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Right ear advantage for conspecific calls in adults and subadults, but not infants, California sea lions (*Zalophus californianus*): hemispheric specialization for communication?

M. Böye,^{1,2,3,*} O. Güntürkün² and J. Vaclair¹

¹Center for Research in Psychology of Cognition, Language and Emotion, University of Provence, France

²Department of Biopsychology, Institute of Cognitive Neuroscience, Fakultät für Psychologie, Ruhr-Universität Bochum, Bochum, Germany

³Tiergarten Nürnberg, Nürnberg, Germany

Keywords: communication, evolution, lateralization, pinnipeds, vocalization

Abstract

This paper explores functional hemispheric asymmetries in the perception of auditory signals in a marine mammal species, the sea lion. Using a head-orienting task toward sounds we found a right ear – left hemisphere – advantage for conspecific calls in adult and subadult California sea lions (*Zalophus californianus*) that was absent in infants. Non-conspecific sounds did not elicit lateralized reactions in any age group. These findings show that maturational steps regarding communication in the brain of pinnipeds are similar to those described in primates. Such a result in a semi-aquatic species distant from primates on the phylogenetic tree speaks for a stability and an ancient emergence of the left hemispheric specialization for vocal communication. The origin of what seems to be a widespread brain feature might be searched in the temporal and spectral communicative sound's characteristics rather than in its semantic value.

Introduction

Since the observations of Broca (1861) and Wernicke (1874), a left hemispheric specialization (LHS) both for speech perception and production has been confirmed by numerous psychophysical and brain imaging studies (for examples, see Hugdahl, 2000). The evolutionary origin of this cerebral bias, however, remains unclear. Recent evidence suggests that gross anatomical equivalents of Broca's and Wernicke's areas are also present in the brain of great apes (Gannon *et al.*, 1998; Cantalupo & Hopkins, 2001). The control of vocal production in animals seems to be devoted to the left brain hemisphere such as in primates (Hook-Costigan & Rogers, 1998; but see Hauser & Akre, 2001), in birds (Nottebohm, 1971, 1977; Floody & Arnold, 1997; but see Williams *et al.*, 1992) and also in anurans (Bauer, 1993). A LHS for the perception of communication sounds has also been reported in animals. Macaques present a right ear processing advantage when trained to discriminate between conspecific vocalizations (Petersen *et al.*, 1978, 1984; Beecher *et al.*, 1979). No advantage is found when discrimination is performed on non-specific (but closely phylogenetically related) calls. Hauser & Andersson (1994), using a head-orienting task, showed that adult rhesus monkeys preferentially orientated their right ear while hearing conspecific calls. Due to the mainly contralateral projections of the auditory system, a right-ear

superiority is assumed to be related to a left hemisphere processing advantage. Interestingly, this study reported a lack of lateralization in infants (4–12 months), leading Hauser (1996) to state that hemispheric specialization for communication in monkeys should need 'a fully mature brain, as well as sufficient exposure to and understanding of the repertoire' (Hauser, 1996). These behavioural asymmetries are consistent with findings made at the neurological level. Heffner & Heffner (1984, 1986), using the same coo vocalizations as Petersen *et al.* (1978, 1984), tested macaques after a lesion of either the left or the right auditory cortex. Macaques with a lesion on the left showed a greater deterioration of their performance and needed more time to relearn the discrimination compared to right lesioned animals. It can be observed that studies concerning the perception of lateralized communicative vocalizations by Japanese macaques reveal that the two hemispheres work in close coordination (Heffner & Heffner, 1994). Thus, if the monkeys displayed the expected ear advantage for perceiving vocalizations presented to the ear opposite to the intact hemisphere, they however, showed no deficit when the vocalizations were presented to both ears, but were lateralized (with time and intensity differences) to the ear opposite to the lesion.

Recently, Poremba *et al.* (2004) measured a superior metabolic activity within monkeys' left temporal poles compared to their right counterparts and this activity specifically occurred when the animals were confronted with conspecific calls. Congruent findings in human and non-human primates (reviewed in Hopkins & Fernandez Carriba, 2002) suggest the existence of a common ancestor living at least 30 million years ago with cerebral specializations for the perception of species specific communication signals.

Correspondence: Dr Martin Böye, at *present address below.
E-mail: m.boye@marine-mammal-cognition.de

*Present address: Planète Sauvage Safari Park, 'La Chevalerie 44710 Port Saint Père, France

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However, LHS for communication in mammals might not be a primate specificity. Thus, mice's reactions to pups' ultrasounds decrease when the right auditory meatus is closed (Ehret, 1987). The supposed LHS for communication in the mice has been recently confirmed and detailed, based on recordings in their left and right auditory cortices (Geissler & Ehret, 2004). Investigations in other vocal mammalian taxa should help us to determine to what extent the treatment of communicative information is lateralized in mammals.

Pinnipeds are marine mammals belonging to the carnivore order that separated approximately 60–100 million years ago from the branch leading to primates (cf. Fig. 1). They present a central and peripheral nervous system that is morphologically and physiologically not different from that found in terrestrial mammals (Glezer, 2002). Their brain, which is similar in shape to dogs' brain, is organized in two clearly distinct hemispheres connected via a corpus callosum (Oelschläger & Oelschläger, 2001). Breeding on land and feeding in water, they are fully adapted to a semi-aquatic lifestyle. Observations of feeding behaviours (Levermann *et al.*, 2003) indicated a predisposition for the use of the right front flipper during feeding in one species, the walrus (*Odobenus rosmarus rosmarus*). Another species, the California sea lion (*Zalophus californianus*), shows a high vocal activity and produces a wide range of in air vocalizations in many contexts of its complex social life (Schusterman *et al.*, 2001), such as alarm calls, mother-pup recognition calls, and aggressive individual vocal signatures by males. [Although the procedure utilized with sea lions and with rhesus monkeys by Hauser & Andersson (1994) differs from those classically used to study human laterality (e.g. dichotic listening), a head orienting task correlated well with other behavioural measures of laterality in human participants (Yazgan *et al.*, 1995).] Based on the head orienting task used in non-human primates (Hauser & Andersson, 1994), in chicks (Miklosi *et al.*, 1996), in raptors, i.e. wild and captive harpy eagles (Palleroni & Hauser, 2003) and in human infants (Ecklund-Flores & Turkewitz, 1996), we present here a study designed to investigate the possible existence of a left brain hemisphere advantage to process conspecific vocalizations in this marine mammal species.

Method

Subjects

The subjects were eight sea lions (*Zalophus californianus*) housed in the Nürnberg Zoo (Germany). The group was composed of one adult male (14 years old), three adult females (17, 15 and eight years old), two subadults (one male and one female, both 14 months old at the beginning of the study). During the experiment, two females were born and tested when they were between 3 weeks and 3 months of age.

The tests were performed outside in a three-million litre pool. Sounds (sampled at 48 kHz) were broadcast via a battery-powered loudspeaker (Psyacoustic, St-Usuge, France, 50 Watt RMS, frequency response 65–14000 Hz) connected to a microcomputer (Compaq Armada, 1700, equipped with an ESS soundcard). The behaviour of the animal was recorded for further analysis on a digital video recorder (Grundig JB-1).

Sounds used to test our animals were divided into four categories regarding their origin (conspecific, Csp; or non-specific, Nsp) and their degree of familiarity (familiar, F or unfamiliar, U). Sea lions' vocalizations used in the experiment were recorded from the studied group (CspF) and from another group living in a distant indoor pool (CspU) using a digital audio tape recorder (Sony TCD-D7) and a microphone (frequency response 80–15 000Hz). Respectively, 20 calls were recorded from four adults and two subadults, and 14 calls from three adults during feeding, aggressive behaviours and interactions between male and females. These 20 calls were selected regarding their quality (good signal to noise ratio). Their duration ranged between 2700 ms and 3440 ms. Although there is so far a lack of classification concerning sea lions vocal productions, we were able to divide our samples into two categories (grunts, barks). We also used 14 vocalization sequences of three primates' species (NspU); chimpanzees copulation barks, vervet monkeys and cotton top tamarins shrill barks and five crows' vocalizations (NspF) chosen within 20 calls recorded in the immediate neighbourhood of the tested animals. The sound pressure level of all sounds was normalized using a sound treatment software (Sound forge 5.0, Sonic Foundry inc.).

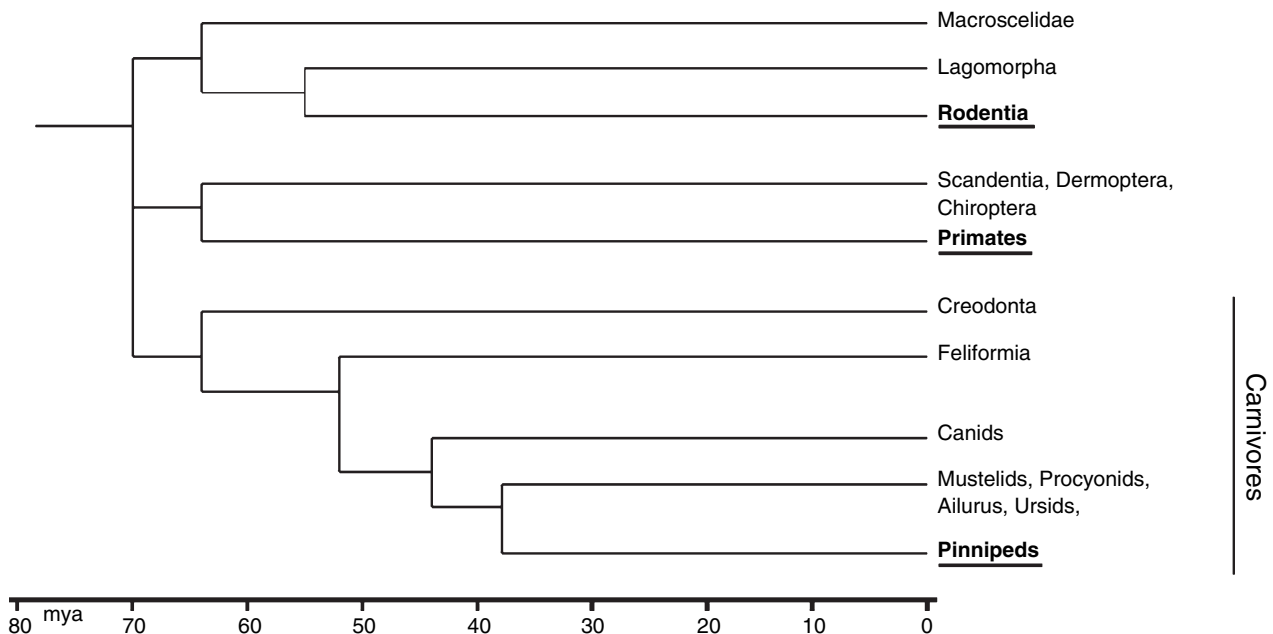


FIG. 1. Phylogenetic tree representing some mammalian species. Underlined species are known for showing left hemisphere specialization for conspecific communicative calls.

The study was performed in two steps; during the first year animals (including the two newborns) were tested with CspF and NspU sounds, and during the second year, in order to evaluate the possible influence of familiarity on lateralization we tested our animals (newborns were then in another pool) with CspU and NspF sounds.

A trial consisted of displaying one sound exemplar behind one animal standing on a rocky artificial beach. The distance between the loudspeaker and the animal was approximately 20 meters. Caution was taken in order to align the loudspeaker on the body axis and on the direction of the head of the animal. As the sounds arrived strictly behind the animal and were aligned on the sagittal axis of its head, the probability that an animal turned its head to the right or to the left was thus equal. In order to prevent any habituation effect, experimental and control sounds were pseudo-randomly chosen. A maximum of four trials were performed within a daily one-hour session. The study ended after a two-year period.

Preliminary observations showed that ~1 h before each of the four daily feeding times, adults and subadults were spending most of their time on the beach inspecting the gate from which the trainers were entering with food. Therefore sessions were performed during one of the one-hour periods preceding feeding time (08:00–09:00 h, 10:00–11:00 h, 13:00–14:00 h or 15:00–16:00 h). Tests were performed when neither vocal nor physical interactions were occurring in the group. Sometimes the tested animal was surrounded by up to four neighbours. As they were slightly located on the left or on the right of the sound's arrival axis, the reactions of these animals were not recorded. The newborns were tested in a different set-up as sounds were displayed to them while they were feeding or resting close to their respective mother on a rocky island.

Video analyses were performed blind regarding sound category. Sound playback was indicated by the appearance of a red square and the videos were inspected without sound. Trials for which the head – loudspeaker alignment was not respected (i.e. when the sea lion's head was slightly directed to the left or to the right), or trials for which the animal was not reacting before the end of the playback were excluded from analysis. Reaction times and head orientation toward the loudspeaker were recorded for each trial. Reaction time was defined as the interval between the beginning of the sound playback and the beginning of the head movement. For newborns, the trajectory of the head movement presented an immature motor control reflected by shaky movements of the head. Consequently, movement onset was difficult to detect on the video and the analysis was restricted to head orientation for the two infants. Moreover, the two newborns were morphologically very similar and it was thus impossible to identify them with certainty. However, both animals were active and reacted to the display of the conspecific and non-specific vocalizations. This is why we have included the newborns in the experiment. This study was in accordance with European regulations and recommendations.

Results

A total of 487 trials were performed, but only 371 trials were retained for analysis. On 116 trials, alignment with the loudspeaker was not respected or/and the animal did not express a reaction before the end of the sound presentation. As concerns the three adult females, it was not possible to establish the identity of the targeted animal between these individuals for 21 trials.

We defined an individual degree of lateralization as the ratio number of right ear presentations divided by the total number of ear presentations (cf. Table 1). For conspecific calls, the ranges of lateralization indices in adults (0.66–0.81 CspF and 0.69–0.79 CspU) and subadults (0.69–0.71 and 0.67–0.73) overlapped. Similarly, the indices of male (0.71–0.81 CspF and 0.67–0.79 CspU) and female sea lions (0.66–0.70 CspF and 0.62–0.75 CspU) were extremely close.

The main results are shown on Fig. 2. Adults and subadults presented 58 times their right ear toward CspF vocalizations and 23 times their left ear (71.6% significant right ear bias, $\chi^2 = 15.12$ d.f. = 1, $P < 0.001$). They also presented 55 times their right ear toward CspU vocalizations and 21 times their left ear (72.37%: significant right ear bias, $\chi^2 = 15.21$ d.f. = 1, $P < 0.001$). Newborns presented 20 times their right ear toward CspF vocalizations and 17 times their left ear. Thus, there was no significant ear advantage for conspecific vocalizations (54.05% right ear bias, $\chi^2 = 0.24$ d.f. = 1, $P < 0.622$) in the infants.

The two groups of adults and subadults presented no ear preference for NspF sounds (adults and subadults 51.65% right ear, i.e. 38 right : 39 left) and also for NspU sounds (adults and subadults 48.23% right ear, i.e. 44 right : 41 left). Similarly, newborns showed no ear preference toward non-specific sound (43.75% right ear, 7 right : 8 left).

Adults and subadults turned their head in the direction of the loudspeaker shortly after the sounds were displayed (on average $773 \text{ ms} \pm 384$). Newborns did not turn their head systematically toward primates' and sea lions' vocalizations and did not react at all while suckling. Females always reacted to the presentation of the auditory stimuli. Interestingly the adult male did not systematically react toward familiar conspecific calls but always did it for non-familiar sea lion vocalizations.

Discussion

Our data show that adult and subadult California sea lions have a right side bias for processing conspecific calls. These results are in favour of possible left hemisphere treatment in the perception of communicative signals within pinnipeds' brain. Although there are indications that the degree of familiarity might influence the degree of lateralization in birds (Cynx & Nottebohm, 1992), it does not seem to be the case in sea lions.

TABLE 1. Numbers of head turns presenting the left (L) or right (R) ear to the sound source and degree of lateralization (DOL) per subject

Vocalisations	Numbers of head turns presenting the left (L) or right (R) ear and degree of lateralization (DOL) per subject																				
	Adult male			Adult female A			Adult female B			Adult female C			Subadult male			Subadult female			Pups ($n = 2$)		
	L	R	DOL	L	R	DOL	L	R	DOL	L	R	DOL	L	R	DOL	L	R	DOL	L	R	DOL
CspF	3	13	0.81	6	14	0.7	3	7	0.7	4	8	0.66	2	5	0.71	5	11	0.69	17	20	0.54
CspU	4	15	0.79	4	12	0.75	3	5	0.62	4	9	0.69	3	6	0.67	3	8	0.72			
NspF	8	7	0.46	9	10	0.53	4	7	0.64	5	6	0.54	3	2	0.4	9	7	0.44			
NspU	6	4	0.4	14	13	0.48	8	7	0.47	4	6	0.6	7	6	0.46	5	5	0.5	8	7	0.46

Vocalisations: CspF, conspecific familiar; CspU, conspecific unfamiliar; NspF, non-specific familiar; NspU, non-specific unfamiliar.

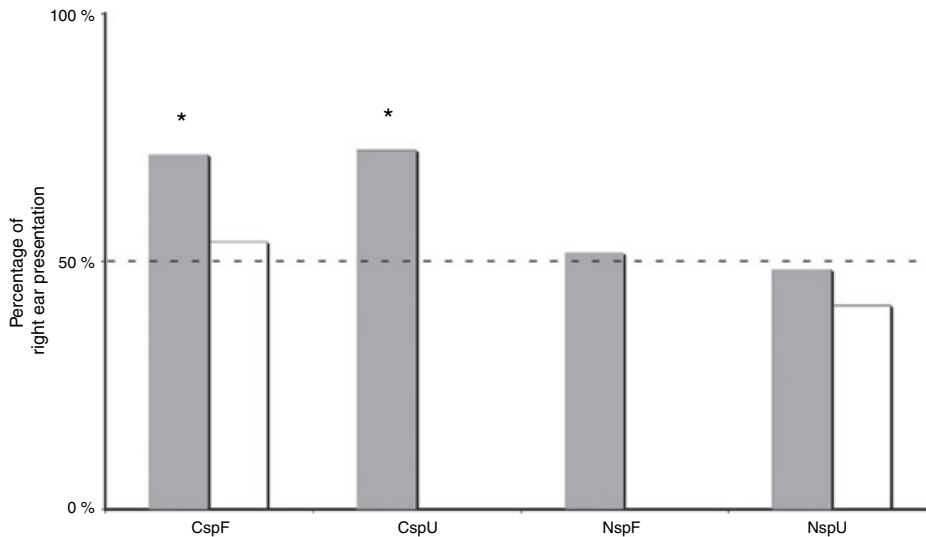


FIG. 2. Percentages of right ear presentations toward conspecific familiar (CspF), conspecific unfamiliar (CspU), non-specific familiar (NspF) and non-specific unfamiliar (NspU) vocalizations in adults, subadults (gray boxes) and in newborn (white boxes) sea lions. * $P < 0.001$ (χ^2 , expected values vs. observed values).

As reported in infant rhesus monkeys by Hauser & Andersson (1994), seal lion pups do not present any ear preference for conspecific calls. It is likely that, as observed in human and in non-human primates, the brain of sea lions might need a maturation phase before treating communicative calls in a specific way. The developmental process responsible for hemispheric specialization for communication seems to occur in the first year of life as our two subadults, tested between 14 months and 26 months of age, already showed this bias. Hauser & Andersson (1994) hypothesized that in rhesus monkeys a sufficient exposure to the conspecific vocal repertoire is needed to develop their ability to communicate. The same explanation might also be suitable for sea lions. In fact, it has been demonstrated in the sub antarctic fur seal, another member of the otariidae, that mother and pups need first a learning phase of approximately 2–8 days before being able to recognize themselves acoustically (Charrier *et al.*, 2001). Then, pups discriminate their mother from other females based mostly on a spectral analysis of the call before being able to use temporal patterns, as is the case for adults (Charrier *et al.*, 2003). Further experiments such as those carried out with non-human primates (reviewed in Seyfarth & Cheney, 1997) would be helpful to detail the ontogeny of communication in pinnipeds.

Our study is the first report of a right side bias and possible left brain advantage for communication in a species which adapted to an aquatic environment in the Oligocene, namely approximately 25 millions years ago. This return to the sea caused important modifications in anatomy, metabolism but also in brain size; thus a greater brain–body size ratio is observed in pinnipeds compared to equivalent terrestrial carnivores (Bininda-Emonds *et al.*, 2001). However, the ecological pressures responsible for such changes do not seem to have affected hemispherical specializations for vocal communication. The existence of similar hemispheric specializations in rodents and primates suggests that this trait is widespread in mammals. If there is a confirmation in other mammal species, it should then be possible to reconsider the origin of human LHS for speech perception.

The presumed older origin of the LHS for communication leads to inquiry into the functions filled out by such hemispheric advantages. Following the discoveries of Broca (1861) and Wernicke (1874), the features of human language's processing have been attributed to the left hemisphere. Although some authors (e.g. Petersen *et al.*, 1984) have argued that the communicative significance of non-human

primate calls was critical to explain hemispheric specialization in the processing of vocal communication, the possible ancient origin of the LHS for communication requires a quest for the more basic features that constitute this asymmetry. Indeed, basic variables of the communicative signals such as the temporal features might be under the control of the left hemisphere (see Fitch, Miller & Tallal, 1997; Johnsrude *et al.*, 1997). For example, Schwartz & Tallal (1980) found a LHS in humans for rapid acoustic changes in speech perception and this regardless of the semantic aspects. Positron emission tomography studies revealed that when confronted to non-speech stimuli (two pure tones separated by one octave alternating with a random duty cycle) left hemisphere was merely responding to temporal features (Zatorre & Belin, 2001). Vocal communication in animals also relies on the use of small and rapid acoustic changes. Japanese macaques (*Macaca fuscata*) contact calls (coo-calls) present a clear frequency peak located differently regarding the social context (Green, 1975). The perceptive salience of the frequency peak position has been demonstrated in call discrimination experiments (May *et al.*, 1988), as well as the direction of the frequency modulation (Le Prell & Moody, 2000) or the relative harmonic amplitude (Le Prell & Moody, 1997). Moreover, the use of the ear presentation preference test in rhesus monkeys led to a shift from right to left side when calls interpulse interval was manipulated (Hauser *et al.*, 1998). This phenomenon also occurred when the calls were played reversed (Ghazanfar *et al.*, 2001). This corpus of evidence suggests that non-human primates rely on temporal cues to recognize conspecific vocal signals. Charrier *et al.* (2002) have shown that temporal structures appear to be a key component for pup recognition in the sub antarctic fur seal; therefore temporal cues might play a determining role also in pinnipeds' communication system (see also Schusterman *et al.*, 1992).

The plausible universality of LHS among vocal mammals might have been driven by basic needs connected to acoustical features within their calls. Investigating relevant acoustical features in other vocal taxa's calls leading to a LHS should give us further information concerning specific abilities of the left hemisphere. Sea lions present, like non-human primates, a LHS for processing the vocalizations of conspecifics. Therefore, we think that this species is an interesting complementary model for undertaking such experiments. Following the same protocol as the one used here we are planning to test the head-orientation in sea lions when they are confronted with manipu-

lated communicative calls. We hope that this kind of approach might help to answer the crucial question as to why the processing of rapid changes in vocalizations is under the control of the LHS.

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Abbreviations

LHS, left hemispheric specialization; Nsp, non-specific; Csp, conspecific; U, unfamiliar; F, familiar.

Supplementary material

Fig. S1. Examples of spectrograms and oscillograms for each sound category used during the experiment.

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