



Original Article

Aggression in young men high in threat potential increases after hearing low-pitched male voices: two tests of the retaliation-cost model

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ABSTRACT

Research suggests that male voice pitch is an honest dominance signal because it indexes men's physicality and because lower-pitched voices are more costly to develop and maintain. Rather than considering these signaler-dependent mechanisms, we tested a receiver-dependent mechanism hypothesized by M. Enquist's (1985) retaliation-cost model of aggressive signaling. The model predicts that, given a competitive scenario, low-pitched male voices will elicit aggression from male listeners (i.e., signal receivers) who are relatively high in threat potential. We confirmed this hypothesis in two experiments. Under a sexual but not control prime and after listening to low- but not average-pitched male voices, increases in heterosexual male participants' trait dominance predicted stronger aggressive cognitions (Experiment 1), and increases in male participants' handgrip strength predicted stronger aggressive intent (Experiment 2). These findings provide the first direct support for the retaliation-cost model in humans, extend research on the effects of male voice pitch on receiver psychology, and demonstrate an additional cost mechanism that explains why voice pitch is an honest signal of dominance in men.

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1. Introduction

Pitch describes the physical frequency of voices and is the perceptual correlate of fundamental frequency (F0). F0 indexes the lowest and most energetic resonance of the vocal folds, is a positive function of the longitudinal stresses on the vocal folds, and is a negative function of their length and density (Titze, 2000). Pubertal testosterone (T) enlarges male focal folds and causes voice pitch to drop at puberty (Pedersen, Møller, Krabbe, & Bennett, 1986). Male voice pitch continues to negatively correlate with T in adulthood (Dabbs & Mallinger, 1999; Puts, Apicella, & Cárdenas, 2012; Puts et al., 2016) and remains lower than female pitch (by as much as half) for most of the life span (National Center for Voice and Speech, n.d.).

This sexual dimorphism in voice pitch was likely selected by female choice (Collins, 2000; Feinberg, Jones, Little, Burt, & Perrett, 2005) and male intrasexual competition (Puts, Gaulin, & Verdolini, 2006). Supporting both mechanisms, men whose voices are naturally lower or experimentally lowered are perceived by women as more attractive (e.g., Borkowska & Pawlowski, 2011; Feinberg et al., 2005) and by men as more likely to win fistfights (e.g., Hill et al., 2013; Hodges-Simeon, Gaulin, & Puts, 2010; Puts et al., 2006). However, the

effect of pitch on men's perceived dominance is more than five times larger than the effect of pitch on men's perceived attractiveness (Puts, 2010). Similarly, Puts et al. (2016; Study 2) found that, when men's perceived physical dominance and attractiveness as short-term mates were simultaneously used to predict men's pitch, only perceived dominance emerged as a significant predictor. Comparative research further showed that, across anthropoids, pitch negatively correlates with body size (especially for males) and pitch dimorphism increases as intrasexual competition increases (e.g., as mating systems transit from monogamy to polygyny; Puts et al., 2016; Study 1). These findings suggest that male voice pitch functions primarily, though not exclusively, as a dominance signal (Puts, 2010; Puts et al., 2016).

Dominance signals are useful for both signalers and receivers. By acquiescing to men with lower-pitched voices (i.e., those who signal dominance), submissive men avoid physical injuries and dominant men gain access to resources without fighting. Indeed, a similar rule employed by red deer stags—retreat when opponents roar at a higher rate—resolves up to 50% of their confrontations (Clutton-Brock & Albon, 1979).

To evolve, signals must be honest on average, with their content reliably correlating with signalers' traits or states above chance (i.e., allowing a small but tolerable incidence of deceit; Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005). For example, red deer stags' roaring rates are honest because they reliably correlate with fighting ability. If roaring rates cannot be used to predict fighting ability, receivers would gain nothing from attending to these signals in contest competition and the signals would ultimately disappear. The existence

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of functional dominance signals strongly implies that some mechanism maintains signal honesty.

1.1. Indexing and cost mechanisms that ensure signal honesty

Signal honesty can be ensured when signal design is physically constrained (i.e., indexing; Maynard Smith & Harper, 2003; Hurd & Enquist, 2005). For example, the pitch of toad vocalizations indexes toads' physical dominance because their vocal folds are proportional to their body size (Davies & Halliday, 1978), which is an important criterion of threat potential (Huntingford & Turner, 1987). Honesty can also be ensured when more intense signals are more costly to develop, maintain, or produce (Grafen, 1990; Hurd & Enquist, 2005; Zahavi, 1975). For instance, high roaring rates signal fighting ability in stags because the energy required for high-rate roars cannot be sustained by weak males (Clutton-Brock & Albon, 1979).

Human male vocal dominance signals may be maintained by both indexing and costly-signaling mechanisms. Suggesting an indexing mechanism, there is evidence that male pitch negatively correlates with height (see for a meta-analysis, Pisanski et al., 2014) and physical strength (among peripubertal Tsimane males, Hodges-Simeon, Gurven, Puts, & Gaulin, 2014). However, the size of human vocal folds is not constrained to body size (Fitch, 2000), and Sell et al. (2010) and Puts et al. (2012) found no correlation between pitch and physical strength among men from America and other populations (e.g., the Hadza). The possibility for indexing exists, but other factors are likely at play.

According to the immunocompetence handicap (ICH) hypothesis (Folstad & Karter, 1992), male pitch honestly signals phenotypic quality because only males in good physical condition can afford to have high T, which facilitates the expression of secondary-sexual traits such as low pitch. Hodges-Simeon, Gurven, and Gaulin (2015) found no evidence that immune function (e.g., levels of secretory IgA) correlated with T or pitch in a sample of peripubertal Tsimane males. But supporting the ICH hypothesis, Hodges-Simeon et al. did find that participants who were in better energetic condition (e.g., those with higher age-adjusted BMI) had higher T and lower pitch.¹ Further supporting the ICH hypothesis, Puts et al. (2016) found that U.S. college males who had higher T had lower pitch, but only if they also had low cortisol levels. Cortisol rises in response to infection (Sapolsky, Romero, & Munck, 2000) and suppresses T (Burnstein, Maiorino, Dai, & Cameron, 1995). It follows that only healthier men (with lower immune system activation and thus lower baseline cortisol) can afford to have higher T and lower pitch. Thus, Hodges-Simeon et al. (2015) and Puts et al. (2016) suggest that men's pitch reliably tracks phenotypic quality by entailing developmental and maintenance costs.

It is unlikely, however, that these indexing and developmental/maintenance cost mechanisms are sufficient to maintain the honesty of men's voice pitch as a dominance signal. Those two mechanisms apply to baseline voice pitch, but do not appear to apply to pitch modulation, which is freely available to men (and women) when they change the amount of tension on their vocal folds (Titze, 2000). Indeed, pitch modulation has been observed in agonistic interactions. In mate competition, men raise their pitch when they address rivals they perceive as more physically dominant, but lower their pitch when they address rivals they perceive as less physically dominant (Puts et al., 2006). There is also evidence that those who lower their pitch are perceived as more dominant than those that raise their pitch (Fraccaro et al., 2013). These findings suggest that male voice pitch not only indexes men's trait dominance, but can also signal their moment-to-moment

assessments of relative threat potential in contest competition. This flexibility invites cheating, and would appear to require additional mechanisms to ensure signal honesty.

2. The present research

Drawing on the retaliation-cost model (Enquist, 1985), an influential animal model of agonistic interaction (Grafen, 1990; Searcy & Nowicki, 2005), we hypothesize that the honesty of men's voice pitch as dominance signal is maintained, at least in part, by the costs incurred by receivers' attack (i.e., retaliation). Considering the weak correlations between men's pitch and physicality (see above), the retaliation cost is a good candidate mechanism because it does not require a direct association between signal intensity (e.g., pitch level) and individual condition (e.g., physical strength). Nor does it require that the signal be costly to develop, produce, or maintain. Instead, the retaliation cost applies to dominance signals that "apparently can be performed equally well by any individual" (Enquist, 1985, p. 1152), so long as the signal chosen (for whatever reason) to advertise threat potential causes different degrees of aggression from signal receivers. There is evidence for this "retaliation rule" in other species, but it is currently unknown whether this mechanism acts on human receiver psychology.

2.1. The retaliation-cost model

2.1.1. The model

Enquist's (1985) model describes a choice between two alternative signals, *A* and *B*, by strong and weak individuals in agonistic interactions. The model assumes that signals do not directly harm opponents or incur production costs, can be performed equally well by all individuals, but are chosen to signal different levels of threat potential—*A* for strong individuals and *B* for weak ones. The model specifies the following rules: 1) If strong, signal *A*; attack if the opponent responds with *A* (the retaliation rule); but, repeat *A* if the opponent responds with *B* and attack if the opponent does not retreat after signaling *B*. 2) If weak, signal *B*; retreat if the opponent responds with *A* but attack if the opponent responds with *B*.

Thus, signaling *A* if strong and *B* if weak are honest strategies, and signaling *A* when weak is a dishonest strategy. Importantly, the dishonest signal does not spread in the population because it is prevented by the retaliation rule: Attack if strong and your opponent signals *A*. When attacks from strong signal receivers are sufficiently costly for weak signalers, honest signaling becomes evolutionarily stable by strategic choice (Grafen, 1990; Guilford & Dawkins, 1995; Searcy & Nowicki, 2005).

2.1.2. Empirical evidence

Tibbetts and Dale (2004) measured the pairwise dominance ranks of paper wasps, which are advertised in facial coloration, and then altered subordinates' facial patterns by applying paint to enhance, reduce, or maintain their rank. As predicted by the retaliation rule, dominant wasps aggressed against cheating subordinates (i.e., those whose face was painted to signal dominance) more frequently than they did against subordinates whose rank was maintained or reduced (see also, Rohwer, 1975). Using playback methods, Osiejuk, Łosak, and Dale (2007) found that, while both young and old ortolan bunting males displayed similar approach tendencies toward non-threatening songs, older males (who had more experience of fighting) showed stronger approach tendencies to more threatening songs. Similarly, Anderson, Searcy, Hughes, and Nowicki (2012) found that song sparrows' baseline aggressiveness, indexed by their approach toward non-aggressive songs, positively predicted their subsequent approach toward aggressive songs. In sum, more dominant signals are more likely to induce aggressive responses from signal receivers who have high threat potential, such as those that are more dominant, experienced with fighting, and dispositionally aggressive.

¹ This intercorrelation between energetic condition, T, and pitch may be due to the fact that people who had more access to food start puberty earlier (Gluckman & Hanson, 2006), which results in higher T and lower pitch. We thank an anonymous reviewer for suggesting this possibility.

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