Eur Arch Psychiatr Neurol Sci (1986) 236:40–43

European Archives of Psychiatry and Neurological Sciences

The Squirrel Monkey as an Experimental Model in the Study of Cerebral Organization of Emotional Vocal Utterances

Uwe Jürgens

Max-Planck-Institut für Psychiatrie, Kraepelinstrasse 2, D-8000 München 40, Federal Republic of Germany

Summary. The different human nonverbal emotional vocal utterances (e.g., laughing, shrieking, moaning) and emotional intonation patterns (e.g., scolding, lamenting, caressing) can be shown to have their acoustic and emotional counterparts in the vocal repertoire of the squirrel monkey. This makes the latter an attractive model for investigations on the neural control of human emotional vocal utterances. Neurophysiological investigations in the squirrel monkey suggest that the cerebral control of emotional vocal utterances is organized hierarchically (Fig. 3). The lowest level – above that of the motorneurons – is represented by the reticular formation of the lateral pons and medulla; here, the motor coordination of laryngeal, respiratory and articulatory movements takes place. The next level is represented by the periaqueductal grey and laterally bordering tegmentum of the caudal midbrain. This area serves to couple specific motivational states to their corresponding vocal expressions. It is a necessary relay station for all vocalization-inducing stimuli. The periaqueductal area receives its input partly from limbic motivation-controlling regions (amygdala, hypothalamus, midline thalamus), partly from sensory pathways (collaterals of spinothalamic tract, fibers from superior and inferior colliculus), and partly from the anterior cingulate cortex. The latter represents the highest level within the system and seems to be responsible for the volitional control of emotional vocal utterances.

Key words: Emotional expression – Vocalization – Cerebral control

Monkey Calls and Human Intonation

Speech consists of a verbal and a nonverbal component; the latter is usually called intonation. While the verbal component is generally accepted to have no counterpart in monkeys, intonation, more specifically emotional intonation, clearly has. Scolding, lamenting, caressing or jubilation as well as the nonverbal emotional utterances, such as laughing, whining, moaning, and shrieking, are characterized by spezific acoustic patterns which do have their homologues in monkeys. Figures 1 and 2 illustrate this.

Figure 1 shows the German word "Du" spoken in eight different intonations. Each panel of the figure represents a frequency-time diagram (so-called sonagram) of another intonation. Grouping of the intonations is undertaken according to a classification system devised by Trojan (1975) using the following three criteria: intensity (low voice – loud voice), vocal pitch (head voice – chest voice) and pharyngolaryngeal tension (strained voice – relaxed voice). A whimpering, lamenting voice, e.g., is characterized by low sound intensity (low voice), high pitch (head voice) and relatively strong pharyngolaryngeal tension (strained voice). If high pitch and strong pharyngolaryngeal tension are maintained but vocal intensity is raised then the whimpering tone progressively changes into an anxious and panic-stricken voice until it corresponds, at high intensity, to a cry of either terror or pain. If vocal intensity is kept low and pharyngolaryngeal tension relatively high, but pitch is diminished, the voice initially assumes an expression of disgust, and at an even lower pitch, one of disdain. If – again starting from a whimpering intonation – vocal intensity is kept low and pitch high, while at the same time pharyngolaryngeal tension is reduced, the whimpering tone switches at first into one of pitiable complaint and then ultimately into an ingratiating tenderly alluring voice. As in the case of the whimpering tone, similar transition profiles can likewise be established for the seven other intonations representing the extreme positions in the classification system of Fig. 1.

The assessment of intonations according to the three criteria of vocal intensity, vocal pitch, and pharyngolaryngeal tension can be used to classify the intonations not only in physical but also in emotional terms.

Vocal intensity, for instance, shows to what extent a given utterance has an appellative character, that is a reaction is invited from a (real or imaginary) interlocutor. An anxious, panicky intonation represents a call for help; an exultant, triumphant intonation constitutes an invitation to partake in the enthusiasm of the person rejoicing; a scolding intonation serves to draw the attention of other persons to the object of the wrath in order to mobilize support against it. Finally, an intimidating intonation expressing vigorous self-confidence represents a dominance gesture which serves to browbeat the interlocutor by means of a (vocal) demonstration of power. In contrast, the more softly spoken intonations of whimpering lamentation, tender ingratiation, contempt, and voluptuous enjoyment rather express an attitude that does not reckon necessarily with a reaction on the part of the interlocutor.

Vocal pitch characterizes a different dimension. Whereas all intonations uttered in a lower register (contempt, furious indignation, voluptuous enjoyment, and intimidation) express awareness of one's own strength, the intonation rendered in, the head register (whimpering lamentation, cry of terror, ten-

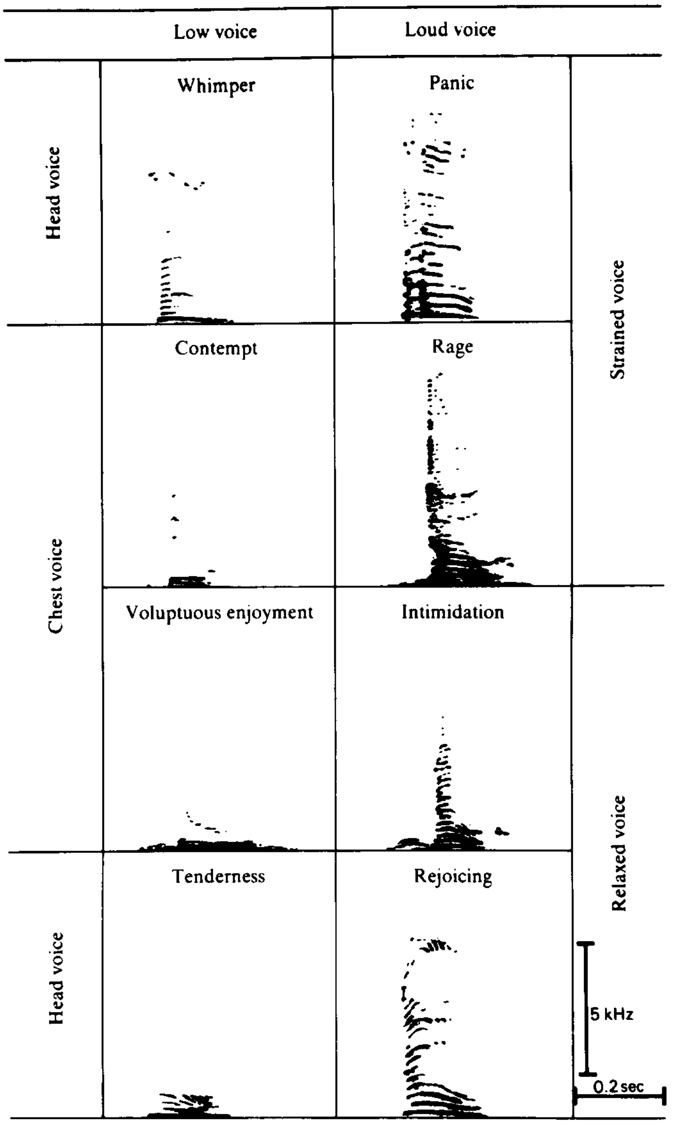

Fig. 1. Spectrographic representation of the German word "Du" in eight different intonations

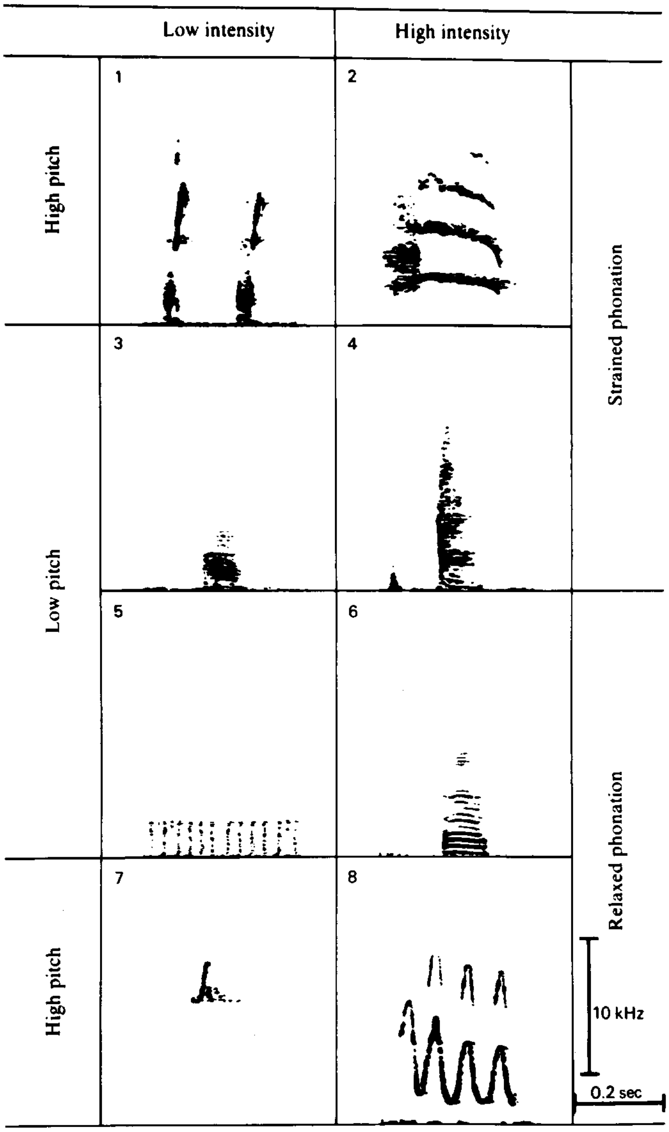

Fig. 2. Spectrographic representation of eight different vocalizations of the squirrel monkey *(Saimiri sciureus)*. Call 1 is uttered by infants trying to regain their mother's back. Calls 2 and 3 express extreme distress and slight uneasiness, respectively. Call 4 is used during mobbing of potential predators. Call 5 is uttered by infants during suckling, and by adults during huddling and between copulatory activity. Call 6 represents a threatening call. Call 7 is a contact call and serves to draw other group members' attention to the vocalizer. Call 8 announces pleasurable events, such as detection of a food source, regaining of group members which had been separated for some time, sun break through after a cloudy period

der ingratiation, and rejoicing) constitute a feeling of being overwhelmed by an external event, thus expressing a reduced self-control.

Pharyngolaryngeal tension, finally, contributes a third emotional dimension: the hedonistic, i.e., it shows the degree to which a specific situation is perceived as either pleasant or unpleasant. All intonations uttered with a strained voice (whimpering, panic, contempt, and rage) are uttered in unpleasant situations, while a relaxed voice (tenderness, rejoicing, voluptuous pleasure, intimidation) points to an emotional state that may be described as pleasant or, at least, neutral.

Figure 2 shows eight vocal utterances of the squirrel monkey *(Saimiri sciureus)*. As in the case of human intonations, the squirrel monkey's calls can be classified according to vocal intensity, vocal pitch, and pharyngolaryngeal tension. Vocal intensity can be measured as sound pressure level, vocal pitch as fundamental frequency, and pharyngolaryngeal tension as the amount of nonharmonic energy in relation to harmonic. Behavioral studies (Jürgens 1979; Winter et al. 1966) have shown that similar to man, high-intensity vocalizations have a strong appellative character, that is, they have a higher probability of being followed by a behavioral response in a conspecific than less intense vocalizations. Furthermore, high-pitched vocalizations express less self-confidence than low-pitched sounds. Thus, alarm calls emitted on the approach of a predator have the highest fundamental frequency of all calls, while threatening calls against conspecifics have the lowest. Lastly, vocalizations under high pharyngolaryngeal tension occur exclusively in aversive situations.

It can be concluded, therefore, that a number of human intonation patterns have their physical and emotional counterparts in the vocal repertoire of the squirrel monkey. The squirrel monkey thus seems to represent, at least on the be-

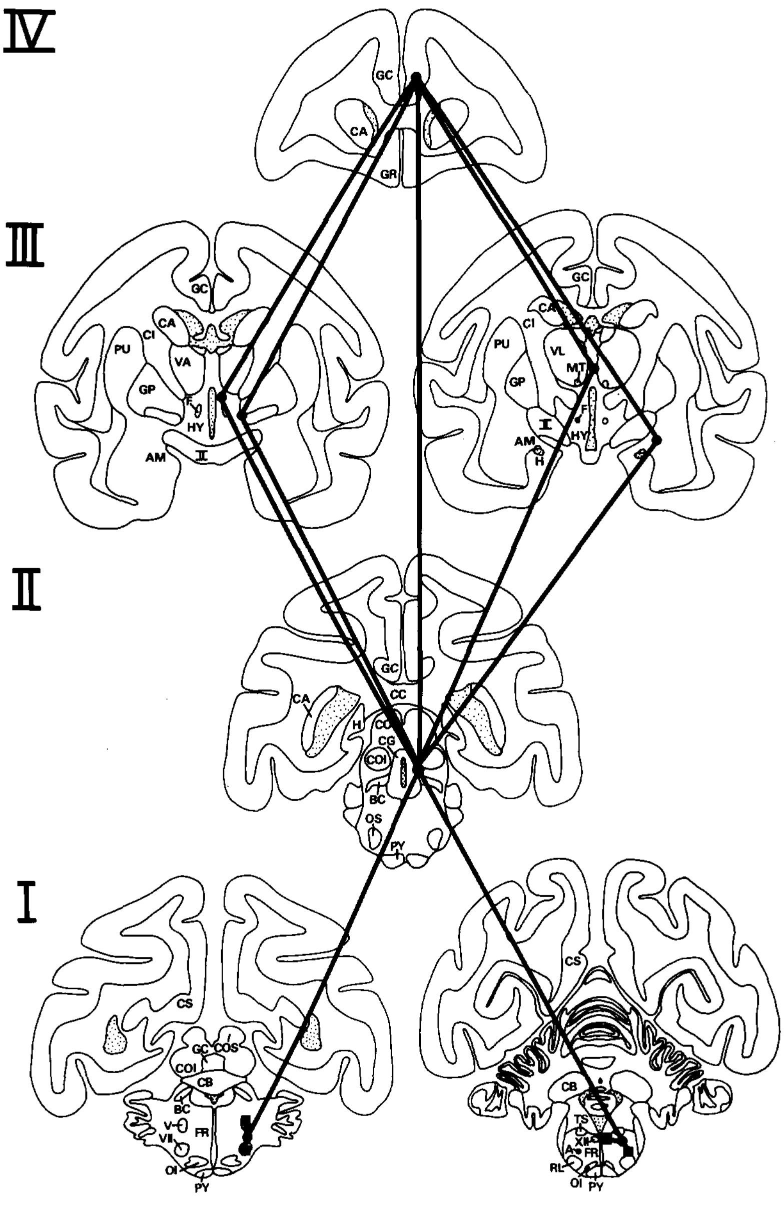

Fig. 3. Scheme of hierarchical vocalization control in the squirrel monkey. All areas marked with a dot yield vocalization when electrically stimulated. Squares indicate cranial motor nuclei involved in phonation. The lines interconnecting the dots and squares represent anatomically verified direct projections in rostrocaudal direction. The dots indicate in **(I)** the reticular formation of pons and medulla, in **(II)** the periaqueductal grey and laterally bordering tegmentum, in **(III)** the mediobasal amygdala, midline thalamus and different hypothalamic areas, in **(IV)** the anterior cingulate cortex. Abbreviations: *A* n. ambiguus, *AM* amygdala, *BC* brachium conjunctivum, *CA* caudatum, *CB* cerebellum, *CC* corpus callosum, *CG* periaqueductal grey, *CI* capsula interna, *COI* colliculus inferior, *COS* colliculus superior, *CS* cortex striatus, *F* fornix, *FR* formatio reticularis, *GC* gyrus cinguli, *GP* globus pallidus, *GR* gyrus rectus, *H* hippocampus, *HY* hypothalamus, *MT* tractus mammillothalamicus, *OI* oliva inferior, *OS* oliva superior, *PU* putamen, *PY* pyramidal tract, *RL* n. reticularis lateralis, *TS* n. tractus solitarius, *VA* n. ventralis anterior thalami, *VL* n. ventralis lateralis thalami, *II* tractus opticus, chiasma opticum, *V* trigeminal motor nucleus, *VII* facial nucleus, *XII* hypoglossal nucleus

havioral side, a suitable model for investigations on human emotional vocal utterances.

Neurophysiological Investigations

Systematic electrical brain stimulation studies in the squirrel monkey have shown that vocalizations can be elicited in this animal from a number of brain structures (Jürgens et al. 1967; Jürgens and Ploog 1970). Such structures are, for instance, the anterior cingulate cortex, amygdala, hypothalamus, midline thalamus, periaqueductal grey and parts of the brain stem reticular formation. It may be assumed that these structures are involved in vocal control in a more or less direct way. From this the question arises of the specific function of these structures in vocal control.

Vocalizations elicitable from the amygdala, hypothalamus, and midline thalamus cannot be distinguished from spontaneously uttered calls. This suggests that these structures are not involved in motor coordination of vocalization: otherwise the interference between electrical stimulus pulses and vocalization-producing neuronal pulse patterns should cause a deterioration of normal acoustic structure (such as is seen in the reticular formation of pons and medulla). Furthermore, vocalizations from the amygdala, hypothalamus, and midline thalamus have relatively long latencies (several hundred ms), habituate quickly (that is, they do not occur over the entire stimulation period but only during the first few seconds) and, finally, are accompanied by specific emotional states (as judged from a self-stimulation study in which the animals received the opportunity to switch on and off the vocalization-eliciting stimulation themselves; Jürgens 1976). These observations suggest that the vocalizations elicitable from these structures do not represent primary motor responses but rather secondary reactions due to stimulation-induced motivational changes. The type of motivational change, and thus the type of elicited call, depends closely on the stimulated structure. For instance, warning calls, expressing a state of intense alertness, can be obtained from the midline thalamus and medial amygdaloid nucleus; mobbing calls, uttered normally during collective aggression, from the dorsomedial hypothalamus; defense calls, representing a mixture of aggression and flight motivation, from the ventral hypothalamus; threatening calls, expressing intimidating self-confidence, from the lateral hypothalamus.

The caudal periaqueductal grey and laterally bordering tegmentum, another vocalization-eliciting area, has in common with the aforementioned structures that it yields normal species-specific calls. It therefore, also seems to be uninvolved in vocal motor coordination. On the other hand, it shows some characteristics distinguishing it from the others, such as very short latencies (< 100 ms), low habituation (prolonged stimulation can produce vocalization for several minutes), and production of a great number of different call types. After destruction of the periaqueductal area, stimulation of the amygdala, hypothalamus, and midline thalamus does not elicit vocalization anymore (Jürgens and Pratt 1979a). Conversely, destruction of the latter is without effect on periaqueductally elicited vocalization (Jürgens 1982; Kirzinger and Jürgens 1985). Lesioning the periaqueductal area, furthermore, not only abolishes electrically induced vocalizations but also vocalizations elicited by external stimuli as well as spontaneous ones. These findings suggest that the periaqueductal grey serves as a necessary relay station for all emotionally induced vocal utterances.

The periaqueductal grey projects, among others, massively into the reticular formation of pons and medulla (Jürgens and Pratt 1979a). Electrical stimulation of these areas also yields vocalizations; but these have an abnormal acoustic structure. Small lesions within these areas also cause severe deterioration of vocalization (Kirzinger and Jürgens 1985). Finally, neuroanatomical studies show that the lateral pontine and large parts of the medullary reticular formation are directly connected with the motorneuron pools involved in phonation, that is, the n. ambiguus responsible for vocal fold adduction, the trigeminal motor nucleus controlling jaw movements, the facial and hypoglossal nuclei responsible for articulatory lip and tongue movements, and the thoracic and upper lumbar ventral horn controlling expiratory movements (Holstege et al. 1977; Thoms and Jürgens in preparation; Tohyama et al. 1979; Westlund and Coulter 1980). These findings suggest that the lateral pontine and medullary reticular formation act as a motor coordination center for emotional vocal utterances.

The periaqueductal grey may be viewed as a mediator between the motivation-controlling forebrain structures and the motor coordinating lower brain stem structures. In the hierarchical scheme of Fig. 3, the motivation-controlling amygdala, hypothalamus, and midline thalamus, therefore, are placed above the periaqueductal grey. Nevertheless, it would be misleading to call the former "higher vocalization centers". They have control only over single call types or a few functionally related ones but not on sound production in general. Nor is a certain call type completely abolished after their lesioning. The only structure located above the level of the midbrain which seems to play a more general role in vocal control – and thus may be considered as a "vocalization center" superior to the periaqueductal grey – is the anterior cingulate cortex (Fig. 3, IV). Electrical stimulation of this area yields a number of functionally different call types with normal acoustic structure, similar to the periaqueductal grey (Jürgens and Ploog 1970). In contrast to the latter, cingular lesions neither abolish spontaneous vocalizations nor calls electrically elicitable from the amygdala, hypothalamus, midline thalamus, or periaqueductal grey (Jürgens and Pratt 1979b; Kirzinger and Jürgens 1982). If, however, monkeys are trained in a vocal operant conditioning task to produce vocalization volitionally in order to get a food reward, and the cingular cortex is then destroyed, animals are no longer able to master the task (Sutton et al. 1974). It is of interest in this context that human patients with bilateral anterior cingular lesions also have severe deficits in the volitional control of emotional intonations (Jürgens and Cramon 1982). These observations suggest that the anterior cingulate cortex plays an important role in the volitional control of emotional vocal utterances. Neuroanatomically, the cingulate cortex is in a well-suited position for such a task as it is connected directly with the periaqueductal grey as well as the amygdala, hypothalamus, and midline thalamus (Fig. 3).

It is worth mentioning that Broca's area and the posteriorly bordering cortical face area which play a crucial role in human speech production are dispensable for the production of monkey calls and, possibly, human nonverbal emotional vocal utterances. Ablation studies in the squirrel monkey and macaque have shown that bilateral destruction of these areas affect neither call structure nor frequency of spontaneous utterances nor volitional (conditioned) vocalization (Jürgens et al. 1982; Sutton et al. 1974).

References

Holstege G, Kuypers HGJM, Dekker JJ (1977) The organization of the bulbar fibre connections to the trigeminal, facial and hypoglossal motor nuclei. II. An autoradiographic tracing study in cat. Brain 100:265–286

Jürgens U (1976) Reinforcing concomitants of electrically elicited vocalizations. Exp Brain Res 26:203–214

Jürgens U (1979) Vocalization as an emotional indicator. A neuroethological study in the squirrel monkey. Behaviour 69:88–117

Jürgens U (1982) Amygdalar vocalization pathways in the squirrel monkey. Brain Res 241:189–196

Jürgens U, Cramon D von (1982) On the role of the anterior cingulate cortex in phonation: a case report. Brain Lang 15:234–248

Jürgens U, Ploog D (1970) Cerebral representation of vocalization in the squirrel monkey. Exp Brain Res 10:532–554

Jürgens U, Pratt R (1979a) Role of the periaqueductal grey in vocal expression of emotion. Brain Res 167:367–378

Jürgens U, Pratt R (1979b) The cingular vocalization pathway in the squirrel monkey. Exp Brain Res 34:499–510

Jürgens U, Kirzinger A, Cramon D von (1982) The effects of deep-reaching lesions in the cortical face area on phonation. A combined case report and experimental monkey study. Cortex 18: 125–140

Jürgens U, Maurus M, Ploog D, Winter P (1967) Vocalization in the squirrel monkey *(Saimiri sciureus)* elicited by brain stimulation. Exp Brain Res 4:114–117

Kirzinger A, Jürgens U (1982) Cortical lesion effects and vocalization in the squirrel monkey. Brain Res 233:299–315

Kirzinger A, Jürgens U (1985) The effects of brain stem lesions on vocalization in the squirrel monkey. Brain Res 358:150–162

Sutton D, Larson C, Lindeman RC (1974) Neocortical and limbic lesion effects on primate phonation. Brain Res 71:61–75

Tohyama M, Sakai K, Salvert D, Touret M, Jouvet M (1979) Spinal projections from the lower brain stem in the cat as demonstrated by the horseradish peroxidase technique. I. Origins of the reticulospinal tracts and their funicular trajectories. Brain Res 173:383–403

Trojan F (1975) Biophonetik. Bibliographisches Institut, Mannheim

Westlund KN, Coulter JD (1980) Descending projections of the locus coeruleus and subcoeruleus/medial parabrachial nuclei in monkey: axonal transport studies and dopamine-β-hydroxylase immunocytochemistry. Brain Res Rev 2:235–264

Winter P, Ploog D, Latta J (1966) Vocal repertoire of the squirrel monkey, its analysis and significance. Exp Brain Res 1:359–384

Received December 10, 1985