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SOCIAL CONTEXT AND RESPONSE TO FEMALE VOICE: AUDIENCE EFFECT IN THE MALE ZEBRA FINCH (*TAENIOPYGIA GUTTATA*)

VPLIV DRUŽBE IN REAGIRANJE NA GLAS SAMICE: »UČINEK POSLUŠALSTVA« PRI ZEBRICAH (*TAENIOPYGIA GUTTATA*)

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ABSTRACT

Social context and response to female voice: Audience effect in the male Zebra Finch (*Taeniopygia guttata*)

How behaviour and underlying brain functions are shaped by social context remains a poorly explored domain. Here, we review two recent studies on Zebra Finches (*Taeniopygia guttata*) which focus on this question. In this species, communication behaviour within male and female pair appears to be strongly regulated by the presence of other individuals. Investigation at brain level shows that the sound-induced immediate early gene response is also highly sensitive to the audience effect.

Key worlds: Acoustic communication, vocal recognition, playback experiments, gene ZENK, songbirds.

IZVLEČEK

Vpliv družbe in reagiranje na glas samice: "učinek poslušalstva" pri zebricah (*Taeniopygia guttata*)

Vpliv družbenih razmer na vedenje in s tem povezane možganske funkcije ostaja slabo raziskano področje. Avtorji prikazujejo dve študiji na zebricah (*Taeniopygia guttata*), ki obravnavata to vprašanje. Pri tej vrsti ščinkavcev izgleda, da na komunikacijsko vedenje med pari močno vpliva prisotnost drugih osebkov. Raziskava na možganih tudi kaže, da tudi na zvočno induciran zgodnji genski odgovor zelo vpliva "učinek poslušalstva".

Ključne besede: zvočna komunikacija, prepoznavanje po zvoku, poskusi s predvajanjem zvoka, gen ZENK, ptice pevke.

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INTRODUCTION

In songbirds, acoustic communications generally take place in a network of signallers and receivers (McGregor 2005). During a communication event, the exchanged information influences the behaviour of "direct" receivers but could also be used by undesired "indirect" receivers: the "eavesdroppers" (Johnstone 2001). Eavesdroppers represent an important regulatory element for acoustic communication, e.g., the vocal intensity (Cynx & Gell 2004) or the attitude towards the other sex depends on the audience of the emitting bird (Marler et al. 1986, Evans & Marler 1994, Baltz & Clark 1997, Evans & Evans 1999, Henry & Hausberger 2001, Striedter et al. 2003). This social regulation of acoustic communication relies on modifications of the emotional state of the protagonists. Indeed, stressful situations like the presence of a predator are known to modify vocal emission by songbirds (McGregor 2005). More generally, social context determines the emitter's motivation that modulates communicative behaviour. Thus, a key issue in research on communication is to elucidate how social factors influence behaviour of communicating animals.

The Zebra Finch (*Taeniopygia guttata*) is a highly gregarious bird. Inside the colony, acoustic communication plays a major role of regulation of social interactions (Zann 1996). Among other vocalizations, both sexes emit a distance call also known as "long call" (Price 1979, Zann 1984, Zann 1996). Although male and female distance calls show different acoustic structures, both are known to contain sufficient information for species-specific recognition among conspecifics and individual recognition between mates (Zann 1984, Vignal et al. 2004). In this monogamous species, distance calls are especially exchanged during separation or reunion of the partners of a pair-bond. This vocal recognition between male and female Zebra Finches takes place inside the communication network of the social group. This bird can thus be considered as a model to investigate the possible influence of the presence of conspecifics on communication processes in a male-female dyad. In two recently published works (Vignal et al. 2004, Vignal et al. 2005), we investigated some behavioural and neurobiological consequences of the audience effect in the Zebra Finch. The present paper aims to review these results.

First study: Behavioural response to mate call in male Zebra Finch (Vignal et al. 2004)

The central question of this study was to assess if the response of a male Zebra Finch to its partner's voice is influenced by the presence of conspecifics. Our results show that the male pays attention to the social relationships between individuals in the audience and uses this information to control its behaviour towards its female partner's calls.

Rationale of the study

Previous studies showed that female Zebra Finches accurately recognize the voice of their mate among vocalizations of other individuals (Miller 1979). Conversely, this abi lity was not observed in males. According to this bird's way of life, it was extremely improbable that this recognition deficience was real, at least for wild birds. As experi-

ments were performed on domesticated strains of Zebra Finches and by playing back females' calls to isolated males, two main hypothesis could be envisaged to explain this "male problem": either domesticated females do not show individually distinct voices, or experiments on males were performed in stressfull conditions where males do not show a normal preferential response to their female's voice.

Method

To determine if females Zebra Finch vocalizations are sufficiently individualized to allow recognition by their male partner, we analysed the acoustic structure of female distance calls by comparing intra- and inter-individual variations of 17 parameters in the temporal and frequency domains. The measured parameters were then subjected to a multivariate analysis.

To assess if the recognition of their female partner's voice by males is affected by social context, the vocal responses of males to their mate's calls and to a familiar female's calls were compared in different audience situations. We chose three different contexts: 1) "unmated males": the tested male is accompanied by two single males placed in a companion cage, 2) "mated pair": the tested male is accompanied by a normal male-female pair in a companion cage, 3) "unmated pair": the tested male is accompanied by a male and a female, not paired, in two different companion cages.

Results

The results of the acoustic analysis clearly show that female calls are highly individualized (Fig. 1). Thus, males have a clear opportunity to differenciate the voice of their partner among vocalizations of other females.

The results of playback tests are also straightforward: male behaviour depends on the social status of accompanying birds (Fig. 2). In the presence of single birds, the tested bird showed no differential response to its partner's calls. Conversely, it emitted two to three times more calls in response to its mate's vocalizations than to the calls of a familiar female when an established male-female pair is present.

First, these results show that the male is perfectly able to recognize the voice of its partner. Second, this bird demonstrates a particular ability to distinguish the nature of social links between congeners. As a whole, this study emphasizes the strong effect that an audience may have on the behaviour of a communicating animal.

SECOND STUDY: Brain immediate early gene response to female call in male Zebra Finch (VIGNAL et al. 2005)

This study explores the modulatory effect of a conspecific audience on the expression of an immediate early gene (IEG), named ZENK, known to be activated in some brain auditory areas in response to calls playback (MELLO 2002). We show that this gene activity is highly sensitive to the presence of an audience.

Rationale of the study

Although sociality is a major characteristic of Zebra Finches biology, experimental

constraints imply that the majority of previous neuro-ethological investigations focused on birds in isolation. As our first study emphasized, this abnormal social situation is certainly stressful for the bird and can therefore generate modifications of behaviour. As we observed that the social context drives behavioural response to acoustic stimuli, this influence was likely to be found at the level of cerebral processes.

Methods

We focused on the response of male Zebra Finches to familiar female calls. Two experimental groups were defined by their social context: whereas each tested individual of the "isolated birds" was in complete social isolation, each subject of the "grouped birds" was accompanied by two companion males. Playback signals were series of familiar female calls. The IEG response to sound stimuli was assessed by immunocytochemistry in the auditory area of the telencephalon thought to realize extraction of biologically relevant information: the NCM (Caudomedial Nidopallium).

Results

We observed a significant effect of social context on the sound-induced activation of the ZENK gene which was strongly enhanced in grouped birds in comparison with isolated ones. Conversely, the basal level of ZENK expression remained identical in both contexts. This is the first unequivocal demonstration that a conspecific audience can influence a gene activation linked to acoustic perception in the songbird brain.

DISCUSSION

From the data reported in our two recent papers, male Zebra Finches react differentially to female voices depending on the presence of congeners, and brain processes underlying this reaction depend also on social context. This audience effect (JOHNSTONE 2001, STRIEDTER et al. 2003) reflects the organization of acoustic communication in gregarious birds: the social group represents a network of emitters and receivers, in which the behaviour of each individual is influenced by the presence of the other members of the network (BALTZ & CLARK 1997, MCGREGOR 2005). This audience effect is one element supporting the existence of high cognitive abilities in some bird species. It might be linked to the cognitive demands of social life, joining the hypothesis of "social intelligence" (DUNBAR 1998) which says that social context is an important selective force for animal cognitive ability. The capability to estimate social relationships between congeners has been studied for a long time in primates (TOMASELLO & CALL 1997, PERRY et al. 2004), but supports for a similar aptitude in birds were lacking. However, evidence of high cognitive faculties in birds is growing, e.g., tool manufacturing (TEBBICH et al. 2001, CHAPPELL & KACELNIK 2004), cultural transmission (MANEY et al. 2003) and transitive inference upon hierarchy (PAZ-Y-MINO et al. 2004). These parallels between mammalian and avian cognitive abilities, reinforced by the resemblances between song learning processes in songbirds and language development in human (BRAINARD & DOUPE 2002, KUHL 2003, WILLIAMS 2004),

have motivated an impressive number of neuro-ethological studies in birds. Recently, the nomenclature of the avian brain has been revised in accordance to the "neo-cortical" functions of the avian pallium (JARVIS et al. 2005).

The complexity of the social regulation of behaviour implies that the brain has a fine representation of the social parameters of the environment. Our studies showed that the presence of congeners modulates cerebral activation induced by hearing conspecific calls. This result confirms that acoustic communication is a very interesting paradigm to investigate how the environment induces rapid and significant modifications of brain activity. A growing corpus of experiments has shown that the cerebral pathways of sound processing in the songbird brain are under the influence of the noradrenergic system (HARDING et al. 1998, MELLO et al. 1998, CASTELINO & BALL 2005). The activity of the noradrenergic system would reflect the animal's vigilance level and would be at the origin of the regulation of the telencephalic neuronal activity linked to stimulus significance (CASTELINO & BALL 2005). Other neuromodulatory networks, as the dopaminergic system, are likely to regulate ZENK expression according to social context (CHARLIER et al. 2005). To achieve a better understanding of how the avian brain processes social parameters of the environment, it will be necessary to monitor ZENK gene and neuromodulators expressions together. Indeed, a recent study observed that ZENK expression is co-regulated with synaptic activity during social behaviour (KOSHIBA et al. 2005). By identifying the involved cellular interactions, we will be able to build a model of the cerebral network which supports the cognitive abilities of birds, and thus to compare this network with what is known about the mammalian brain.

Finally, by emphasizing the impact of social context in laboratory investigations with rather simple paradigms, the results of our studies reinforce the importance of paying attention to the audience effect when designing experiments and interpretating results of research works that use behaving animals.

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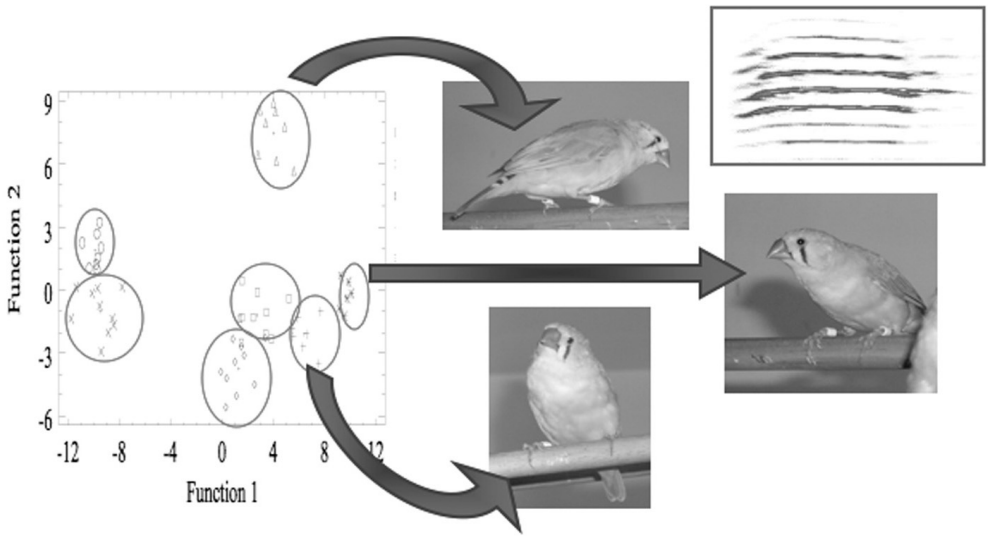

Figure 1: Results of a Principal Component analysis showing that Zebra Finch female calls are highly individualized. Each point on the graph represents a recorded call, each symbol corresponds to a different female (part of the figure is from Nature, 2004, 430, 448-451).

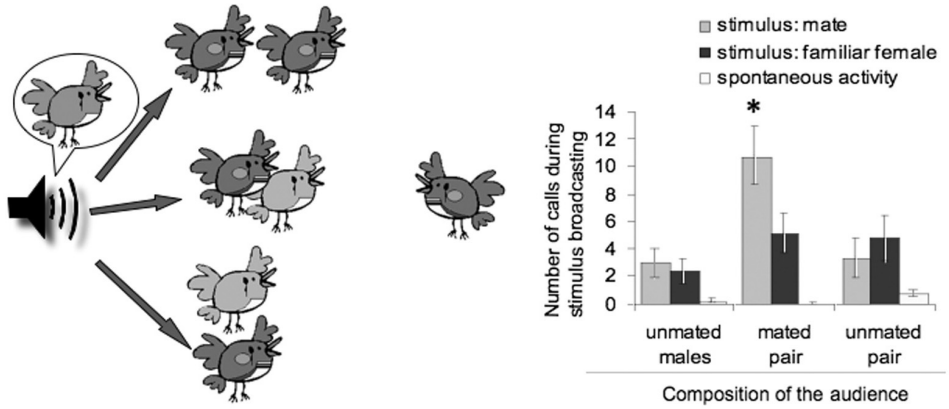

Figure 2: Audience effect and male response to female voice. Males were tested in three different contexts (accompanied by two single males, by a male-female pair, or by a single male + a single female). The male response to its mate's calls depends on the composition of the audience (part of the figure is from Nature, 2004, 430, 448-451).