Animal Behaviour 143 (2018) 83–91

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Commentary

Signal or cue? Locomotion-induced sounds and the evolution of communication

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ARTICLE INFO

Article history:
Received 23 November 2017
Initial acceptance 15 January 2018
Final acceptance 8 June 2018

MS. number: AS-17-00935R2

Keywords:
communication
cue
locomotion-induced sound
signal
sonation

The thrumming motor of an approaching car is salient to a pedestrian or cyclist. The source is usually an internal combustion engine, which intrinsically makes a fair amount of noise during operation. At low speeds, this internal combustion is the primary source of automobile noise. Despite its relevance, this noise is clearly a cue and not a signal, because the sound is an incidental by-product of the motor. After all, internal combustion cars have a muffler to reduce motor noise. A few years ago, electric automobiles arrived on the market, which have intrinsically quieter electric motors. Their relative stealth has posed a new risk to pedestrians and cyclists, who could not hear these new cars as well. As a result, the U.S. National Highway Traffic Safety Administration requires that, starting in 2019, electric cars must produce extra sound when they drive at low speeds (NHTSA, 2016). The addition of a noise-maker that produces extra sound during motion is clearly a signal to pedestrians. This sound, initially just a cue of an internal combustion engine, has been converted into an intentionally produced signal in electric cars. A new communication signal has 'evolved'.

This automotive example has many similarities to the sounds animals make as they move, which I call 'locomotion-induced sounds'. The study of locomotion-induced sounds and the role of these sounds in communication is not well advanced. Here, I explore a topic that was not entirely resolved in my recent review (Clark, 2016). Specifically, I explore the criteria used to decide whether a poorly studied locomotion-induced sound is a signal or a cue.

There are two models of how signals arise. The ritualization (Huxley, 1923; Tinbergen, 1952), or 'sender precursor' (Bradbury & Vehrencamp, 2011), model of how signals initially arise out of cues over evolutionary time is the model we apply below. The other model of signal evolution is the perceptual bias model, in which receiver responses arise prior to sender traits (Ryan & Cummings, 2013). The arguments below are couched in the context of ritualization, because cues are central to the arguments presented below, but it is unclear whether the concept of a cue has any utility in the perceptual bias model.

The 'evolution' of electric car noises reflects the stages of ritualization, which are as follows. (1) Exaptation (Gould & Vrba, 1982): a motion evolves that generates adventitious sound as a by-product. For example, the noisy internal combustion engine is invented and cars with internal combustion engines begin to replace horse-based transport. (2) Receivers respond to the cue, raising the possibility of selection exerted on the sender. For example, once internal combustion engines are familiar, pedestrians use this sound to detect an approaching car. (3) Ritualization: mechanisms that produce the sound respond to selection on the sender, the sound becomes evolutionarily modified, thereby becoming a signal (Darwin, 1871; Maynard Smith & Harper, 2003; Prum, 1998). For example, electric cars, as they are not intrinsically

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https://doi.org/10.1016/j.anbehav.2018.07.009

noisy, acquire noisemakers. Extant animals and the sounds they make as they move may fall anywhere within these three stages (e.g. Scott et al., 2010).

Not all sounds produced by animals as they move are already ritualized. The world is full of noises that are cues. As you sit and read this, perhaps the fan on your computer whirrs, or the toenails of a dog or cat click on the floor as it walks by. Within a medium (air, water, soil), all motions make sound, and all sounds arise from motion (Clark, 2016). Sometimes this axiom is trivial, because many motions are functionally silent. For example, heartbeats generate sound that is inaudible (except with a stethoscope). But the broader point holds: sounds arising from animal motion are ubiquitous. Hereafter I call these locomotion-induced sounds; this term is neutral to function. Locomotion-induced sounds cannot all be signals, although they have evolved into signals many times in animals including various birds (Clark & Prum, 2015; Clark, 2016), the footdrumming of rodents (e.g. kangaroo rats, *Dipodomys* spp.) and other mammals (Randall, 2001, 2013), or wing clicks used for echolocation in certain bats (Boonman, Bumrungsri, & Yovel, 2014). Motion-induced sounds are present in many insects, such as the wing hum of midges and mosquitoes (Cator, Arthur, Harrington, & Hoy, 2009; de Silva, Nutter, & Bernal, 2015), or crepitation of grasshoppers (Otte, 1970). Some of the recent surge in interest in 'nonvocal' sounds of birds was inspired by Bostwick and Prum (2003), who used the term 'sonations' to mean nonvocal sounds that serve as signals. Sounds that are not sonations are 'adventitious sounds', or cues that are simply a by-product of locomotion, such as ordinary human footsteps.

Researchers studying putative vertebrate sonations, particularly of birds, often have a background in the study of vocalizations. Studies of sonations thus get coloured by implicit assumptions borrowed from the study of vocalizations. (Vocabulary too: what does 'nonvocal' actually mean? Can the vocal tract really produce nonvocal sound?). Vocalizations are noises produced by the respiratory and digestive tract, parts of which (e.g. larynx, syrinx) are specialized for the production of sound. Vocal adventitious sounds, such as coughs, wheezes or burps, seem to be relatively rare. Therefore, acoustic emissions of the vocal tract are often reasonably assumed to be signals, even if their function is unknown. But this is neither a safe nor a conservative assumption in the study of locomotion-induced sounds.

The rigorous approach to establishing that a sound is a sonation is to apply the same standard that applies to any other putative signal. One definition of a signal entails three criteria: a signal, on average, conveys information that both (1) increases the fitness of the sender (2) and the receiver, and (3) has evolved to do so (Bradbury & Vehrencamp, 2011; Maynard Smith & Harper, 2003; Scott-Phillips, 2008). Anything else is a cue: it has not evolved for the purpose of conveying information. It is not sufficient for a putative signal to contain information useful to both sender and receiver, as cues can do this as well (Maynard Smith & Harper, 2003; Scott-Phillips, 2008) — saliency arises in stage 2 of the evolution of sonations. Recognizing and responding to the sound of the internal combustion of an automobile might increase the fitness of a pedestrian, and perhaps also of the driver, but it is not a signal until it becomes evolved for that purpose, as in noisemakers on electric cars. According to these three criteria, an animal signal can be identified through experiments that demonstrate a benefit to sender, a benefit to receiver, and that it has evolved. Demonstrating all three of these criteria has been done for relatively few signals, and even fewer sonations (e.g. Murray, Zeil, & Magrath, 2017).

Evidence arising out of experimental manipulations designed to test the above criteria will always be the most rigorous approach to diagnose signals from cues. As the necessary work to do such manipulations is time consuming, most examples of possible sonations have not been studied in this way. It is these poorly studied examples that are the focus here. When there is limited information, for example, when males of a newly discovered species of tyrant flycatcher are observed making a noteworthy sound in a flight display, and found to have distinctively twisted wing feathers (Lane, Servat, Valqui, & Lambert, 2007), what are the criteria by which we decide this sound is a likely signal?

To answer this question, I outline below five theoretical properties of locomotion-induced sounds that have practical bearing on their diagnosis, building on ideas and terminology presented in Clark (2016). While these five properties are not unique to locomotion-induced sounds, they are useful to enumerate, since the contours of the problem differ from those for vocalizations. For example, a property may be hard to assess in vocalizations because invasive techniques (e.g. surgery) are needed, but it can be easy to ascertain by eye/ear for locomotion-induced sounds (see Property 1, below). Other properties can be trivial to assess with vocalizations, but are not trivial with locomotion-induced sounds (see Properties 3, 4 and 5 below). I convert these theoretical properties into a practical set of criteria for assessing whether a given sound is a signal, along with a heuristic set of seven questions to guide assessment of empirical examples (presented in Supplementary Table S1). I then apply these criteria to some recently studied examples of locomotion-induced sounds that authors have stated are sonations. The arguments and examples presented here are mostly couched in the context of flying animals, especially birds, as birds have been a recent focus of research. The term 'locomotion' used here follows the extremely broad definition of Barlow (1968, p. 228): 'Thus in the end [all of behaviour] is locomotion, respiration, or feeding'. The arguments presented here are intended to be valid for most sound produced by motion of an animal's integument, including gestures, although certain integumentary structures (e.g. air sacs, buccal cavity, human lips) contribute to production of sounds best regarded as vocal.

FIVE PROPERTIES OF LOCOMOTION-INDUCED SOUNDS

Property 1

Locomotion-induced sounds have a kinematic basis. This property is an axiom underlying the study of locomotion-induced sound (Clark, 2016). Sound does not arise de novo, it arises out of relative motion within a fluid medium such as air or water. While the source motions that produce vocalizations arise hidden inside the animal (in the larynx or syrinx), and so are not readily observed, locomotion-induced sounds are produced by observable external motions of the animal. This means that there is a '1 to 1' match between a component of the animal's kinematics (motions) and the ensuing sound (Clark, 2009). If an experimenter has correctly identified the mechanism, and thus knows the source of sound (Clark, 2016), then a regression of timing of motion against timing of a sound element, in theory, has a slope of 1.0 and an r^2 of 1.0, after accounting for measurement error. The motions and sounds are simply two manifestations of the same phenomena. This also means that one can use either modality, motion or sound, to analyse sonations. Video or sound recordings of a sonation provide complementary lines of evidence of the same underlying phenomena.

Property 2

The mechanism that produces a sound can be specific, subtle or hidden, and thus hard to identify. The 1:1 match can be difficult to discern from other kinematic events that are correlated with the mechanism. Consider the example of a person that takes five steps.