



## Waltzing *Taeniopygia*: integration of courtship song and dance in the domesticated Australian zebra finch



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Multimodal signalling can improve or maximize information exchange. A challenge is to show that two independent signals, such as vocalizations and visual displays, are deliberately coordinated. Male zebra finches, *Taeniopygia guttata*, signal visually and acoustically during courtship, performing a stereotyped dance while singing. The male approaches the female hopping in a zig-zag pattern, turning his body axis, and wiping his beak repeatedly on or above the perch. The only previous quantitative study of song and dance choreography in zebra finches revealed that the distribution of all movements during song was not strongly patterned across birds but very similar in fathers and sons. This raises the possibility that particular movements may follow a choreography. Here we report that three operationally defined dance movements, 'beak wipe' (BA), 'turn-around' (TA) and 'hop', occurred with different frequencies and speed during singing than during silence. BW, TA and hops clustered significantly at the start and end of song bouts and were arranged in a nonrandom fashion. In addition, BW, but not TA, were performed faster during song than nonsong. Finally, hops coincided significantly more often than expected by chance with particular notes. Together, these results suggest that male zebra finches integrate their song and dance during courtship. This may help females to identify courting males in a noisy environment and evaluate the intensity and quality of the courtship performance. Our results underscore that the choreography of movement gestures with learned vocalizations, such as hand gestures accompanying speech, is a further parallel between human and avian signalling. They invite future investigations into the underlying neural mechanisms and consequences for mate choice.

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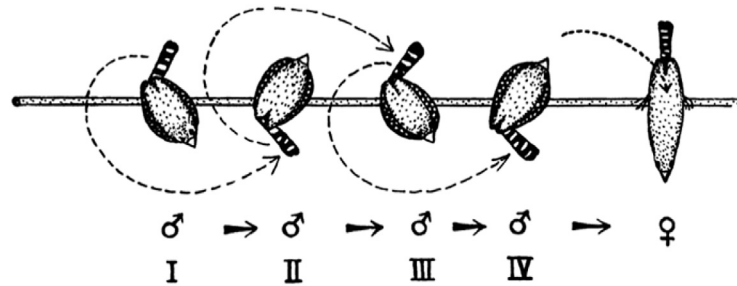
Communication is essential for organizing the social interactions of zebra finches, *Taeniopygia guttata*, that live in large flocks (Immelmann, 1969). Both sexes use several types of calls but only males sing songs (Slater, Eales, & Clayton, 1988; Zann, 1996). Males direct their song towards females during courtship but also sing so-called 'undirected song' in nonreproductive contexts, e.g. when alone or in the company of males (Dunn & Zann, 1996; Immelmann, 1959; Jarvis, Scharff, Grossman, Ramos, & Nottebohm, 1998; Morris, 1954; Sossinka & Böhner, 1980). Males can rapidly switch between directed and undirected songs (Caryl, 1981), which differ bioacoustically and in the underlying neural processes (Cooper & Goller, 2006; Jarvis et al., 1998; Kao & Brainard, 2006; Sossinka & Böhner, 1980; Woolley & Doupe, 2008). Courtship song is accompanied by a characteristic dance during which the

male advances towards the female turning 180° with each hop, twisting his head and tail towards the female while continuing to sing. When facing the female, he also rhythmically swings his head from side to side while singing (Barclay, Harding, & Waterman, 1992; Immelmann, 1959; Kunkel, 1959; Morris, 1954; Zann, 1996, pp. 170–174; Fig. 1).

When animals use multiple signalling modes to attract a mate, those signals need not necessarily be coordinated with each other in their fine temporal pattern (e.g. butterfly coloration and pheromones for mate attraction). However, in some animals it has been shown that courtship can involve two signalling modes that are integrated into a coherent performance, providing the basis for an integrated percept in the receiver. For instance, jumping spiders, *Habronattus pugillis*, coordinate visual and seismic signals using limbs and body appendages (Elias, 2006). Golden-collared manakins, *Manacus vitellinus*, and club-winged manakins, *Machaeropterus deliciosus*, integrate acoustic wing-snaps with visual displays during courtship (Barske, Schlinger, Wikelski, & Fusani, 2011; Bostwick, 2000). Barbary doves, *Streptopelia risoria*, perform visual bows accompanied by acoustic bowing-calls during

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**Figure 1.** Schematic representation of a male zebra finch courtship dance facing a female bird. Reprinted with permission from Morris (1954, p. 286).

courtship. The onset of both signals is not temporally synchronized, but the intervals between bowing and calling are rhythmically correlated, leading to an integrated complex signal (Fusani, Hutchison, & Hutchison, 1997). Male superb lyre-birds, *Menura novaehollandiae*, integrate acoustic and movement signals voluntarily and within a predictable pattern during courtship (Dalziel et al., 2013). Nonvocal bill-clicking patterns and specific song note sequences in Java sparrows, *Lonchura oryzivora*, are closely integrated. They occur for instance more frequently with the beginning of song, which might be an outcome of cultural transmission (Soma & Mori, 2015). In various species, female recipients are known to be sensitive to the multimodality of these signals. For instance, females of the estrildid family have a complex dance in species in which males also have a complex dance (Soma & Garamszegi, 2015). Also, wing-spread displays in cowbirds, *Molothrus ater*, accompanying song (Cooper & Goller, 2004) elicit longer lasting copulation solicitation displays from females than presentation of song or wing-spread displays alone (O’Loughlin & Rothstein, 2010). Audiovisual playback experiments revealed that the female’s sexual behaviour varies with the intensity of the male’s body movements (O’Loughlin & Rothstein, 2012). Interestingly, wing movements and song were integrated even in males that had been reared without visual or auditory input from male tutors (Hoepfner & Goller, 2013). Female golden-collared manakins are influenced by speed and frequency of the displays by courting males (Barske et al., 2011). Female túngara frogs, *Physalaemus pustulosus*, prefer a robotic frog that correctly coordinates the visual signal of the vocal sac inflation with the produced calls (Taylor, Klein, Stein, & Ryan, 2011). In humans, the integration of gesture and speech is intimately linked to learning and creating language (Goldin-Meadow & Alibali, 2013). These examples stress the additive effect of two signalling channels, and the relevance of temporal integration of the two signals with each other. In contrast to these examples, in other birds visual and vocal displays are not synchronized. For instance, long-tailed manakins, *Chiroxiphia linearis*, and starlings, *Sturnus vulgaris*, perform visual and acoustic signals in a parallel, but not in an integrated fashion (Böhner & Veit, 1993; Lukianchuk & Doucet, 2014).

In male zebra finches it is not clear whether the dance movements accompanying song are synchronized to the song. The only study that examined whether song and dance are coupled in specific ways found no significant association of stereotypic body movements with acoustic features of song (Williams, 2001).

Here we operationally defined two dance elements, beak wipes and turn-arounds, characteristic of high-intensity courtship (Barclay et al., 1992), as well as a third dance element, hopping behaviour, and analysed their relationship to vocalizations in videotapes. We hypothesized that these movements were associated with song more so than when birds were silent. We further

speculated that movements were associated with specific positions in the song motifs.

## METHODS

### Subjects

A total of 20 captive-bred male zebra finches (9–45 months old) participated in three variations of the experimental set-up, seven in 2010 (experiment A), four in 2011 (B) and 10 in 2013 (C). One male was tested twice (2010, 2011) and his data were averaged. Before experiment A male birds were housed in groups of seven males for several months. Birds were transferred from large aviaries into smaller group cages 1 week before experiments B and C. Experiment B was performed in May outdoors, and before, during and after testing, birds were also kept outdoors. Indoor conditions were kept at  $25 \pm 3$  °C and 12:12 h light:dark cycle. All subjects had access to seed, water, grit and cuttlebone ad libitum.

### Recording

An adult male was introduced to the experimental set-up containing one female that he could hear but not see. After at least 2 h the visual separation was removed for 5 min and the male could see the female. Males that performed courtship dances and directed their song to females during this time were audiorecorded and videotaped. During 2 days at least three video sessions per bird, separated by 20 min or more, took place. All recorded songs were directed to the female, accompanied by the typical courtship-associated movements and body posture. We varied the experimental set-up during the three experiments with respect to location, cage size and video/audio equipment which ensured that our findings were not affected by the physical constraints of a particular experimental set-up (Fig. 2, Table A1). Because zebra finches in the wild court on branches rather than on the floor, we equipped our cages with a perch in contrast to a former study (Williams, 2001). Video and audio streams were digitized and stored on hard disks or on SD cards.

### Behaviour Definitions, Audio and Video Analysis

Audio files (22.05 kHz, 16 bit resolution) were converted into sound spectrograms using Avisoft-SASLab Pro 4.38 software (Avisoft Bioacoustics, Berlin, Germany; settings: FFT\_256 points, Hamming window, overlap 50%). Video recordings were analysed frame by frame using Noldus Observer 9 XT (Noldus Information Technology, Wageningen, The Netherlands) and dance-associated

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