



Commentary

Studying audience effects in animals: what we can learn from human language research



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Communication involves the transmission of information through the use of signals, which are produced by a sender and influence the behaviour and physiology of receivers (Bradbury & Vehrencamp, 2011; Endler, 1993). There are two main types of receivers: intended receivers, who are the targets of the signal, and unintended receivers (e.g. predators, eavesdroppers). Although unintended receivers are not the targets for the signal, they can sometimes exploit information from an intercepted signal, often at a cost to the signaller (Fichtel & Manser, 2010; Peake, 2005). Signallers may respond to differences in the presence, characteristics, or composition of receivers by initiating or inhibiting signal production, and by varying the rate, type and properties of the signals they produce. This sensitivity to the presence or nature of receivers is called an ‘audience effect’ (Fichtel & Manser, 2010; Marler, Dufty, & Pickert, 1986; Zuberbühler, 2008). Although nonvocal behaviour can also vary depending upon the characteristics of the receiver(s) (Chen & Fernald, 2011), the discussion that follows will primarily focus on vocal behavioural sensitivity to audience characteristics. In this commentary, we argue that a commonly used method to study vocal sensitivity to audience in humans – namely, an analysis of the fine acoustic structure of sounds – could strengthen our ability to

detect and interpret audience effects in nonhuman animals (hereafter, animals).

Audience effects are important phenomena in animal communication for at least two reasons. First, audience effects suggest signallers have volitional control over signal production (Townsend et al., 2016). In one seminal study, Sherman (1977) demonstrated that female Belding’s ground squirrels, *Urocitellus beldingi*, produce more alarm calls when direct kin are present, relative to when the audience is composed primarily of nonkin. In a second study, Evans and Marler (1994) found that male domestic chickens, *Gallus gallus*, increase their production of food-related calling when in the presence of a female compared to when they are alone. Increases in signal production suggest the signaller has control over its signalling in response to audience characteristics. The second reason audience effects are important is because some examples suggest that signallers are aware of receivers’ perceptual states, and can modify their signal use accordingly (Chen, Matheson, & Sakata, 2016; Tomasello & Zuberbühler, 2002; Townsend et al., 2016; Zuberbühler, 2008). For example, when male Thomas langurs, *Presbytis thomasi*, detect predator stimuli, they continue to produce alarm calls until all members of their group respond with a countercall (Wich & de Vries, 2006). For some researchers (although not necessarily Wich and de Vries), this kind of audience effect suggests signallers have theory of mind (Call & Tomasello, 2008), because they seem to be aware of what receivers know. This

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interpretation, however, is controversial (e.g. Barrett, Lindquist, & Gendron, 2007; Heyes, 2015).

Research on audience effects in animals, and on vocal communication more generally, has vastly increased our understanding of the development, ecology and evolution of behaviour. However, common approaches in this field may underestimate the occurrence of audience effects in animals. Consequently, our understanding of developmental and evolutionary flexibility in vocal signalling remains limited. In this commentary, we briefly review the typical ways in which audience effects are studied in both animals and humans. We suggest that a key methodological approach used in studies of human communication – specifically, a focus on examining the fine acoustic structure of signals – could provide a useful tool to explore audience effects in animal communication. This approach, in turn, may increase our understanding of sensory, perceptual and cognitive abilities of animals.

Most studies on audience effects in animals assess whether a given audience influences the signaller's rate of signal production or latency to produce a signal (Slocombe & Zuberbühler, 2007). This research has typically focused on food, predator and social signals. For example, capuchin monkeys, *Cebus capucinus*, who search for food in groups, give food-associated calls more quickly when there is a lower density of individuals in the group, and/or when the group is physically further from the food source (Di Bitetti, 2005). Di Bitetti argues that this is either evidence that an individual calls less when it can monopolize the food resource (a deceptive lack of calling), or that the signaller is aware of when others have noticed the food. In response to a variety of predators, adult female vervet monkeys, *Chlorocebus pygerythrus*, produce more alarm calls in the presence of their offspring than in the presence of unrelated juveniles, and males produce more alarm calls when adult females are around than when females are absent (Cheney & Seyfarth, 1985). These findings raise the possibility that signallers are aware of key, biologically relevant audience members, and strategically signal more when these key individuals are present. Juvenile male brown-headed cowbirds, *Molothrus ater*, decrease singing rates when adult males are in the area, although they readily sing to other juvenile males, and to females (White, King, Cole, & West, 2002). Juvenile males seem to adjust their singing rates flexibly to avoid possible aggression from adult male cowbirds, which are typically more dominant. Although obviously not an exhaustive review, these examples illustrate the typical reliance on measuring variation in call rates and latencies in audience effects research in animals. In contrast, research on human communication has typically incorporated a more fine-grained approach to assess speaker (hereafter, signaller) sensitivity to listener (hereafter, receiver) characteristics.

Like animals, humans have a remarkable ability to change vocal signals in response to the presence of other individuals, and often modify their vocalizations depending on the characteristics or identity of the intended receiver. The term 'audience effect' is not typically used to describe human communication, although many of the terms used to discuss animal communication (e.g. eavesdropping) can be used to describe everyday human experiences (Matos & Schlupp, 2005). A key way human research differs from animal research on the question of audience effects is in its focus on measuring variation in the acoustic structure of sounds in addition to more gross measures such as the rate and latency of signal production.

A well-known example of signaller sensitivity to audience in human communication is the characteristic speech produced by caregivers whenever an infant is present. In addition to having a slower signalling rate and simplified sentence structure as compared to adult-directed speech, infant-directed speech is characterized by longer pauses, higher average fundamental

frequency, exaggerated pitch contours and more distinctive speech sounds (Fernald & Mazzei, 1991; Gleitman, Newport, & Gleitman, 1984; Trainor & Desjardins, 2002). Kuhl et al. (1997) examined how vowel space (i.e. the dispersion of vowel sounds in acoustic space) within infant-directed speech differs from that of adult-directed speech in three different languages. In each of the languages studied, mothers addressing infants stretched their vowel space, making vowels more distinctive. Liu, Kuhl, and Tsao (2003) found that the size of mothers' vowel spaces is significantly correlated with infants' ability to discriminate speech sounds, and they suggested that the enhanced vowel distinctiveness found in infant-directed speech may help infants quickly home in on the relevant vowel categories of their native language. Taken together, the adjustments caregivers make when directing speech to infants function to attract infant attention (Trainor & Desjardins, 2002), and have been shown to facilitate speech segmentation (Thiessen, Hill, & Saffran, 2005), word recognition (Fernald, Pinto, Swingley, Weinberg, & McRoberts, 1998) and novel word learning during early development (Graf Estes & Hurley, 2013).

Humans also modify their vocal signals when they interact with their pets. Pet-directed and infant-directed speech may sound similar to the casual observer, but these two types of signals are acoustically distinct. The two speech types share higher overall fundamental frequency and more exaggerated pitch contours (Fernald & Kuhl, 1987), yet pet-directed speech does not display the same type of vowel modifications seen in infant-directed speech (Burnham, Kitamura, & Vollmer-Conna, 2002). Whereas pitch variations likely function to attract attention of pets and infants, unlike for infants, expanded vowel spaces are of little use to pets. Interestingly, signals directed to second-language learners also exhibit vowel space expansion (Knoll & Uther, 2004), which may be particularly useful for learning the sound categories in a new language. Signals directed to second-language learners are also slower and more deliberate than those directed towards same-language adults (Biersack, Kempe, & Knapton, 2005), but lack the attention-grabbing higher pitch characteristics of infant- and pet-directed speech (Uther, Knoll, & Burnham, 2007). Together, these findings suggest that human signallers modify the acoustic structure of their speech in a manner that is tailored to the individual needs of their receivers.

Signallers also modify their speech based on social pressures from surrounding audience members. Much of the research on this kind of modification of speech focuses on the fine acoustic structure of the words produced by speakers. One major kind of modification is vocal accommodation (Coupland, 1984), whereby the signaller's speech patterns will start to converge on the speech patterns of their conversation partners (Thakerar, Giles, & Cheshire, 1982). For example, adult signallers from one dialect area will often shift the acoustic features of their words and phrases in ways that converge upon, but do not mimic, those features of their target audience from a different dialect (e.g. Giles & Coupland, 1991). Furthermore, gay men tend to modify their production of stop consonants (e.g. b, p, d, t, g, k) when they believe they are in the presence of another gay man (Dickson & Turner, 2015). A second major kind of modification is vocal convergence, whereby the sounds produced by two or more speakers in a social group become more similar over time. For example, the acoustic parameters of phonemes converge in college roommates over a period of weeks, particularly in the vowel space of words, and stronger relationships between the roommates are associated with greater convergence (Pardo, Gibbons, Suppes, & Krauss, 2012). Thus, speakers vary the style of their language – not just what they say, but how they say it – to match the region, social class, ethnic background, sexual orientation and gender of receivers (Bell, 1984; Wolfram & Schilling-Estes, 2005). These processes of vocal accommodation and phonetic convergence are thought to

function to increase communicative efficiency, as well as to increase social approval, affiliation and bonding, among the speakers and their audiences (Locke & Snow, 1997).

This review provides a snapshot of human signallers' sensitivities to characteristics of the audience, and reveals the remarkable flexibility of signal production in humans. Some of this flexibility relates to the actual words and phrases used, and the rates at which they are produced. Beyond these measures, though, research indicates that humans have an incredible ability to modify the fine acoustic structure of their signals in response to their particular audience. In addition, this work has found that the modifications made by speakers are often functional, revealing biologically meaningful information about the communicative relationship between signallers and receivers. It is an obvious but important point – these patterns in behaviour might have remained undetected had researchers not assessed, in detail, the acoustics of the sounds produced in the context of different audiences. In turn, certain audience effects in humans, and what they tell us about the complexities of human communication, might have gone undetected without this focus on detailed acoustic structure of signals.

Additional subtle, yet biologically relevant, patterns of behaviour are likely present in animal communication systems as well, but may be missed by research that focuses exclusively on measures of signal rate or latency. We suggest that studies of audience effects in animal signalling may similarly benefit from exploring the fine acoustic structure of signals. A few examples of studies that have taken this approach do exist. Slocombe and Zuberbühler (2007) demonstrated that chimpanzees, *Pan troglodytes*, who are the victims of an attack by a conspecific modify the acoustic structure of their screams along several acoustic parameters depending on the group ranking of members in the audience. More specifically, when the audience contains an individual of equal or higher rank than the aggressing chimpanzee, the victim will increase the frequency (Hz) of the scream. According to Slocombe and Zuberbühler (2007), these findings suggest that chimpanzees are aware of third-party relationships and can modify signals to their advantage depending on the composition of the surrounding group. Chacma baboons, *Papio cyncephalus ursinus*, vary the relative amplitudes of their vocal tract resonances (i.e. the first two formants) in their grunts depending upon whether the signaller is interacting with an infant or with its group in the context of movement (Owren, Seyfarth, & Cheney, 1997). Furthermore, receivers respond differently to playbacks of grunts that are recorded in these two contexts and that differ maximally in the relative amplitudes of the first two formants, suggesting baboons attend to these changes in grunt fine structure in adaptive ways (Rendall, Seyfarth, Cheney, & Owren, 1999). Finally, male red-legged partridges, *Alectoris rufa*, alter both rate and spectral (i.e. frequency-based) features of alarm calls, depending on audience composition (Zaccaroni, Binazzi, Massolo, & Dessi-Fulgheri, 2013); the presence of conspecifics increases the rate of alarm calls to predator stimuli, and the presence of the signaller's mate lowers the peak frequency (Hz) of the signaller's calls. Lower peak frequencies (Hz) are harder to detect. Thus, this type of modification to the calls' spectral features presumably makes these calls less susceptible to eavesdropping, which is potentially advantageous for mate investment (Zaccaroni et al., 2013).

Although we have focused on audience effects in vocal signals, audience effects can occur in any signalling system. Audience effects have been well studied in visual signalling systems, and in a wide range of taxa. As one example, male Atlantic mollies, *Poecilia mexicana*, court females with more nips and gonopodial thrusts if those females are bigger rather than smaller, or are conspecific rather than heterospecific (*Poecilia formosa*; Plath, Richter, Tiedemann, & Schlupp, 2008). However, they only do this when

no male eavesdroppers are present – if a male audience is present, the signaller will direct these visual courtship displays to the smaller or heterospecific female as frequently as it does to the larger or conspecific female, respectively. Since mate choice copying is common in many fish species, male signallers likely decrease mating competition by deceptively adjusting their courtship signals to females.

Audience effects in visual signalling systems occur in more than just fish species. Male fiddler crabs, *Uca perplexa*, adjust the fine-scale movements of their large claw in courtship interactions with females depending on the proximity of those females (How, Hemmi, Zeil, & Peters, 2008). Males possibly make these adjustments to increase efficacy of signal transmission based upon distance-related changes in female receiver visual perception. In other words, male fiddler crabs may be sensitive to what their female audience can effectively detect visually. Males are also sensitive to the reproductive state – and therefore the courtship responsiveness – of females, and adjust their claw waving appropriately (Murai & Backwell, 2005). In many lizard groups (for example, many species of the *Anolis*, *Liolaemus* and *Sceloporus* genera), males move their heads in highly stereotyped broadcast visual displays called headbobs, which function in territorial and aggressive interactions with other males and in courtship interactions with females. In the Neotropical lizard *Liolaemus pacha*, this broadcast display is produced with longer durations and higher amplitudes of headbob movement if a male receiver is present, compared to when a male receiver is absent (Vicente & Halloy, 2015). These examples demonstrate how fine-grained analysis reveals audience effects in visual as well as vocal communication systems.

In future research, a greater focus on analysing the fine acoustic structure of signals produced in the context of different audiences should improve our ability to detect audience effects in animals. It is also likely that considerable relevant data already exist (from animal studies that have collected audio recordings) that could be used to assess the potential effects of audience on the fine acoustic structure of signals. A greater focus on fine acoustic structure may also better reveal the functions of these communicative patterns. Finally, and more proximately, a fine-grained approach might put us in a better position to understand underlying affective, perceptual and cognitive mechanisms involved in animal communication. For example, this type of approach may allow us to address the debate over the relative contributions of cognitive versus affective mechanisms in communicative flexibility (Fischer, Wheeler, & Higham, 2015; Marler, Evans, & Hauser, 1992; Watson et al., 2015b, 2015a). From one perspective, audience effects suggest signallers are using and potentially modifying their signals strategically, in consideration of how their signals might affect the behaviour of different receivers (Zuberbühler, 2008). Conversely, different audiences represent different social contexts, which inherently generate different levels of arousal and stress in signallers, and these changes in arousal are often reflected in the characteristics of the signals produced (Morton, 1977; Owings & Morton, 1998). More detailed acoustic analyses of signals will help inform these types of debates, particularly if combined with experimental playbacks to receivers to determine how they respond to the acoustic variation signallers produce (as in Rendall et al., 1999). Based on findings from fine-grained analysis of human audience effects, we propose some predictions about possible audience effects in animals.

First, animals should alter signals to increase attention-getting aspects when signal transmission to a particular receiver is urgent, as in the case of alarm calls. Alarm calls can alert others to potential danger, such as when an actively hunting predator is detected (Marler, 1955). Alarm calls tend to be high-frequency (Hz)

signals, which can be modified to be even higher in frequency and longer in duration when produced in response to predators of greater threat (Ficken & Witkin, 1977). Krams and Krama (2006) found that male great tits, *Parus major*, were more likely to produce more alarm calls, and alarm calls of longer duration, if their mate was in the immediate environment compared to when their mate was not in the immediate area. Given the link between increased predatory risk and higher-pitched alarm calls, we would additionally expect signallers to produce higher-frequency (Hz) and longer-duration alarm call notes when they detect a predator if biologically valued receivers (such as kin or mates) are in the audience, compared to when they are not.

Second, animals should alter signals to increase attention-getting aspects when signalling to an inattentive receiver. As an example, chimpanzees are more likely to produce sequences of visual gestures if their receiver is not responding to them, and are generally more likely to use visual gestures when they are in the visual space of receivers as opposed to being out of view of receivers (Liebal, Call, & Tomasello, 2004). We would expect signallers to produce signals of greater intensity – such as louder calls, more exaggerated visual displays, or exaggerated frequency modulations – if the intended receiver is not attending to the signaller. It has been argued that the use of signal modification to gain receiver attention is relatively rare in animals, and perhaps restricted to great ape species (Tomasello, 2008). However, increased assessment of signal fine structure in the context of different audiences and a broader taxonomic approach may reveal wider occurrence of attention-getting behaviour in nonhuman animals.

Finally, animals should adjust their signals when communicating with relatively naïve receivers, such as inexperienced young or individuals with different signal sets. For example, in a parallel to infant-directed speech in humans, noninfant gorillas, *Gorilla gorilla*, alter their visual, tactile and acoustic signals when the receiver is an infant, through greater signal use in all modalities (Luef & Liebal, 2012). These types of signal modifications may also be more taxonomically widespread. Recent evidence from birds shows that adult zebra finch, *Taeniopygia guttata*, tutors that direct songs to young male learners (pupils) include more repeated elements and longer spacing between song elements (Chen et al., 2016). These authors also found that tutors altered the fine structure of their songs by modifying mean frequency, spectral entropy and goodness of pitch in ways that appear to increase pupil attention and may improve pupil song learning. A similar type of accommodation may also occur when individuals signal to those with different signal sets; for example when signals are directed to an individual with a different regional dialect. Vocal dialects are found in many songbirds and parrots (see review in Sewall, Young, & Wright, 2016), as well as cetaceans (e.g. Gero, Whitehead, & Rendell, 2016; Rendell & Whitehead, 2005), and future studies could focus on whether and how individuals at the border of dialect regions may dynamically alter aspects of their signals depending on the dialect of their intended receiver. When signals are directed across dialects, signallers may converge on the signal patterns of the other individual to more closely match aspects of the other's signals, similar to the process of vocal accommodation in humans.

A key challenge remains. Many animal signals are graded, and it may be difficult to determine (1) whether, and which, graded variation in fine acoustic structure serves to increase receiver attention or arousal and (2) whether that variation fundamentally alters the meaning of the signal (Leger, Owings, & Gelfand, 1980; Marler, 1976). Although labour intensive, we believe that a multi-step experimental approach could distinguish these possibilities. First, observational data and signal quantification could be used to determine whether signallers alter signals, and link those signal

changes to audience composition. Second, recorded signals could be played to receivers to determine whether these signals elicit different responses. Third, aspects of signals hypothesized to be relevant could be experimentally manipulated and used again in playback experiments to test whether they elicit the predicted responses in receivers. Combined, these methods will allow us to determine the situations and audiences for which signallers alter signals, how the signals are altered and how those alterations affect receiver behaviour.

Nearly 10 years ago, Zuberbühler (2008, p. R189) argued 'Audience effects are probably widespread in animal communication, although surprisingly little research has addressed the problem directly'. We agree that more research on audience effects and their biological significance is needed, and the fine-grained analyses we endorse here offer another tool to detect and understand these effects. If a key goal of research in animal communication is to understand signal variation that is biologically relevant to both signallers and receivers, then we should embrace relevant methodologies from other fields that have proven highly successful at answering similar questions.

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