

S35-4 Social experience, vocal learning and social cognition in the European starling, *Sturnus vulgaris*

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Abstract European starlings are well known for their rich and varied social life. Recent studies reveal a social organization based on same-sex preferences, spatial proximity and vocal sharing in captive groups. Much less is known about social cognition and the possible role of social experience on the development of cognitive abilities. Experimental results described here show how the social conditions under which starlings are raised affect not only the quality of vocal copying (for the same auditory experience), but also perception of mirror images, relationships to people and organization of neuronal selectivity in the brain. Thus hand-raised birds placed either in groups with adults, or in pairs as young naive birds, or in isolation, react very differently when confronted with familiar or unfamiliar humans. Intraspecific social experience, therefore, influences the relationships of birds with their environment, including interspecific interactions. Different modalities are involved and include the visual and auditory worlds, as revealed by a mirror test and electrophysiology respectively..

Key words Social learning, Vocal learning, Cognition, Starlings

1 Introduction

Despite an apparently less sophisticated brain structure, birds have been shown to be capable of cognitive tasks generally considered restricted to mammals. A number of examples have been revealed through exhaustive studies on the African gray parrot (e.g., Pepperberg, 1990). Another remarkable feature of avian ability is the vocal complexity of song, which led Marler (1970) to suggest parallels between song learning in birds and language development in humans. Long-term memory, categorization, discrimination and recognition have all been found to be involved in learning and perception in birdsong (Hausberger et al., 1999).

Complex vocal learning is often involved in social contexts (Baptista and Gaunt, 1997). Many songbird species spend at least part of their lives in social situations: colonies, foraging groups, wintering flocks, leks. Therefore, social cognition in songbirds, although little investigated, should be a fruitful field for study. Birds, through song signatures, discriminate neighbors from unfamiliar birds (Beecher, 1982), evaluate distance (Wiley and Godard, 1996), and form preferential social associations (Freeberg, 1999). In many species, song learning appears to be modeled under social influences, although the precise modalities involved (auditory-visual-physical contact) remain unclear. Moreover, birdsong has led to fascinating discoveries in neuroethology revealing a complex system where learning, plasticity and therefore, experience, play a role in modeling brain structure (e.g., Doupe and Solis, 1997).

It is still difficult, however, to integrate these differ-

ent lines of knowledge, especially where social cognition is involved. Essential questions concerning perceptions of conspecifics or social partners, why a young bird chooses a particular tutor, the roles that vocal versus visual channels play in communication, and the neuronal bases involved, must all be solved in order to understand how birds view their social world. In the present study, we present evidence of social cognition in European starlings and investigate the effects of social experience on the development of social perception and brain structure.

2 Behavioral evidence

Song characteristics enable starlings to gather information about species, population and individual identities. Playback experiments in the field reveal clear dialectal discrimination as well as an ability to recognize specific song types despite variation (Adret-Hausberger, 1982). Studies on captive groups indicate that social organization is reflected best in spatial proximity and that song-sharing is a sign of social affinity: pairs of females and groups of males emerged that shared most of their song repertoires (Hausberger et al., 1995).

Social affinities tend to remain stable for long periods. It is possible that birds may have an image of some kind in their memory for a preferred social partner. Thus we devised an experiment to investigate whether shared songs had special meaning for the sharers and whether separation affected their memory. Playback experiments were performed on female starlings. We broadcast their own songs (unique

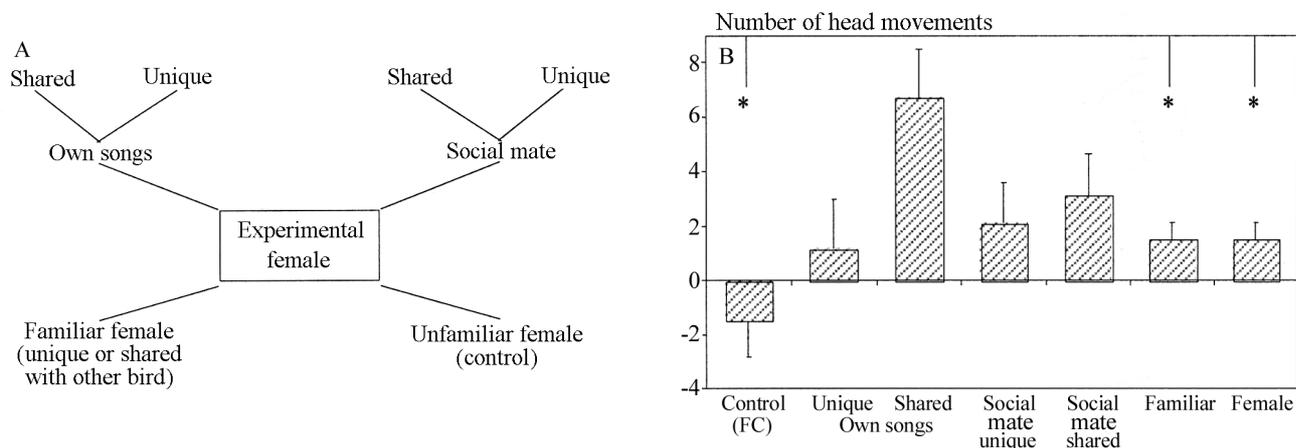


Fig. 1 Responses of the three social types of European starlings to broadcast song

A: the categories of songs broadcast to experimental females; B: head movements after playback of female whistles to females — means and *SD* (from Hausberger et al., 1997).

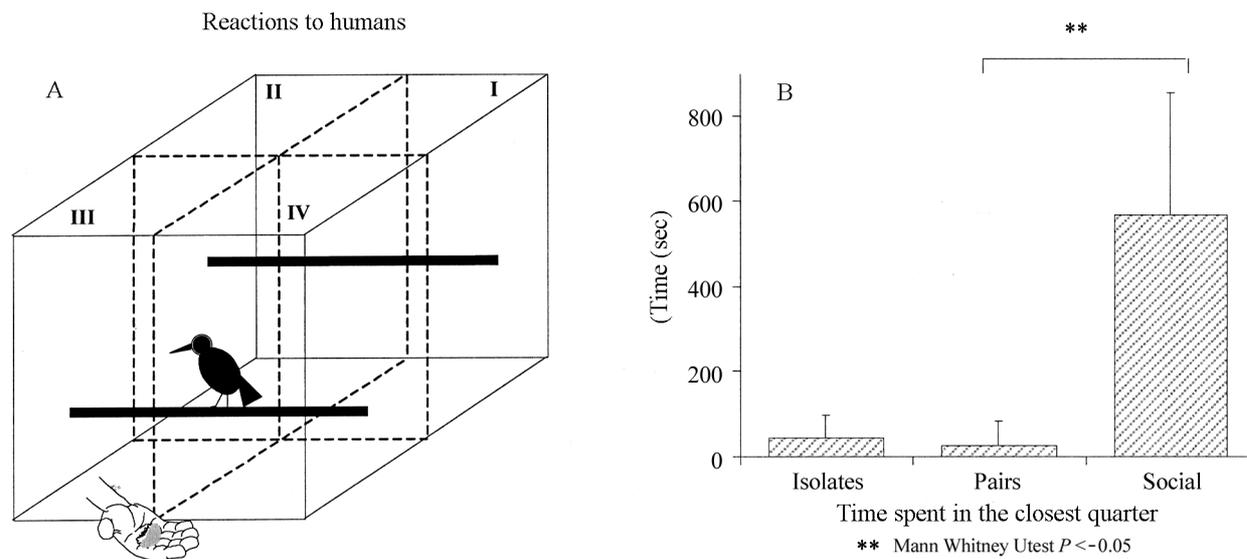


Fig. 2 Responses of the three social types of European starlings to humans

A: experimental setting to assess reactions in male birds raised in their first year in different social contexts in aviaries (1) with adult males and other young birds (social), (2) in pairs of inexperienced birds (pairs), and (3) in isolation. Pairs and isolated birds were kept in soundproof chambers (Poirier et al., submitted). Appetizing food was presented at the door of the cage. The cage was divided in four parts: I and II = back of cage, III and IV = front of cage. B: average time spent by birds in the front part of the cage (III and IV). Clear differences appear between birds raised socially, in pairs or in isolation.

or shared), the songs of partners (unique or shared), and songs of familiar or of unfamiliar females, and recorded all behavioral responses (Fig. 1A). The females increased their head movements (changes in orientation, gazes) for some stimuli more than for others. Whereas the songs of a strange female inhibited head movements, shared songs (own and partner's) elicited a significant increase (Fig. 1B). Obviously, shared song had special meaning for the birds which seemed to exhibit searching behavior through visual cues. Interestingly, the females had been separated from their social partners for several months before being tested, suggesting that shared songs may recall a perception of a social bond.

Social experience has important effects on vocal

sharing. Thus young females raised only with adult male tutors shared only their warbling motifs (Table 1). It also affects visual perception. Reactions to mirror images differed according to whether starlings have been raised in social groups, in pairs as naive birds, or in isolation. Birds raised in pairs appeared less disturbed, whereas those that had been isolated or raised in social groups were more active in response, gazing or pecking at the mirror (Henry et al., in prep.). The perception of what is a conspecific clearly differed among the three groups, a perception probably most difficult for the birds raised socially.

We then asked the question: could the perception of a nonspecific individual be affected by experience and, moreover, if that perception differed according to social

experience? So reactions to humans were tested by presenting appetizing food to birds at the door of their cage (Fig. 2A). We compared time spent by birds in the back of their cage (parts I and II) and in the front of their cage (parts III and IV) close to humans. Social experience clearly affected their reactions to humans. Socially-raised birds spent longer than isolated and pair-raised birds in the parts of their cages closest to humans (Fig. 2B). Thus in starlings, social experience affects both the perception of conspecifics and non-conspecifics, including humans.

3 Neuroethological evidence

Playback experiments clearly indicate capacities for categorization and generalization in starlings (Hausberger and Cousillas, 1996). We investigated the neural bases of these abilities. Thus, a study on wild-caught adult male starlings, involving single cell electrophysiological recordings of field L, the main auditory area of the brain, revealed that about 80% of over 300 auditory neurons responded only to whistles (Hausberger et al., 2000). Thus, many neurons appear to select precise elements in songs, which were also identified as key elements for categorizing songs in behavioral experiments. A mapping method, using multicellular recordings, indicated that such selectivity is organized spatially (Cousillas et al., submitted).

Both neuronal selectivity and their spatial distributions appear to depend on social experience. Comparisons revealed that most auditory neurons in birds raised in isolation responded to any sound (e.g., on/off responses), those in paired birds were intermediate in selectivity, and only those in birds raised in social groups were proportionally similar to those in adult wild animals (Cousillas et al., in prep.).

Thus these data indicate that, even though they may hear adult songs, birds raised in isolation develop poor perceptual abilities that certainly affect the way they view, categorize and memorize their social world. Social experience obviously plays a major role, auditory experience in solitary starlings preventing them from constructing a "normal" auditory field.

4 Discussion

Both behavior and neuro-ethological data converge to show that social cognition does exist in starlings, and that it depends very much on social experience acquired during development. Social organization differs between males and females, and this difference is reflected in the stronger reactions of females to shared songs.

Moreover, female starlings do not seem to learn from male models. Song learning along sexual lines has been described in a few species (review in Baptista and Gaunt, 1997), and in particular in the Indian hill mynah (*Gracula religiosa*), another sturnid (Bertram, 1970). This is particularly intriguing, as here the young females had no adult female model. Baptista et al. (1993) did not succeed in tutoring young female white crowned sparrows; this may have been due to the fact that only male models were available

Table 1 List of motif types found in the repertoire of 3 adult males and four one-year old females

	Wild birds			Experimental birds		
	M1	M2	M3	Social birds		
				S3f1	S3f2	S3f3
W1		+	+			
W2		+	+	+		
W3		+	+	+		
W4		+	+			
W5		+	+			
W6		+	+			
W7		+	+			
W8		+	+			+
W9		+	+	+		
W10		+	+	+		
W11		+	+	+		
W12		+	+	+		
W13		+	+	+		
W14		+	+	+		
W15		+	+	+		
W16		+	+	+		
W17		+	+	+		
W18		+	+	+		
W19		+	+	+		
W20		+	+	+		+
W21		+	+	+		
W22		+	+	+		
W23		+	+	+		
W24		+	+	+		
W25		+	+	+		
W26		+	+	+		
W27		+	+	+		
W28		+	+	+		
W29		+	+	+		
W30		+	+	+		
W31		+	+	+		
W32		+	+	+		
W33		+	+	+		
W34		+	+	+		
W35		+	+	+		
W36		+	+	+		
W37						+
W38						+
W39						
W40						
W41						
W42						
W43						
W44						
W45						
W46						
W47						
W48						
W49						
W50						
W51						
W52						
W53						
W54						
W55						
W56						
W57						
W58						
W63				+	+	+
W64				+	+	+
W65				+	+	+
W66				+	+	+
W67					+	+
W68					+	+
W69				+	+	+
W70					+	+
W71					+	+
W72					+	+
W73					+	+
W74					+	+
W75				+	+	
W76				+	+	
W77				+	+	
W78				+	+	
W79					+	
W80				+		+
W81			+			
Within each pair						
Non shared motif types	19	32	26	3	1	1

The four females were housed with male M3 from fledging and could hear and see males M1 and M2 living in adjacent aviaries. Note song sharing among males and among females respectively, but no overlap between them (from Poirier et al., submitted).

(Baptista, pers. com.). Song sharing seems to be linked to social affinity in a variety of species, including starlings (Hausberger et al., 1995; Mann and Slater, 1995; Brown and Farabaugh, 1997; Smith et al., 2002). We also found that female starlings form close bonds. Therefore, the cues used for learning a song may be correlated with cues used to develop social affinities (West et al., 1997).

As it is, sharing a song seems to give particular status to the song and to elicit long-term memories. Exactly what sort of perceptivity this is is difficult to assess but, in our experiments, females clearly responded with searching behavior when a shared song was broadcast. Moreover, socially-raised birds approached humans more readily. Social experience in early life affected perception of non-conspecifics as well.

Social experience appears to build both the visual and auditory worlds of starlings. Mirror images elicit very different responses in birds raised socially, in pairs or in isolation. Only those individuals habituated to one companion settled down rapidly; both solitary and socially-raised groups appeared disturbed. At least the paired and socially-raised birds seemed to recognize a conspecific (some social males were even aggressive), but birds raised in isolation spent much more time looking at the mirror image and did not resume feeding during the experiment (Henry et al., in prep.). Parrots also respond to mirror images (Pepperberg et al., 1995).

The construction of social cognition through social experience requires plasticity. This emerges clearly in our investigations of song perception. Developmental plasticity has been demonstrated in field L in the brain of starlings (Cousillas et al., submitted), and has been shown to exist in a variety of song nuclei and species (Doupe and Solis, 1997). Here we have demonstrated that social experience is a key in the development of complex selectivity in auditory neurons in field L.

The nature of social experience appears crucial in the development of the perceptual world of birds. Being raised with another naive young bird is sufficient to elicit a higher quality of song than when raised in isolation (Chaiken et al., 1997), but this is nothing compared to the effect from being raised with adult models, whatever the auditory experience.

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