How studies on vocal communication in birds contribute to a comparative approach of cognition

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ABSTRACT. How studies on vocal communication in birds contribute to a comparative approach of cognition. - Study of communication is certainly a useful tool to investigate animal cognition, and specially comparative cognition. Different approaches are possible from language-training experiments, field observations to neurophysiological studies. Studies on birds' vocal communication are a good illustration of how all those approaches can be used in cognitive science. Authors have looked at aspects like referential signalling or categorical perception, for example. Another useful approach is a global approach that integrates the different types of studies going from precise observation of the animal's natural behaviour (social interactions, context analysis) as a first step to experimental studies in captivity and the field to an analysis of the neurophysiological bases of cognition and communication. The present paper describes how observations of the singing behaviour of starlings (Sturnus vulgaris) in the field have led us to raise questions about cognitive issues like learning, memory and categorical perception, how this knowledge has helped us designing experiments and what a neurophysiological study can bring to the understanding of cognitive processes.

KEY WORDS. Vocal communication, Cognition, Birdsong, Starling, Perception, Learning

The different approaches to the study of animal cognition

Study of animal cognition, that is of the "processes or faculties of knowing" has been dominated in the last decades by the methods of comparative psychology. Using highly controlled experimental conditions and precise recordings of behaviour (mainly in conditioning procedures), this approach has proved useful in revealing some cognitive processes like categorical perception, same/different concept in animals like apes and pigeons in particular (Thompson, in press). However this is mainly a "protoevolutionary" approach, aiming more at understanding which human processes might or might not exist in animals rather than at looking at phylogeny or ecological adaptations (Timberlake, 1990). Hodos & Campbell (cited in Wasserman, 1993) criticize the way species have been chosen for comparisons and attribute this problem to a lack of a broad evolutionary theoretical foundation for the field.

A more recent approach is that proposed by
FIGURE 1. The main song types of male European starlings. The species-specific whistle types are present in the repertoire of all or most males with the same characteristics and variation ranges. From the left: inflection theme (IT), theme with harmonics (HT), simple theme (ST), composed theme (CC), rhythmic theme (RT). The individual whistle types characterize one bird in its colony and can be interspecific mimicries. At the bottom, short parts of the warbling song of these three birds including two motifs each time.

Griffin (1984) and defined as "cognitive ethology". It tries to understand animal behaviour by looking at animal minds in terms of intentionality and consciousness (see e.g. Ristau, 1990). However this approach does not give us an explanation about more "basic" cognitive processes like learning, memory, categorization, or recognition. These processes do not necessarily require consciousness but do play an important role in the natural life of animals. Therefore an approach like that suggested by Yoerg & Kamil (1990) aiming at integrating precise ethological observations with analyses of the processes involved should be very fruitful, specially in comparative cognition. Two models of evolution have to be considered: the more "classical" divergent one following phylogeny; the convergent one
suggesting that animals at different phylogenetical levels might have evolved similar responses to particular ecological conditions (e.g. Snowdon, 1987). Since "behaviour is determined by the interaction of environmental and cognitive events" (Yoerg & Kamil, 1990), the second model should be very useful in comparative cognition, in helping us understanding the evolutionary history of cognitive processes. This implies examining 1) how different species within and between phylogenetic groups "react" to similar or different environmental constraints, 2) what range of variation in the cognitive processes a species can exhibit in varied environmental conditions.

One interesting aspect in comparative cognition is the role of communication in social cognition: how animals recognize each other, "know" about the social status of the other group members but also how social environment shapes or influences cognition and communication. There is a large range of possible social structures and environmental constraints within a phylogenetic group or even within a species. It is interesting to see how cognitive processes like memory, learning or perception can both be influenced and play a role in the adaptations to given conditions.

From this perspective, I will show here how our descriptive studies on starlings' singing behaviour have led us to become interested in cognitive processes and the role they might play in the plasticity shown in this species' social structure according to environmental constraints.

**From describing to experimenting: how observing behaviour raises questions on cognitive processes**

The starling is a good model because it is present in many parts of the world and therefore lives in many different environmental conditions. It is also a highly social animal that generally forage in flocks of varied sizes and sleeps in communal roosts of several hundred to several thousand birds. According to nest availability, starlings breed in colonies of a few nests (Europe) or individually (Australia for ex.,

![FIGURE 2: Distribution of the dialectal variants for the different species-specific themes. Dialectal boundaries are figured as lines: within these boundaries all birds share the same variant of the theme considered. From the left, inflection theme, harmonic theme, simple theme (variations are limited to total duration) and composed theme in the same general area. Note that the dialectal areas are of different sizes according to the theme (from Adret-Hausberger, 1983, modified). Darker areas are forests. For the composed theme, the areas with points are those where this theme is present, the others where it is absent.](image-url)

[Distribución de las variantes del dialecto para los diferentes temas específicos de la especie. Los límites del dialecto se representan como líneas: dentro de esos límites todas las aves comparten la misma variante del tema considerado.]
Hausberger

Adret-Hausberger, 1988). The song is present in all social situations, every morning in the colony in sedentary populations, during the day in flocks and at night roosts. Field recordings of more than 400 males in 10 different populations on three continents have revealed that two universal big categories of songs exist: the whistles and the warbling.

The whistles are short, loud and rather stereotyped and are found with the same general structures everywhere (Adret-Hausberger, 1989; Motis subm.). Each male has a repertoire of 3 to 12 different whistle types (fig. 1). Some of them are shared by all males ("species-specific themes") and are found with the same characteristics and variation ranges in all populations. The others ("individual themes") are characteristic of each bird in its colony (Adret-Hausberger et al., 1989, 1990). They include some interspecific mimicries and can also be found in other birds of other colonies (Hausberger et al., 1991). The species-specific themes are involved in numerous vocal interactions between neighbours in the colony but also in flocks and roosts. Interacting birds reply to each other using the same theme (song matching; Adret-Hausberger, 1982). Each of these themes can be subdivided into variants that vary locally. A complex system of dialects reminiscent of human isoglosses therefore appears (Adret-Hausberger, 1983, 1988, Adret-Hausberger & Güttinger, 1984) (fig. 2).

The warbling is mainly a quiet song, produced in long continuous sequences of notes (fig. 1). The notes are grouped in motifs. A sequence is typically composed of repetitions of one motif type before switching and ends up with clicks and high pitched trills (Adret-Hausberger & Jenkins, 1988; Eens et al., 1989; Böhner et al., 1990). Each male has a repertoire of motif types that is highly individual. We never found the same motif type in two different males. This song seems to be involved in the attraction of females (Henry et al., in press) and the repertoire tends to be larger in polygynous males than in monogamous males (Adret-Hausberger et al., 1990; Eens et al., 1991).

The starlings' songs can therefore be subdivided into shared songs (species-specific whistles) and individual structures (whistles and warbling). This is found also at the temporal level: shared songs show a high stability over time in a colony whereas the individual structures especially the whistles change from one year to the next for a given bird (Adret-Hausberger, 1990).

The possible song learning abilities of females are not well known from the field studies. Females sing occasionally in the colony but in short and soft bouts and it is not known whether or not they sing outside the colony. It was once possible to record songs in a polygynous trio where male-females and female-female vocal interactions occurred. We found that the male and the two females had individual structures in common but also that the two females were sharing even more structures, suggesting some female-female learning (Hausberger & Black, 1991).

In conclusion song variations as revealed by field recordings can bring informations at different levels from species-identity to individual identity (see table III).

Many questions have arisen from those results, some of which clearly are related to basic cognitive processes:

- song learning processes: how can such complex dialects arise, does song sharing reflect in some ways the social structure of the birds?; what are the females' learning abilities?; when and in which conditions does learning occur?
- recognition processes: do individual structures in particular play a role in individual recognition? Can shared songs be recognized as reflecting a social status?
- memory: do birds "forget" the songs they do not sing anymore or do they keep them in memory? how long can they "remember" the song of another bird?
- categorization: the species-specific whistles have universal characteristics and variation ranges
Despite local variations, might starlings discriminate them in some categorical ways? Might songs enable starlings to recognize social categories?

In order to try and answer such questions we designed experiments in different conditions: observations of captive groups, field playback experiments and neurophysiological analyses of perception.

Song learning and memory in adult male and female birds: the importance of social interactions

In order to better understand to which extent song variations might reflect the social structure, we designed an experiment where possible song changes
Spontaneous singing of females occurred in the aviaries but only in short bouts and mostly in interaction with another female. Also females did not sing spontaneously in isolation. Therefore, we chose to inject the females with testosterone with the aim of determining what they had in memory and also to increase their singing behaviour. This procedure has been used successfully with different songbird species (e.g. Konishi, 1965). Female starlings started singing a few days after the testosterone injection. Their songs included both warbling and whistles (see also Hausberger & Black, 1991). However the species specific themes were always missing, apart from the theme with harmonics heard sometimes in a few females. Therefore the songs of the females are composed essentially of what was defined as "individual structures" in males. Recordings made at several month interval showed changes in both song repertoire and song composition of the females from one recording session to the next. For example some new motif types appeared at each new "testosterone" recording (fig. 3). However some of the motif types recorded at the previous session disappeared. Some of the females therefore modified almost entirely their repertoire in one year. However it is important to note that some of the elements recorded in November and dropped in May were recorded again either in spontaneous songs in the aviaries or in the following October. This means that even a testosterone treatment does not reveal everything a bird has in memory.

Observations of the social structure were made using instantaneous scan sampling (for more details see Hausberger et al subm.): activities, interactions and distances between birds were noted. We observed very few agonistic interactions and these were mainly between males and females. The social structure appeared based on very few male-female pairs, but mostly on female-female pairs and male-male pairs (fig. 4). In all groups we observed this sex-dependent social structure, with only a few birds remaining isolated. This seemed a general trend outside the breeding time. This social structure was moreover clearly reflected in the degree of song sharing. Thus, for example, two females that came originally from the same aviary arrived with many songs in common. We then separated them and observed that one of them had a new "social mate". She then started sharing several motif types and whistles with this new female: they both copied each other and even developed new songs in common (table II). This reveals a very high plasticity in adult female song. Such song sharing
FIGURE 4. Representation of the social structure (in terms of proximity) of one of the groups observed in March, after the birds had spent 3 months together. Two circles together correspond to animals that significantly spent most of their time in close proximity. The black arrows correspond to birds that significantly avoided each other. The other arrows correspond to a tendency to be close but to a lesser degree than in the "social pairs".

[Representación de la estructura social (en términos de proximidad) de uno de los grupos observados en marzo, después de que las aves hayan pasado tres meses juntas.]

occurred for all the "female-female pairs" we observed. The quality (as measured by similarity) of this learning is quite high (fig. 5).

The different males had different variants of the species-specific themes when they arrived. We observed gradual changes in the structures produced by the different males so that after 6 months spent together, all males were sharing the same variant, a feature typical of colonies in the wild. However, they also started copying each other's "individual structures" (warbling and whistles) and even develop new songs in common. The degree of song sharing depended on the tendency for two birds to stay together: we found a correlation between the degree of song sharing and the time spent in close proximity ($r=0.85 \ p<.02$). Again this reveals the ability of adult starlings to adapt to new social conditions. This is specially remarkable since male starlings in the wild colonies we observed never shared any of the individual structures. This is probably reflecting a different type of social interaction. In wild colonies, males tend to stay each on its nest and interact vocally from a distance and it might be more important to maintain individuality. However, we do not know what types of interactions there are outside the colonies in the wild. Birds are often close to each other in flocks and roosts and maybe we would find there some similarity with our captive studies.

Only a few whistles and motif types were common between males and females in our study and those structures were then generally first heard in females (Hausberger et al. subm.).

From our results we can conclude that the development of new songs is quite possible in adult starlings, both males and females, that there is a sex-dependent learning and that they learn better from a "good friend".

The degree of song sharing does appear to reflect the social structure.

The unexpected social structure and the results on song sharing are not due to artefacts (e.g. testosterone injections). Henry et al (subm.) found similar results in American captive groups where female song was recorded without testosterone injection. They found moreover that young females learn their songs from adult females including their mother and young males from adult males including their father. Eens et al. (1992) also found that young males learn from adult males.

It is difficult to know in our adult birds whether there is really adult acquisition of new songs or a choice among the songs they already have in memory. Females obviously could sing again songs they had abandoned for a while so that such a
TABLE II. Song sharing in females as illustrated with warbling. The squares correspond to the motif types sung by a given female. At the bottom are indicated the remaining motif types of the female considered ("unique songs") and underneath the total number of motifs obtained for this female. Note the increase in song sharing between R and N and B and Or from November and May, which corresponds to these pairs of females becoming socially associated.

[Sonidos compartidos en hembras ilustrado con trinos.]

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process is quite possible. De Wolfe et al (1989) in white crowned sparrows and Nelson (1992) in field sparrows found that young birds arrive on a territory with several song types amongst which they will selectively keep only those shared with a close neighbour. Dominant cowbirds prevent subordinate ones from producing some song elements, but the latter will still be able to produce them if placed in another social context (West & King, 1980). May be a similar phenomenon is responsible for the avoidance of sharing of individual structures in male starlings living in wild colonies.

Birds' memory of songs is probably very large since they also remember some of their neighbours' song types even though they do not produce them (Mc Gregor & Avery, 1986; Kreutzer, 1987). Song sparrows can easily memorize 64 song types without producing them (Stoddard et al., 1991). Playback experiments with female starlings revealed that they could discriminate the non-shared songs of a past "social mate" from which they had been separated for more than six months (in prep.). Also they only reacted to their own songs if the structures broadcast were shared ones. Therefore songs might be a way of remembering social affinities or "social categories", the same way some calls of vervet

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FIGURE 5. Examples of unique and shared whistled songs. The two whistles on the top correspond to a whistle sung first by the female vcj and was then also produced by vf. The songs shared by vcj, r and n (left side) were first produced by vcj and r and then n (after association with r socially). The whistles on the right are unique to b, j, and n respectively.

[Ejemplos de silbidos únicos y compartidos.]
monkeys are reflecting social links for the group members (Cheney & Seyfarth, 1982) (table III).

**Song categories: behavioural evidence and neurophysiological bases**

Analyses of structures have shown that each of the species-specific whistle types shows the same characteristics and variation ranges in all populations studied up to now. The characteristics differ from one theme to the other: presence of an inflection for one, of two superimposed elements ("harmonic theme") or a given frequency modulation (simple theme) (Adret-Hausberger, 1989).

A contextual analysis of starlings' singing behaviour in the field has suggested that the different species-specific whistles sung by males might correspond to different categories. The frequency of production of each of these whistle types shows a particular seasonal curve (Adret-Hausberger, 1984), depends on nest proximity (Hausberger & Guyomarc'h, 1981; Hausberger, 1991), and clearly varies according to the social context. Thus starlings tend to sing mainly the inflection theme if they are in a flock of about 150 birds whereas they produce mainly the rhythmic theme if they are in the roost (Adret-Hausberger, 1982). They also reply to each other using the same whistle type during vocal interactions.

It is interesting that birds in flocks reply to each other using the same type since in flocks birds from different dialectal areas mix, that is with different variants of a given type.

Playback experiments revealed that in fact male starlings are able to recognize the whistle type even if they hear an unknown variant of it (Fig. 6). If an unfamiliar variant is broadcast, the bird replies by song matching, but using its own variant of this theme. This means that some characteristic features of those songs must enable them to recognize the themes despite the variations (Adret-Hausberger, 1982). Playback experiments using modified versions of a species-specific theme revealed that several features are important and that the different features have different weights (in prep.). There seems therefore to be a hierarchical perceptual analysis as suggested by the feature analysis hypothesis (Roitblat & von Fersen, 1982).

We can therefore wonder whether there are key-parameters defining a given category and whether some particular neuronal specifications might be responsible for identification of these features.
FIELD OBSERVATIONS + CAPTIVE STUDIES

SPECIES

Whistles: in males: species-specific themes (same characteristics and variation ranges in different populations)

Warbling (o + o): basic organization - ends of sequences

POPULATION (♂): complex local variations (see isoglosses in human dialects)

more colonies → 5

individual nests → 3

levels of dialects

COLONY (males): all species-specific themes shared

SOCIAL GROUPS

Males: song sharing correlated with social bond

"Individual" whistles + warbling

Females: pairs sharing same structures

PAIR (♂ / ♀): a few individual whistles and motifs shared

INDIVIDUAL: individual whistle types + warbling: (♂ + ♀)

but degree of individuality depends on social context:

very high in "natural" colonies, very low in some captive conditions.

TABLE III. The relation between starlings' songs and social structure as revealed by field and captive studies.

Leppelsack & Vogt (1976), using natural sound stimuli, found that some neurons in the auditory field L of starlings responded selectively to particular complex combinations of parameters and not to pure tones. This suggested that some neurons might be selective towards particular features of some species-specific sounds. An experiment was therefore designed where we looked at the responses of auditory neurons to the different categories of whistles in this brain area. We broadcast different natural variants of those whistle types but also synthesized versions (where we modified different parameters) to awake starlings placed in a neurophysiological set up. Both multicellular and single cell recordings were made. Multicellular recordings distributed regularly in the area being studied enabled us to construct "maps" corresponding to the localization of the neurons being activated. This mapping procedure revealed that different parts of a stimulus (e.g. whistle) elicit responses in different places, that is different neurons are activated by different features of the stimulus. This can not always be explained by simple tonotopical organization and shows that different sub-areas might exist with different types of selectivities (Leppelsack, 1992). We never found
a neuron responding to a whole whistle. They only respond to particular parts of the whistle. Therefore there does not seem to be any "song category" detector as such.

Within these areas, the selectivity could be better studied by looking at single cell responses. We found that large differences appeared in the responses of different neurons, some of which showed very short responses to particular parts of a given stimulus whereas others showed very little selectivity. In order to identify which parameters elicited responses in given neurons, we developed a method of backwards correlation analysis (see also Eggermont, 1990). It consisted in recording all the instances of responses of one given neuron and build an average sonogram from the sonograms of all the parts of stimuli that occurred just before this neuron responded (more details in Richard et al. in prep.). This visualisation enabled us to confirm the very high selectivity of some neurons. Some of them responded to one simple parameter, e.g. a particular frequency. Many other neurons responded to complex combinations of parameters, from particular slopes to inflection points in the frequency modulation (Fig. 7). In many cases, inhibition and excitation are combined and define a very precise "shape". Therefore the analysis of neuronal responses in a central auditory area of starlings reveal that some cells are selective towards particular features present in particular in the species-specific whistles (in prep.). This type of encoding could be a first step in the recognition and categorization process.

Neighbouring neurons tended to have similar or complementary types of selectivities and therefore "groups" of neurons appeared. Different groups might "work" together to determine a first level of feature integration. Margoliash (1983) in particular found in white-crowned sparrows that auditory neurons are present in the motor song center HVc which show a selectivity towards precise songs, specially the bird's own song. Only further studies will show us whether there are different degrees of integration in different parts of the song central system.

Conclusion: what is the interest of integrative studies for a comparative approach of cognition?

Our field observations and experimental studies on starlings' songs have revealed that:
- learning processes are under strong social influence and show a high plasticity even in adults
- memory is important and enable birds to select songs according to the social context even in a "past repertoire" and to remember another bird's characteristics over a long period (at least 6 to 8 months)
- recognition processes enable the birds to extract different information (in particular social) from song structures
- categorization helps starlings recognizing important song types despite population, colony or individual variations
- perceptual processes (encoding) are based on selectivities of auditory neurons towards particular features

Environmental constraints can act on the social structure at different levels. Their influence on the types of cognitive processes that are used as well as the importance these processes might have in the adaptation to those constraints are illustrated by some of our results:
- nest availability determines whether or not colonies occur as well as the size of the colonies. This influences the system of dialects that varies according to whether colonies occur (ex: Australia/ Europe) or their distribution (ex: Brittany/ Palatinate)
- time spent together: ex: aviaries and possibly particular ecological conditions, also migratory versus sedentary populations appears to influence the amount of repertoire that is shared.
FIGURE 7. Examples of neuronal selectivities as revealed by the backwards correlation method. Selectivities of 12 auditory neurons are represented here. For each neuron, the feature eliciting an activation is on the left, the one eliciting an inhibition on the right. When the spontaneous activity is low, no significant inhibition could be detected (ex: NA6SO2.013 or NA4SO4.O10).

The frequency scale is from 0 to 6 kHz and the time is from minus 128ms (128 ms before the spikes appeared) to 0. The sonogram here correspond to an average sonogram of all parts of the different stimuli that elicited a response of the neuron considered: every time a significant response occurs, the program recorded the stimuli features that preceded it. All occurrences of responses and the characteristics of the stimulus that preceded them were thus recorded for each neuron and enabled us to build this average sonogram (Richard et al. in prep.). Two types of selectivities are illustrated on the top row with four neurons: towards an inflection point in the frequency modulation (left) or pure frequencies (right). Note that an inhibition occurs for other parts of the spectrum. The middle row correspond to neurons selective towards frequency modulations with an inflection in the slope (left) or time delimited signals (right). The last row illustrates selectivities towards a particular slope (left) or two different frequencies (right).

Note for NA6SO7.008 and NA6SO6.008 how activation and inhibition contribute together to the detection of the feature.

[Ejemplos de selectividades neuronales puestas de manifiesto por el método de correlación hacia atrás.]
Song sharing seems to be indicative of a certain social tolerance. This might also be important in places like flocks where birds with different dialects mix. Memory might play a role in long term individual recognition in migrant populations. Distribution of resources can determine the number and sizes of foraging flocks as well as the distribution of roosts. Categorization and therefore perceptual processes enable (through song matching in particular) interacting birds to have information on the species and population identity of the other birds in situations where birds from different areas mix (ex: roosts).

Therefore an interdisciplinary approach on one species can shed light on how and why particular cognitive processes have arisen. We here combined the interests of ethologists (studies in an ecological context), psychologists (information processing perspective) and neurophysiologists (perceptual processes). The diversity of environmental situations in which starlings can be found as well as their highly social life are reflected in the plasticity of the learning processes in particular. Similar integrative studies on other species living in similar or different conditions should prove useful to understand the evolutionary history of cognitive processes.

"Because behavior is determined by the interaction of environmental (ecological) and cognitive events, an interdisciplinary approach to the study of behavior is demanded" (Yoerg & Kamil, 1990).

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Resumen

Cómo los estudios sobre la comunicación vocal en aves contribuyen a una aproximación comparada de la etología cognitiva.

El estudio de la comunicación es a todas luces una herramienta útil para investigar la cognición animal, y especialmente la cognición comparada. Son posibles diferentes aproximaciones, desde experimentos de adiestramiento del lenguaje, a observaciones de campo, a estudios neurofisiológicos. Los estudios sobre comunicación vocal en aves son una buena ilustración de cómo todas estas aproximaciones pueden usarse en la ciencia cognitiva. Los autores han dirigido sus miras, por ejemplo, a aspectos similares a la señalización referencial o percepción categórica. Otra aproximación útil es una global que integra los diferentes tipos de estudios que van desde la observación precisa del comportamiento natural del animal (interacciones sociales, análisis contextual) como una primera etapa, a estudios experimentales en cautividad y en la naturaleza, hasta un análisis de las bases neurofisiológicas de la cognición y la comunicación. El presente trabajo describe cómo las observaciones del comportamiento de canto de los estorninos (Sturnus vulgaris) en la naturaleza nos han permitido hacernos preguntas acerca de problemas cognitivos similares al aprendizaje, memoria y percepción categórica, cómo este conocimiento nos ha ayudado a diseñar experimentos y cómo el estudio neurofisiológico puede llevarnos a comprender los procesos cognitivos.
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