired an auditory category and were not simply memorizing individual sounds. Moreover, the dogs also correctly classified a type of dog sound that had not been presented during training—howls. Thus, there is reason to believe that the dogs were classifying the sounds into dog and non-dog categories.

However, a note of caution is in order: although one can devise tests to determine if an animal is responding on the basis of a particular alternative category, such as familiar vs. unfamiliar sounds, there is no way to exclude the possibility of other unthought of categories (Herrnstein, 1985; Thompson, 1995). Nevertheless, the ease with which animals learn to discriminate natural sounds, as opposed to the difficulty encountered in training them to respond to arbitrary tonal patterns, is impressive because it suggests that animals naturally respond to sounds on the basis of the objects or situations with which the sounds are associated (Heffner and Heffner, 1986).

2.6. *Vocal communication within species*

Vocal communication between members of a species is widespread among animals and numerous species of vertebrates and invertebrates use vocalizations for seeking mates (e.g., Sebeok, 1977). The common technique for studying intraspecies communication is to playback natural sounds to an animal to determine its unconditioned response to those sounds. This technique has been used with farm animals by making use of the vocal interactions between mothers and their offspring. These studies have demonstrated that sows respond more vigorously to the vocalizations of piglets that are hungry (because such piglets themselves vocalize more vigorously), that female sheep respond differentially to the bleats of their own newborn lambs, and that calves, piglets and chicks respond differentially to their own mothers' vocalizations (Barfield et al., 1994; Kent, 1987; Walser et al., 1981; Walser, 1986; Weary et al., 1996).

The degree to which vocal signals can convey information has been indicated by the study of the reactions of vervet monkeys to playbacks of their alarm calls (Seyfarth et al., 1980). Vervets appear to emit different alarm calls for different predators (Struh-saker, 1967) and the playback of three different calls demonstrated that the animals

respond differentially to them. 'Leopard' alarm calls were more likely to cause the monkeys to run to trees, 'eagle' alarm calls caused them to look up and/or run into cover, and 'snake' alarm calls caused them to look down. Thus, some animals can use vocalizations to signal different events as well as to recognize individuals of their species.

2.7. Using human speech to communicate with animals

When the subject of the language abilities of animals arises, one usually thinks of studies of chimpanzees using visual symbols or signs (e.g., Gardner and Gardner, 1978; Savage-Rumbaugh and Rumbaugh, 1978; Premack, 1986). However, one of the most impressive series of studies to date has been the demonstration of the ability of an African grey parrot to produce and respond appropriately to English words. This linguistic ability has then been used to study the parrot's cognitive abilities (for a review, see the work of Pepperberg, 1991). Although the focus of these cognitive studies has been on visual concepts, the parrot's use of English words indicates that some species may be able to communicate with us by using our own speech sounds.

The particular parrot in question has been trained to use English words much in the same way as one might train a human infant (Pepperberg, 1991). This includes the use of two trainers, one of whom models the appropriate use of words, and the reliance on the use of the attention or social reinforcement of the human trainers as the main reinforcer for correct responses (such attention evidently can be as powerful a reinforcer for parrots as it is for humans; cf. Harris et al., 1964). Over time, the parrot has learned the names of over 30 objects (such as paper, key, grain, grape), 7 colours, 5 shapes, 5 numbers, as well as the appropriate use of words such as 'want', 'come here', 'no', and 'what's this?' The animal's vocabulary has then been used to demonstrate its ability to categorize visual objects on the basis of colour, shape, material, and number. Moreover, the animal can distinguish between 'identical' objects and objects that are the 'same' with respect to only one characteristic, such as colour or material, thus demonstrating cognitive abilities that have yet to be found in monkeys. In terms of auditory awareness, it has demonstrated its ability to use sounds to represent objects, the characteristics of objects, and relationships between objects. Although such linguistic ability has not yet been demonstrated with mammals, which generally lack the ability to mimic sounds, one wonders how well other animals, such as dogs, can learn to understand human speech.

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