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Amplitude regulation of vocalizations in noise by a songbird, *Taeniopygia guttata*

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ABSTRACT

Bird vocalizations are produced under various noise conditions. It could therefore benefit birds to alter the amplitude of their signals as noise conditions change. We tested this by recording male and female zebra finches, *Taeniopygia guttata*, as they were subjected to various levels of white noise. Both sexes increased amplitude levels of vocalization in response to increased levels of noise. Similar results were obtained with humans (the 'Lombard effect'). The results are discussed in terms of the 'active space' of bird song and honest signalling.

The world can be a noisy place. Animals that use sound to communicate may be expected to have evolved adaptations that mitigate such interference. One adaptation is amplitude regulation, in which animals adjust their vocalizations to compensate for changes in background noise. As environmental noise increases, subjects increase vocal amplitude. Some form of this phenomenon has been shown experimentally in humans, *Homo sapiens* (Lombard 1911); Old World monkeys, *Macaca fasicularis* and *M. nemestrina* (Sinnott et al. 1975); Japanese quail, *Coturnix coturnix japonica* (Potash 1972); budgerigars, *Melopsittacus undulatus* (Manabe et al. 1998); and white-lipped frogs, *Leptodactylus albilabris* (Lopez et al. 1988). These data suggest that amplitude regulation constitutes a widespread form of plasticity in adult vocal performance. It appears to be an unlearned, largely reflexive response, although there are no developmental data on amplitude regulation except in humans (Amazi & Garber 1982; Siegel & Kennard 1984). Whether songbirds regulate the amplitude of their vocalizations has not been experimentally determined. The ability of adult songbirds to control amplitude would be a novel form of vocal plasticity. It might or might not be mediated by whether the vocalization is learned, and by the sex of the producer. Amplitude regulation would also provide more evidence of a feedback loop in adults between auditory perception and song production (Nordeen & Nordeen 1992; J. Cynx & U. Von Rad, unpublished data).

Amplitude regulation has functional implications as well, regarding the costs and benefits of vocal behaviour (Krebs & Dawkins 1984). Production studies have looked at the costs in terms of power output (Brackenbury 1979; Calder 1990). The rate and amount of singing or calling in a species may be constrained by any number of covarying proximal factors, such as aerobic metabolism, ambient temperature and neuromuscular fatigue (Lambrechts 1996). In a similar way, singing more loudly than necessary may be costly. Amplitude regulation would provide birds with a way of limiting this cost. Bird songs and calls may also be designed for particular 'active spaces' (Marler 1955; Brenowitz 1982), that is, some kinds of vocalizations are produced to be transmitted short distances, and others to maximize distant recognition. Vocalizations may be produced to propagate optimally in specific habitats (Morton 1982; Wiley & Richards 1982). Some of these studies contained the assumption that sound amplitude levels remain constant, or at least contain negligible variance. Others have suggested the possibility of individual amplitude variation, but provided no direct evidence. There are nonexperimental reports that individuals of some species of songbirds vary the amplitude of their vocalizations (red-winged blackbirds, *Agelaius phoeniceus*: C. Harding, personal communication; chestnut-sided warbler, *Dendroica pensylvanica*: D. E. Kroodsma, personal communication; white-throated sparrow, *Zonotrichia albicollis*: Falls 1969; ovenbirds, *Seiurus aurocapillus*: Falls 1963; Kentucky warblers, *Oporornis formosus*, Spector 1992). Finally, Kroodsma (1979) presented evidence for a relation between amplitude and dominance in long-billed marsh wrens, *Cistothorus palustris*.

This study provides experimental evidence for amplitude regulation in one species of songbird. We tested for amplitude regulation in male zebra finch, *Taeniopygia*

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