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Gamma activity in the piriform cortex and behavioral thresholds for electrical stimulation in the olfactory bulb

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Abstract. The olfactory bulb was stimulated by trains of electrical pulses in freely moving rats. Evoked responses resembling damped oscillations at the gamma frequency of 30-60 Hz were recorded in the anterior and posterior piriform cortex. Different types of unconditioned sniffing were induced by stimulation of the olfactory bulb. They were similar to those evoked by an odorant (amylacetate) but differed from the behavioral patterns evoked by non-olfactory (auditory) stimulation. Rats were trained to avoid foot-shocks following electrical pulses into the olfactory bulb as conditioned stimulus in a two way shuttle-box paradigm. Threshold electrical intensities for inducing evoked responses in piriform cortex, unconditioned behavior, and learned avoidance were compared. Thresholds for unconditioned and conditioned behavior were significantly higher in comparison with those for evoking gamma discharges in anterior and posterior piriform cortex. The results suggest that fast time-locked synchronization in the gamma range in the piriform cortex induced by synaptic input from theolfactory bulb is not sufficient for inducing corresponding behavior. Thus behavioral detection and probably also olfactory recognition do not seem to be direct consequences of this fast time-locked neural synchronization. Additional neuronal processes that are connected with further elevation of stimulation intensity seem to be necessary for that.

Key words: neural oscillations, behavioral control, olfactory perception, electrical stimulation of the brain

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INTRODUCTION

It has been described previously that neurons fire synchronously in a time locked manner at frequencies of about 30 to 90 Hz in various brain nuclei (Freeman 1960, 1968a,b, 1974, Galambos et al. 1981, Marcel 1982, Freeman and Skarda 1985, Gray et al. 1989, Eeckman and Freeman 1990, Singer 1990, Llinas and Pare 1991, Llinas and Ribary 1993). This type of fast time-locked firing was first observed for neuronal populations in the olfactory system, involving the olfactory bulb (OB), piriform cortex (PC) and other olfactory nuclei, in response to synaptic input during inspiration (see also Ottoson 1959). It can be easily registered by means of gross electrodes as electroencephalographical (EEG) oscillations at gamma frequencies. Bursts of gamma oscillations can be evoked in the olfactory bulb or cortex also by low-frequency electrical stimulation of the olfactory nerve or olfactory tract (Freeman 1960, 1968a,b, 1974, Freeman and Skarda 1985).

It was demonstrated that neuronal responses or changes in ongoing activity in sensory nuclei evoked either by sensory stimuli or by direct electrical stimulation, do not constitute human percepts, neither are they behavioraly detected in animals per se (Libet et al. 1979, 1991, Barlett and Doty 1980, Kirk-Smith et al. 1983, Holender 1986, Gustavson et al. 1987, Kulli and Koch 1991, Llinas and Ribary 1993). This finding suggests that neuronal activity has to be organized in a specific way to constitute percepts and determine behavior. It has been proposed that temporal synchrony among firing activity of groups of neurons could be an essential mechanism of functional organization of neural processing, and that fast time-locked oscillations could reflect this temporal organization (Damasio 1989, Crick and Koch 1990, Singer 1990, Madler et al. 1991, Jirsa et al. 1992, von der Malsburg and Bohman 1992, Wilson and Bower 1992).

Consequently, it has been proposed that awareness of stimuli could be the direct consequence of fast time-locked organization of neural activity (Crick and Koch 1990, Llinas and Pare 1991, Madler et al. 1991, Llinas and Ribary 1993). According to this hypothesis neuronal activity induced in sensory nuclei by stimulation should be perceived just after it becomes suprathreshold for inducing or resetting fast time-locked oscillations. There is some experimental evidence supporting this hypothesis. It was observed that sensory stimuli reset the gamma oscillations in the thalamocortical circuits in awake, but not in sleeping human subjects (Llinas and Ribary 1993). Suppression of awareness of auditory stimuli caused by anesthetic drugs correlates with the disappearance of gamma waves evoked by these stimuli (Madler et al. 1991). It was also shown that the threshold for sound-evoked gamma waves was close to the perceptual threshold in awake humans (Galambos et al. 1981).

The aim of the present paper was to test whether the threshold for inducing fast time-locked gamma oscillations in the PC by stimulation of the OB, correlates with thresholds for unconditioned and conditioned behavioral responses in the attending alert rat.

METHODS

Seven male Long-Evans rats weighing 250-350 g were used. Bipolar teflon insulated silver electrodes (diameter 120 μm) were implanted under pentobarbital anesthesia (50 mg/kg) into the left OB at the level of glomerular layer (stimulating electrodes), and into the ipsilateral PC (recording electrodes) using a stereotaxic atlas (Paxinos and Watson 1982). The tips of stimulating electrodes were separated by 0.3 mm, those of recording electrodes by 0.7 mm. Recordings were performed from anterior parts of PC (rostral to the level AP: +1.7) receiving fibers from both types of OB output neurons (mitral and tufted cells), and from posterior PC (caudally to the level AP: -1.8) with only mitral cells projections (Haberly and Price 1977).

All rats were allowed to recover 14 days following surgery. The experiment was performed in a 40 x 30 x 40 cm plexiglass cage in a sound-attenuated chamber. Series of 200 μs rectangular pulses, delivered with a frequency of 9/s, that corresponds to the frequency of sampling the air flow by sniffing (Welker 1964, Clarke and Trowill 1971, Macrides et al. 1982) were adopted as stimuli. Trains lasted 5 s. The intensity of electrical stimulation was increased in 10-20 μA steps to the level at which the first induced sniffing reactions were evoked (see below). This procedure was repeated 3 to 10 times for each rat on 3-5 days and the corresponding mean threshold was estimated.

The behavioral effect of electrical stimulation of OB has been compared with the application of amylacetate (AA), and for control purposes also with auditory stimulation. OB stimulation consisted of a train of pulses with intensities being set 40-70 μA above individual thresholds for evoking sniffing. AA was applied for 5 s into the air flowing through a glass turbine positioned 10 cm above the cage and exhausted from the ground of the cage. Auditory stimulation consisted of 5 kHz, 80 dB SPL, 5 s lasting tones presented by means of a miniature loudspeaker positioned 20 cm above the cage. Trains of 10-20 stimulations have been delivered respectively, intervals between trains ranging from 15 to 90 s. Each rat was tested in 3 to 6 sessions on consecutive days. The rat's behavior was recorded on video tape for off-line analysis. Sixteen single EEG evoked responses (ERs) recorded from PC and band-pass filtered between 0.5-200 Hz were averaged.

As mentioned, sniffing in the rat is characterized by regular rhythmic respiration at the frequency of 6-9 Hz, correlating with EEG activity of the same frequency registered in the OB (Clarke and Trowill 1971, Macrides et al. 1982). For our purpose sniffing was defined as rhythmic movements of nostrils and chest corresponding to the actual frequency of 6-9 Hz rhythmic EEG activity in the OB induced by administration of AA into the experimental cage. EEG in this case was recorded by the implanted stimulation electrodes. Two types of unconditioned sniffing were delineated: Type I was characterized by sniffing toward the walls of the cage or the floor and/or into wind performed during locomotion and during the pauses between sequences of locomotor activity (exploration - E). Duration of sniffing during these pauses did not exceed two seconds. Type II behavior was characterized by continuous sniffing lasting above three seconds and performed without locomotion, or during long pauses in the course of locomotor activity. Type II could be divided into 4 specific sequences: (1) repetitive sequential "air-gathering" with elevation of the head (vertical sniffing into wind - VSW; (2) sniffing toward the floor, to walls of the cage and/or to oneself's body (continual sniffing toward objects - CSO); (3) rearing accompanied by sniffing and head rotation (rearing- R); (4) repetitive half-circle movements of the body with the nose stretched forward along the body axis (horizontal sniffing into wind- HSW). A video-scanner was used for analyzing off-line the behavioral patterns induced by stimulation.

In five rats the reward/punishment properties of electrical stimulation of OB were investigated using the video system. Two 25 x 6 cm stainless plates were positioned into the right and left corner of the cage. Each rat was used in 6 sessions on consecutive days. Placing the rat into the cage at the onset of session induced exploratory activity lasting for about 10 min usually. Electrical stimulation of OB with the parameters adopted for evoking unconditioned behavior described, was switched on only when the rats positioned their head over the plate on the right side of the cage during exploratory activity. The incidence of positioning of the head above the plates, and duration of sniffing during these periods were evaluated.

After completing this experiment, the rats were first trained to avoid foot-shocks conditioned by electrical stimulation of OB, performed as described above, in a two way shuttle box. Foot-shocks were delivered at the end of electrical stimulation of OB. When the rats learned to run to the opposite side of the shuttle box before the end of stimulation of OB in more than 65% of trials, the second phase of training started. The intensity of OB stimulation current was lowered in 10-20 μA steps. If the animal did not perform the required response three times consecutively, the intensity of stimulation current was increased by one step, whereas the correct performance led to the decrease of stimulation intensity again etc., up to estimating the intensity of stimulation current, the animal was not able to react to with a probability higher than 5% after five days of training. After completing this procedure the third phase of the experiment started. Behavioral and electrophysiological thresholds were measured simultaneously. The intensity of stimulation was lowered successively as described, and ERs were recorded in response to intensities at which ERs were still detectable by averaging 16 single ERs. This level was defined as electrophysiological threshold. The threshold for triggering learned avoidance was set as the lowest current intensity below which the avoidance response did not occur any more. The procedure of successive lowering of intensity of stimulation current was repeated 3 to 6 times for each rat in five days and the resulting behavioral and electrophysiological thresholds were then compared. Further details have been described previously (Jirsa et al. 1992, 1993).

RESULTS

Unconditioned behavior induced by electrical stimulation of the OB

Figure 1A shows the relative incidence of various behavioral sequences induced by AA, electrical stimulation of OB and sound (adopting AA and sound intensities as described, and using electrical currents corresponding to medium suprathreshold intensities). The sound evoked mostly reactions of type E, i. e., locomotion without prolonged sequences of sniffing during pauses be-

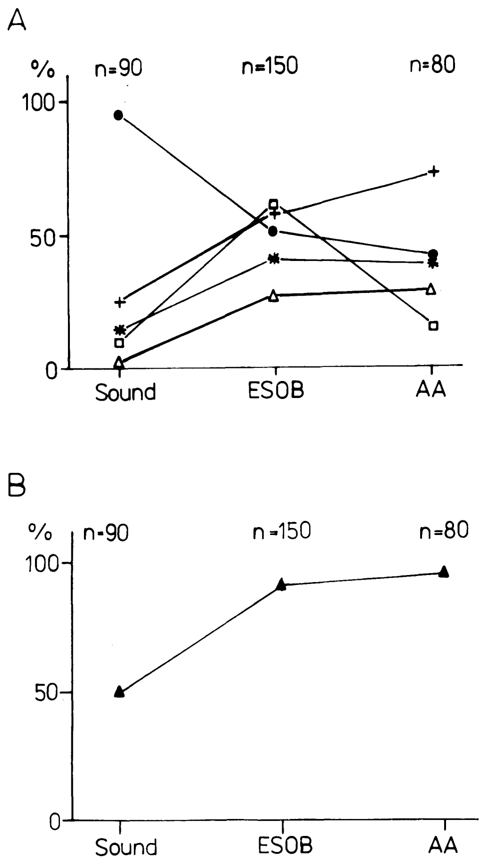

Fig. 1. Incidence (%) of various behavioral sequences evoked by electrical stimulation of the olfactory bulb (ESOB), by administering amylacetate (AA), and by sound stimuli. A, incidence of type I of behavior (exploration, E) and of various sequences of type II behavior (CSO, continual sniffing toward objects; VSW, vertical sniffing into wind; HSW, horizontal sniffing into wind; R, rearing). B, incidence (%) of trials in which at least one behavioral sequence of the type II induced by stimulation could be delineated; *n*, number of trials in which any behavior of type I and/or II) could be detected. For further explanation see text.

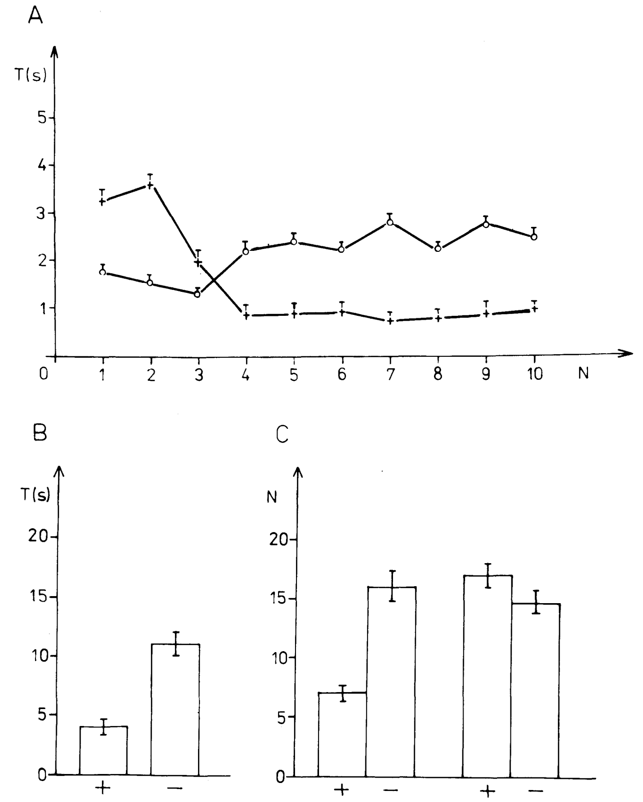

Fig. 2. Exploration of the place above the metallic plate associated with electrical stimulation of the OB after placing the rat into the experimental cage. A, mean time (T) ± SE of exploring the place associated with stimulation during the first ten explorations (abcissa) of this place (crosses) in comparison with control sessions when no electrical stimulation was delivered (circles). All differences between stimulation and control sessions were significant ($P<0.05$, *t*-test). B, mean time (T) ± SE between the second and the third explorations of the metallic plate during the sessions when stimulation was delivered (+) and in control sessions without stimulation (-). C, mean number (M) ± SE of explorations of the plates associated (left two columns) and unassociated (right two columns) with electrical stimulation of OB during first ten minutes of stimulation (+) and control (-) sessions. Data averaged from 30 stimulation and control sessions, respectively, in the group of five rats.

tween single sequences of locomotion. AA and electrical stimulation of OB evoked mostly behavioral patterns of CSO, VSW, HSW and R type, i.e., behavior of the type II. Figure 1B shows the occurrence of at least one behavioral sequences of the type II.,i.e., CSO, VSW, HSW or R, induced by electrical stimulation of the OB, AA or the sound. The incidence of evoking type II behavior by electrical stimulation of OB was significantly higher in comparison with that by sound (Chi-square = 223.6, $P<0.05$), but did not differe significantly from that evoked by AA (Chi-square = 2.22, $P>0.05$). The mean number of behavioral sequences of the type II behavior evoked by single stimulation was 1.77 ± 0.76 for electrical stimulation of the OB, 1.59 ± 0.70 for AA and 0.51 ± 0.50 for sound, the mutual differences being significant ($P<0.05$, *t*-test). This result indicates that AA and electrical stimulation of OB evoked often more than one behavioral sequence of the type II, whereas sound typically evoked only a single or no behavioral sequence of type II at all.

Figure 2 illustrates the effect of electrical stimulation of OB upon the frequency and duration of sniffing over the metalic plate associated with stimulation, placed in the cage. Electrical stimulation significantly prolonged the duration of sniffing toward the reinforced plate in comparison with the control one in the first three stimulations trials. During the later phase of experiment, however, the time of exploring the plate became shorter in comparison with control conditions (Fig. 2A). The animals tended to return to the place of stimulation during the first contacts with the stimuli, as indicated by the short interval between two consecutive sniffings over the reinforced plate (Fig. 2B). However, later the animals avoided the place of stimulation, as documented by the reduced number of explorations (Fig. 2C). As also shown in Fig. 2C, the mean number of explorations over the plate unasociated with stimulation was not reduced during the stimulation sessions.

This circumstance suggested that the reduction of explorations over the place associated with electrical stimulation of the OB was due to a tendency to avoid the stimulation, and not to a reduction of overt exploratory activity.

Electrical evoked responses in PC

ERs in all rats consisted of sequences of waves with decreasing amplitudes corresponding to frequencies of oscillations 30-60 Hz (Fig. 3A). Oscillations were absent in anterior PC in one rat (Fig. 3A, rat No. 38). Figure 3B shows the occurrence of consecutive cycles of oscillations in PC in the group of rats during inducing unconditioned behavior. As the first peak does correspond to initial synaptic input more than to induced activity of neurons in PC (Haberly and Bower 1984, Schwob et al. 1986), the measurment of cycles started with peak "b" (see Fig. 3A). Only the initial cycle defined by peaks b-c-d could be registered regularly (Fig. 3B). Only this first cycle was used for ER threshold measurment, and the ER thresholds were evaluated as those for inducing b-c-d wave complexes. As the later cycles occurred only occasionally, they were not adopted for this purpose.

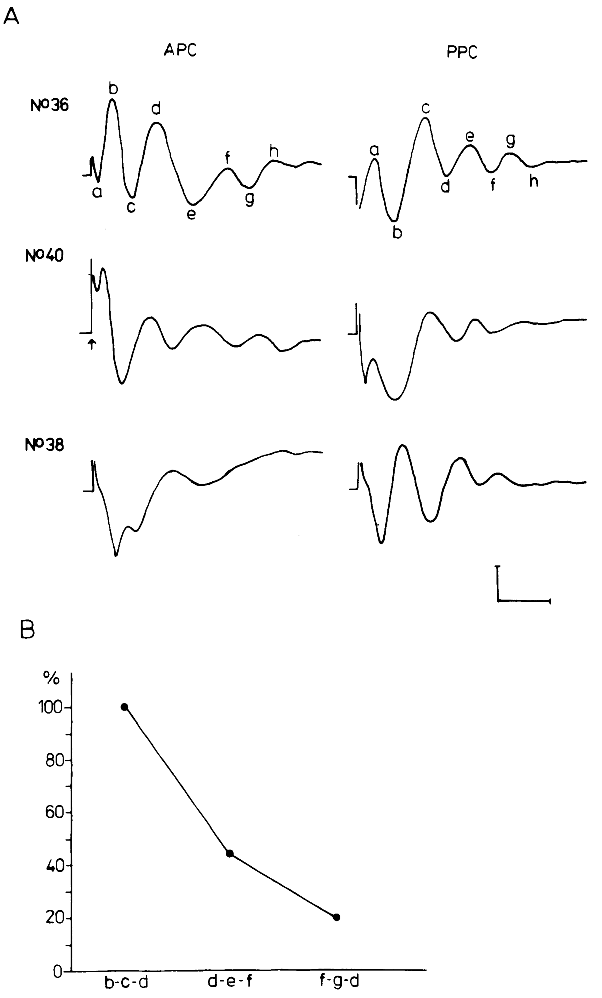

Fig. 3. A, examples of averaged ($n = 16$) evoked responses in anterior (APC) and posterior (PPC) piriform cortex in response to electrical stimulation of the olfactory bulb in three rats. Stimulus intensity was set 100% above individual electrophysiological threshold in anterior PC. For details see text. Calibration: vertical 200 µV; horizontal 25 ms. Arrow indicates stimulus onset. B, probability of recording single cycles of averaged evoked responses from anterior PC by electrical stimulation of the OB in the group of six rats. Evoked responses were evaluated only when unconditioned behavior was induced by the same stimulation train simultaneously. Data averaged for each rat from ten stimulation trains inducing unconditioned behavior. Stimulation intensity was set 50% above individual behavioral threshold in each rat.

Mutual comparison of electrophysiological and behavioral threshold

Five rats of the group of seven learned to perform in the shuttle box regularly in response to 9/s OB stimulation. During step-wise decrease of current intensity the learned behavior usually disappeared at a certain level, but it could still be relearned after 4-12 additional conditioning trials with the same (low) intensity. However, when a critical minimal intensity was reached, learned behavior did no appear at all and could not be relearned even after three days of repeated conditioning using the same intensity of stimulation of OB, although the behavioral response remained still preserved after increasing

TABLE I

The mean thresholds ± SD for evoking unconditioned behavioral patterns to electrical stimulation of the olfactory bulb, conditioned avoidance, and the main components of evoked responses in anterior (APC) and posterior (PPC) piriform cortex by pulse trains at frequency 9/s in the group of rats. See text for details

Treshold in microamperes			
Unconditioned behavior	Conditioned behavior	Main components of ERs in: APC	PPC
175 ± 60 (n = 150)	140 ± 40 (n = 100)	95 ± 32 (n = 100)	105 ± 36 (n = 100)

current intensity. The mean threshold values for evoking unconditioned and conditioned behavior, and for inducing ERs in anterior and posterior PC, are given in Table I. The mean learned avoidance threshold value was significantly lower than the threshold for evoking unconditioned behavior (t-test, $P<0.05$). The learned avoidance threshold, however, was significantly higher ($P<0.05$) than the electrophysiological threshold in both anterior and posterior PC. Figure 4 illustrates the relations between ERs and learned behavior in two representative rats.

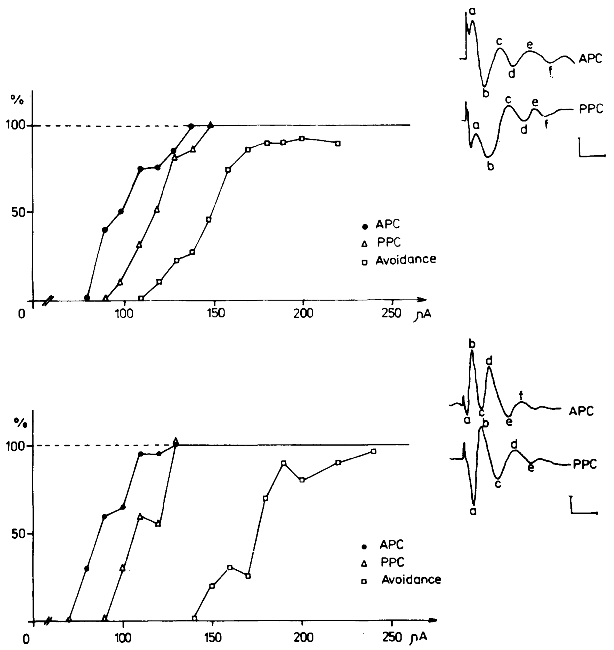

Fig. 4. Probability of correct avoidance performance in a shuttle box and of inducing corresponding evoked responses (right top corner) in anterior (APC) and posterior (PPC) piriform cortex, for different intensities of electrical stimulation of the olfactory bulb in two rats. The probability of inducing evoked responses holds for the components marked b-d (main components). Calibrations: vertical, 300 µV; horizontal, 30 ms. Each point in the curves was averaged from 40 experiments.

DISCUSSION

Elctrical responses in PC

The shape of gamma-discharges evoked by electrical stimulation of OB in PC in rats was similar to that shown in cats, and induced also by electrical stimulation of the lateral olfactory tract (Freeman 1960a, 1968a,b). It differed, however, from the shapes described by various authors in other species, including the rat, characterized as a nonoscillatory wave complex (Haberly 1973, Haberly and Bower 1984, Schwob et al. 1986, Patnau and Stripling 1992). Our results showed that gamma type discharges could by evoked also in the rat in response to electrical stimulation of OB, although their frequency was sometimes close to thelower limit of the corresponding frequency range (about 30 Hz). Two most probable explanations why other investigators did not register gamma responses could be offered. First, some previous studies were performed in anesthetized animals. It is known, however, that anesthetics can abolish gamma discharges (Ottoson 1959, Freeman 1968a, Madler et al. 1991, Jirsa et al. 1992). Second, high intensity electrical stimuli were usually adopted.It was, however, proposed on the basis of computer modelling recently, that oscillatory responses of PC networks in response to single shocks administered to the lateral olfactory tract, should develop only when using relatively weak stimuli (Wilson and Bower 1992). That was our case, as intensities did not exceed the 200% level above thresholds for evoking ERs.

The main result of this experiment was that the threshold for inducing time-locked activity in the gamma range in both anterior and posterior PC was lower than both unconditioned and learned behavioral thresholds. The main components of ERs (onset latencies above 10 ms) that served for determining the electrophysiological threshold do correspond to time-locked firing of neurons in the PC (Freeman 1968a, Schwob et al. 1986, Haberly and Bower 1989, Wilson and Bower 1992). Thus our results suggest that time-locked gamma activity in the PC (both anterior and posterior) *per se* does not trigger the chain of neuronal events enabling control of specific behavior. Additional neuronal processes triggered by elevation of the strength of synaptic input from OB to PC, due to increased stimulation intensity in the OB, seem to be necessary for that.

Neural patterns induced by electrical stimulation of the OB do differ in some respect from those evoked by olfactory stimuli. The frequency band of oscillations within the gamma bursts in PC, 30-60 Hz, induced by electrical pulses into OB, represents only the lower half of the band of olfactory inspiration-linked gamma bursts, that ranged between 35-90 Hz in the rat usually (Eeckman and Freeman 1960). Moreover gamma bursts induced by sniffing an odorant contained more periods of oscillations (Freeman 1960, Freeman and Skarda 1985) and possibly could spread over larger spatial distances in PC. It has been assumed, however, on the basis of computer modelling that gamma bursts evoked in PC by electrical stimulation and those induced by odorants should reflect identical neuronal processes (Wilson and Bower 1992). The shape of oscillations should reflect therefore the dynamic activation of similar subsets of neurons in PC in both cases. Thus the difference between electrophysiological and behavioral thresholds should not be caused by differences in the neurophysiological mechanism of generation of the gamma oscillations in PC by electrical stimulation or odorants, probably. Synaptic inputs from OB to PC as well as excitatory/inhibitory synaptic connections mediating gamma discharges within PC are organized diffusely, involving large regions of the PC (Haberly and Price 1977, Haberly and Bower 1984, Wilson and Bower 1992). The presence of ERs in both anterior and posterior PC thus indicated that the gamma burst did spread spatially over the whole PC, probably. Thresholds for inducing time-locked electrical activity were lower than the behavioral ones both in anterior and posterior PC. Thus the difference between electrophysiological and behavioral thresholds was not due to limitation of spatial distribution of gamma oscillations by weak intensities of stimulation.

Informational content of neural patterns evoked by electrical stimulation of the OB

It might be worth mentioning related experiments in humans. It has been described that direct electrical stimulation of sensory nuclei in the brain evoked vivid sensory feelings in humans (Libet et al. 1979, 1991). When the train of electrical pulses was shorter than a critical duration, no sensory feelings were reported by the subjects in these experiments. However, after the experimental paradigm was changed so that subjects were forced to press one of two buttons depending on their judgment concerning the presence/absence of electrical stimulation, they were still able to make this choice correctly, although they had no subjective feelings evoked by the stimuli (Libet et al. 1991). Similar dissociations between subjective perception of stimuli and the ability to initiate and control behavior based upon this stimulation was described also in other experiments. Patients with damaged primary visual cortex were not aware of visual stimuli in their blind field and did not initiate volitional movement toward them in spite of being motivated to do so (Marcel 1982, Cowey and Stoerig 1991, Weiskranz 1991). They did not reach for example for a glass of water when being thirsty. However, when told that a glass of water was placed in front of them, they were able to direct their hand movement correctly to the glass (Marcel 1982). They could also detect light stimuli presented into their "blind" field correctly when a forced-choice paradigm was used and reported then that they made the choice on the basis of "guessing" (Marcel 1982, Cowey and Stoerig 1991). An analogous phenomenon is "anosmic olfaction", detection of weak olfactory stimuly the subjects are not aware of, by guessing (Radil and Wysocki 1996). These experiments suggest that specific behavior can be controlled by neuronal patterns evoked by sensory stimulation without the stimulus being recognized subjectively.

In our experiment with the two-way shuttle box the animals had to associate initiation of their avoidance reaction with any information available enabling to predict the foot-shocks in order to avoid them. Foot-shocks represented additional external information to which electrical stimulation of OB could be associated. The ability to behave correctly in the two-way shuttle box in response to electrical stimulation of OB indicated therefore that the rats were able to use patterns of neural activity evoked by this electrical stimulation for predicting the foot-shocks. That does not mean per se, however, that these neuronal patterns were recognized as "olfactory". Any information, similar to that mediating the non-specific "guessing" behavior described in humans, could enable the rat to detect the electrical stimulation of OB.

The unconditioned behavior, however, was triggered only by electrical stimulation of the OB without any additional external information about stimulation. The question is what was the informational content of neuronal patterns controlling behavior in this case. It has been already described that electrical stimulation of the OB can have reward properties in the rat (Olds 1958). Unconditioned behavior under this condition could therefore indicate that stimulation was recognized as something pleasant by the rats, and animals tried to find then the locus of maximal reinforcment. However, our rats did avoid the place of stimulation more often than they were attracted to it. Stimulation had neither clear-cut punishment properties, like those evoked by painful stimulation, as the rats returned to the place of stimulation more often and did stay there longer during the first three stimulations. Moreover, no tendencies to escape from the box during electrical stimulation of the OB was observed in unconditioned rats at any intensity of stimulation in the experiment dealing with unconditioned behavior. The probable interpretation of this behavior might be, that electrical stimulation of OB was interpreted by the rats as something more unpleasant than pleasant. The animals tried at first to explore this information in more detail and returned therefore to the place of stimulation. After this exploration phase, however, they did try to avoid the stimulus. When the same stimulation was delivered in motionless animals, it induced patterns of behavioral activity containing at least one behavioral sequence of the type II, i. e., that of continual sniffing without locomotor activity, in most cases. The incidence of type II behavior did not differ depending on the stimulation adopted, i.e., electrical of the OB, or olfactory (AA). Exploratory activity induced by non-olfactory stimulation (sound) was accompanied, however, by much lower incidence of type II behavior. This observation could suggest that neuronal patterns evoked by AA and electrical stimulation of the OB represented similar information for the animals, differing from that induced by auditory stimulation. It has also been described (Monod et al. 1989), that electrical stimulation of the OB evoked similar vegetative reactions as odors in rat. Similar procedure performed in human subjects evoked vivid olfactory sensations, which were subjectively interpreted by them as strong unpleasant odors (Penfield and Erickson 1941). All this evidence seems to support the hypothesis that the rats "recognize" the neuronal activity induced by electrical stimulation of the OB as if it was an odor, during the unconditioned behavior described.

Possible role of gamma oscillations in olfactory processing

Analysis of our results suggested: (1) Fast time-locked synchronization of neural activity induced in PC was not sufficient per se for triggering and controlling of both unconditioned and conditioned behavior; additional neuronal processes triggered by elevation of stimulation intensity seemed to be necessary for that. (2) At least the unconditioned behavior in the rats could have corresponded to olfactory interpretation of the neural activity induced, i. e., to olfactory perception in humans. The probable conclusion was that behavioral detection and olfactory interpretation of neural activity induced in the PC was not an immediate consequence of its fast time-locked synchronization.

On the other hand It has been demonstrated by adopting different psychological and psychophysiological paradigms that emotions and vegetative reactions in humans can be influenced by administering low concentrations of odors, which do not evoke olfactory feelings in the subjects (Kirk-Smith et al. 1983, Gustavson et al. 1987). These findings suggest that olfactory information is being analyzed and does affect particular neuronal systems of the brain (i. e., emotional and vegetative) before the threshold for perceptual interpretation has been reached. Thus it is possible that gamma activity participates in pre-perceptual analysis of olfactory information. As long as the intensity of stimulation remains weak, the output of this analysis is not being perceived. It might be, however, "recognized" by some neural subsystems (i.e., vegetative), that are not connected with conscious perception. In case of stronger stimulation, additional neural processes are being triggered, which also enable conscious awareness of the output of the pre-perceptual analysis of olfactory information connected with gamma oscillations.

ABBREVIATIONS

AA - amylacetate
CSO - continual sniffing toward objects
E - exploration
ERs - evoked responses
HSW - horizontal sniffing into wind
OB - olfactory bulb
PC - piriform cortex
R - rearing
VSW - vertical sniffing into wind

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