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Neural correlates of odor-guided behaviors

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Key words. Olfaction; behaving subjects; chronical electrophysiology; multiunit/unit recording; organization level.

Introduction

To the same extent as audition, the olfactory processes contribute to extract information from distal sources. Close to gustation, they are also affected by proximal cues. Thus odorous signals can subserve any decision to start, maintain or interrupt behavioral sequences. Besides that, the olfactory pathways are extensively open to electrical self-stimulation[43]. Odors in themselves may be reinforcing[25], and are able to modulate the electrical reinforcement[41]. Their hedonic value turns out to be a conspicuous factor in multidimentional evaluation[46]. Therefore the sense of smell is likely to subserve the identification of odors not so much as chemical species, but even more as indices of possible reward.

In man, the hedonic dimension of food odors, but not that of control odors, is biased by the metabolic status of the subject, in an adaptative manner, which gave rise to the general definition of alliesthesia[5]. In most examples, finalism is satisfied with the statement that external stimuli are pleasant, as far as they signal a goal useful to individual or specific survival. In such models, the pleasantness of odors is their proper behavior-guiding dimension. Which does not exclude that odors in themselves are gratuitous goals for cognitive behavioral sequences, such as exploration. In any case, optimalized sensory mechanisms do require that the internal state of the subject should control the olfactory processing[24]. As a consequence, the definition of behavioral events has to be extended to internal events subserving behavioral sequences.

In fact the internal processes could interfere with the treatment of olfactory information at various functional levels, from the nasal cavity to the central integrative areas, through metabolic, endocrine, autonomic and central nervous processes. Various chapters in this issue illustrate it from the organizational, functional and psychophysical points of view. But although we know much about the hardware, data from acute experiments can seldom be extrapolated to those cases with numerous degrees of freedom, when sensory cues are perceived by behaving subjects. One has rather to try to construct a neurophysiology of the unrestrained model, by integrating various fields of neurobiology, developing accurate methods, defining the proper functional units and the relevant conceptual tools.

Since no language common to neurology and to psychology has been elaborated so far, one cannot pretend to determine either functional level from the other one. Therefore the neurophysiologist studying the behaving subject is limited to a search for neural correlates of behaviors, i.e. for the most probable occurrence of simultaneous neuronal and behavioral events, as they were defined previously. So as to match particular behavioral sequences with specific spatio-temporal patterns of neuronal activity, it is necessary to find a common space- and time-scale for both phenomena, and to question the accuracy of the recording techniques and data processing to detect the relevant brain figures.

Chronical central electrophysiology was first represented by electro-encephalograms (EEG) summating the activity of wide heterogeneous neuronal populations for nearly unlimited periods. Spatial resolution was improved with the multiunit (MU) approach, bringing information on the mean activity level in a limited group of neurons, especially meaningful in homogeneous structures. Both EEG and MU studies revealed sustained electrical phenomena, correlated with cognitive processes, such as selective attention[31,34], expectancy[47] and memory[42]. In chronical conditions, the individualized action potentials from single units are presently the ultimate resolution level; on the behavioral time-scale, they may be expected to carry more information than could be interpreted without additional elements. In the following review, it will be considered whether neuro-behavioral correlates can be disclosed in the olfactory system at the available resolutive levels, whether the correlates observed at these various levels are congruent to each other, and if they could help, as a whole, to define the functional principles of the system itself.

Multiunit correlates of behavioral events in the olfactory pathways of unrestrained animals

The olfactory bulb level. Being a well delimited and accessible laminar structure, the olfactory bulb (OB) has been investigated in chronical conditions in preference to the other olfactory stages[22,32]. The dynamics of the experimental schedule resulted from conditioning, or from the manipulation of behavioral arousals, which did not end in performing sequences, because the specific target, food, sexual or social partner was not accessible to the subject.

Learning experiments. A pioneer work in the cat had pointed to the plasticity of OB evoked responses, when the repetition of a given stimulus altered its meaning[18]. One approach used the electroencephalography of the OB and frequency component analysis. The EEG activity was collected at 64 points on the OB surface of rabbits conditioned to associate olfactory stimuli and electric shocks[13]. The data processing allowed the construction of the most probable maps of the superficial EEG amplitudes. The spatial distribution of the most active spots was an individual characteristic of the subjects; it was not related to the nature of the stimulus, but changed along with the associative training and the habituation to the cage.

In another approach, the MU activity from the OB mitral cells was recorded from indwelling electrodes by telemetry[33]. Available water was signalled to thirsty rats by liminal concentrations of isoamyl acetate; pure air was used as a control stimulus. The olfactory electrical responses were enhanced on correct trials, a phenomenon supposedly mediated by centrifugal influences.

Nutritional experiments. On this practical basis, a corpus of works was achieved, in which male rats were used on a standard schedule. The MU activity of mitral cells was collected between 300 and 3000 Hz, in the same satiated or food-deprived subjects receiving 20 puffs of isoamyl acetate or food odor, alternated every 2 min or more, each lasting for 10 s. Although the hungry rats were not fed till the end of the recording sessions, the concentration of the alimentary stimulus was high enough to suggest immediate food. Isoamyl acetate also was presented far above the olfactory threshold. The MU activity was summated with a 0.2 or 0.5 s time constant; an increase in the summated activity above the background level during a stimulation was noted as a positive response.

The probability of observing a positive response decreased along with repeated stimulations, but the decay was attenuated significantly in hungry animals receiving food odor, selectively[17] (fig. 1). Insulin administered to fed animals reproduced the response patterns proper to food depletion[40] (fig. 2), while gastric distension in deprived rats was able to elicit the satiety response pattern[9]. Exploration, or at least activated respiration, could be noted at the time of positive electrical responses in the OB. Thus some metabolic and visceral parameters taking part in the definition of the hunger internal state adjusted the OB responsiveness to a familiar food odor. The olfac-

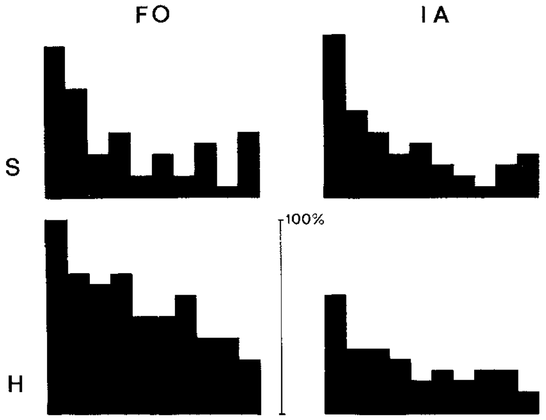

Figure 1. Time-course of the occurrence of positive MU responses in the mitral cell layer of 25 unrestrained food-satiated (S) or deprived (H) rats. FO: food odor. IA: isoamyl acetate. Abscissa: rank order of the stimulation. Ordinate: percentage of positive responses. The amplitude of the nutritional modulation of responses to an odor was expressed from the significant differences between the patterns obtained in the same H and S animals.

tory cues from novel or aversive food odors did not elicit modulated responses, while a control odor associated with food during infancy did acquire this ability[35,44]. So far, the amplitude of the nutritional modulation of the MU mitral cell activity (cf. legend to fig. 1) has been noted to vary in a parallel with the palatability of the stimuli, which illustrates the life-long plasticity of behavioral energy-regulating mechanisms, as seen from their neurosensory components.

Other behavioral arousals. The nutritional model was extended to other experimental situations, related to non-consummatory behaviors. In female unrestrained rats, estrus enhanced the MU responsiveness of mitral cells to the odor of intact males and to a lesser extent, of castrated males, but not to the odor of isoamyl acetate[29]. The adaptative character of a preferential treatment of relevant odorous signals was as prominent for sexual behavior as in the case of food and fluid intake. But the observations ought not to be interpreted in a unimodal manner. An adjacent experimental paradigm involved rat conspecific pheromones and predator odors. It brought out that the mitral cell MU responses were biased to positiveness when the stimuli could be regarded as reassuring and the other way round, for the frightening ones[8].

Underlying neural mechanisms

The same schedule as before was applied to rats with surgical or electrical lesions in the olfactory pathways, or with the olfactory mucosa treated with zinc sulphate. The modulation of OB responses according to the internal state and to the relevance of the stimulus required an intact olfactory mucosa, and medial plus lateral ascending pathways, although enough information was carried through the medial pathways alone to subserve an aversive olfactory conditioning to food odor[45] or to waken sleeping animals in an adaptative manner [7,15]. The modulating processes were probably calling for a full recognition and affective evaluation of the stimulus. An argument in this direction is that it was observed in waking animals only; during slow-wave and REM sleep, the OB excitability was changed following other factors[14].

When medial fibers to the OB had been interrupted in one side, the responses to food odor in the corresponding OB were no longer modulated[36]. This suggested that the modulating processes were mediated by the OB centrifugal innervation. Complementarily, the modulation was amplified in one OB, selectively, after the ipsilateral destruction of the noradrenergic OB terminals by local 6-hydroxydopamine treatment[16]. It seems therefore that the modulation, first interpreted as an all-or-none gating process, resulted in fact from multifactorial influences contributing to adjust the mitral cell excitability.

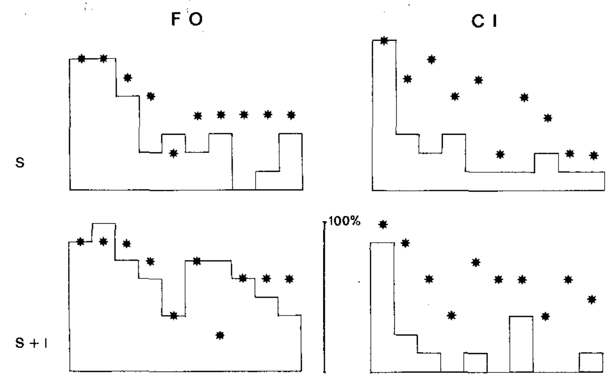

Figure 2. Time-course of the occurrence of positive responses to food odor (FO) and to citral (CI) in 8 unrestrained satiated rats (S) after a control or an insulin injection (+I). Histograms: mitral cell MU responses. Stars: respiratory responses. Abscissa: rank order of the stimulation. Ordinate: percentage of positive responses.

Multilevel neural processes

In a review of anatomical and functional data, with a special interest in the olfactory-hippocampal synchronism in sniffing animals, it was justifiable to investigate the olfactory processing not only with the step-to-step linear strategy, but also considering the OB as a knot in a looped circuitry[27]. In fact, EEG data were obtained simultaneously from several points in the olfactory pathways and in other brain areas. Initial work pointed to the similarity of the spectra from the OB and piriform cortex of expecting or licking cats[3]. The most conspicuous events, in the vicinity of 40 Kz, were interpreted as spreading oscillations related to respiratory activity. The EEG analysis between 35 and 85 Hz was extended to several mammals and to various olfactory and other areas including the striatum, pallidum and neocortex[4]. The results supported the hypothesis that neuronal populations interacted reciprocally in circuits where they induced oscillatory phenomena, with maximal amplitude close to 40 Hz, in determined behavioral circumstances. A preliminary spectral analysis of the mitral cell MU activity in the rat between 0 and 3000 Hz did not reveal any consistent peak at 40 Hz. But it remained that the modulation of responses to food odor was observed concomitantly in other olfactory, diencephalic and limbic areas[38] (fig. 3). Some of the modulated sites were located on cholinergic or noradrenergic pathways to the OB. In

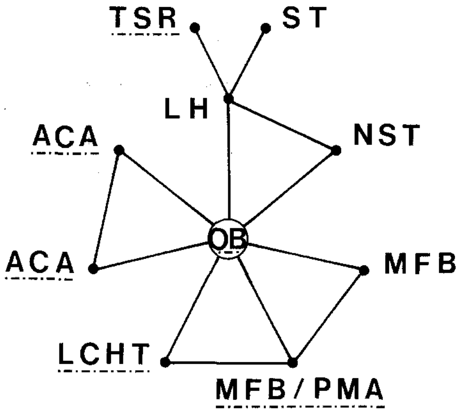

Figure 3. Correlated multiunit responses in the olfactory bulbs (OB) and in central sites of unrestrained food-deprived and satiated rats stimulated by food odor and isoamyl acetate. ACA: anterior limb of the anterior commissure, both sides, LCHT: lateral cortico-habenular tract, LH: lateral hypothalamus, MFB: medial forebrain bundle, NST: nucleus of the stria terminalis, PMA: median preoptic area, ST: stria terminalis, TSR: thalamo-striate radiatio. The black lines join structures in which the simultaneous responses were qualitatively identical in 95% of the cases at least. In the underlined structures, a respiratory modulation of the activity was noted on anesthesia during surgery.

several of them, and in some others, as in the OB, the MU activity included a respiratory frequency component, disclosed in the anesthetized rats[37] (fig. 3).

The correlation between the response pattern of the OB and of each central site was evaluated; the corresponding index decreased while the number of interposed synapses increased. But in spite of one synaptic relay or more, the resting activity in the OB could sometimes be nearly superposed on that of more central areas, e.g. preoptic loci. The correlation index could be included as a parameter into models of oscillatory interactions between neuronal groups in the olfactory system. It is relevant to the concept of cerebral functional distance, elaborated from the results of dual task experiments in man[21].

In unrestrained cats, the evoked potentials and MU activity at several stages of the olfactory pathways were modified by hypothalamic stimulation or by estrogen treatment, in a way likely to subserve sexual behavior[1,6]. Thus relevant olfactory stimuli, able to release and maintain behavioral arousal and performances, elicited sustained electrical phenomena in heterogeneous neuronal networks, as had been noted in a more general experiment[2]. But the distribution of the activity within the circuits could not be determined any more precisely without reaching the unit level of the analysis.

Unit correlates of behavioral sequences

In behaving animals, unit recording was developed later in the olfactory pathways than in other neuronal systems. An experimental compromise was to collect single cell activity from awake but restrained animals. In the rabbit, with this preparation, the respiratory influences on the OB deutoneuron activity appeared with their full complexity[11]. In the Goldfish, the natural prey extract most suitable for guiding food intake was noted to elicit the most conspicuous unit responses in the OB deutoneurons, compared with its amino acid constituents or to control odors[49].

Unit recording in the OB of unrestrained animals was used to study active olfactory perception[20]. Rabbits were conditioned to push covers and disclose an odorous cue for available food while unit OB activity was collected. The 96 recorded cells seemed to be driven by various determinants: respiratory activity, olfactory stimulation, the animal's decision to act. The author suggested that some neurons were likely to subserve olfactory discrimination, while most of them were devoted to integrative processes, and yielded behavioral rather than olfactory responses, properly speaking. Complementary experiments were useful to test this interpretation, and to examine which unit processes could account for the nutritional modulation of MU mitral cell responses.

Olfactory units in the OB of behaving rats

The following results represent a synthesis of published material[39] and of additional data. They were obtained in 10 male rats prepared behaviorally and surgically for the simultaneous recording of respiration and of unit activity in one OB during simple behavioral sequences. The MU activity was also collected as before in the controlateral mitral cell layer (5 rats) or in more central areas (5 rats). A removable microdrive allowed the displacement of a tungsten microelectrode with stereotaxic indications. The rats had to associate a food odor puff (F) and the immediate distribution of one edible pellet; interposed isoamyl acetate stimuli (IA) did not announce any event.

The animals were tested on mild food deprivation, and the pellets could be seized and eaten spontaneously; the neglected pellet, when presented at the mouth, was either accepted or refused actively. These behavioral outcomes determined the F+, F(+) and F− sequences, respectively; their occurrence was not determined by the experimental schedule.

At this time, 34 OB neurons could be recorded for 5–30 min. Among them, 19 mitral cells and 2 cells in the external plexiform layer were identified from electrical lesions. The units yielded 154 workable sequences, lasting for 15 s, with a 5-s stimulus in the middle part. The stimuli were distributed as follows; 79 IA, 35 F+, 17 F(+) and 23 F−. Individual sequences were analyzed as a succession of 30 bins, each lasting for 500 ms and characterized by the number of spikes from the same unit (U), the terminal level of summated multiunit activity (M) and the number of inspirations (R). Sniffing corresponded to the values of R greater than 1.

The unit activity. In quiet awake subjects, the OB unit activity was steady for all the observation time, as far as it was expressed by the mean discharge rate in 15-s periods. At a shorter time-scale, the firing rate was ever-changing, and apparently not linked either to the spontaneous behavioral sequences, such as displacement, exploration and grooming, or to respiratory cycles, at least in a regular manner. Besides that, the time when the olfactory stimulus reached the sensory receptors could not be determined except with a half-second precision. Therefore the resting activity and the responses were evaluated from the mean firing rate over 10 bins at least; temporal reorganization of the discharge was inferred from changes in variance, but it was smoothed inside each bin. A significant increase of the variance and/or mean defined a positive response, and inversely.

In identical experimental conditions, the responses of a neuron to the same stimulus were scarce but consistent and discriminative at the 0.001 probability threshold. At more tolerant levels, significant responses were more numerous, but they happened to vary qualitatively. Since the occurrence of a positive, negative or null response was hard to predict at the unit level, the first aim of the data processing was to examine whether the activity of the neural population observed could be statistically correlated to the behavioral responses or to functional parameters.

The unit responses. The concomitant respiratory, multiunit and unit responses to the olfactory stimuli are represented in figure 4. In experimental conditions giving the rats access to food, a nutritional modulation of the MU bulb responses – and of the respiratory frequency – appeared as a greater occurrence of positive MU and respiratory responses to those food odor stimuli giving rise to immediate or encouraged pellet intake. The data were more diversified at the unit level. Although deutoneurons were activated when the rats were sniffing spontaneously between the stimuli, the respiration was not the main correlate of neuronal responses.

When the responses of the mitral cells (19/21 deutoneurons) and of the other cells were processed separately, isoamyl acetate and food odor elicited distinct response patterns in either population (fig. 5). The deutoneuron responses to food odor were biased in a positive direction as the readiness to eat increased. The other units, mostly interneurons in the granular layer, displayed the opposite trend. Thus, in the lack of any metabolic data the OB unit response pattern could help to predict the behavioral outcome of an alimentary odorous stimulus.

Some information about the internal state of the subjects could be deduced from the level of electrical activity in central areas. The mitral cell unit discharge was significantly correlated to the integrated MU activity in the medial hypthalamus (but not in the paraventricular nucleus), to that in the reticular part of the thalamus, and, on the first stimulation only, to that in the vicinity of the dorsal noradrenergic bundle. The unit discharge in the granular layer was correlated to the MU activity in the lateral cortico-habenular tract, where fibers traveled from the olfactory cortex to the thalamus. In spite of the great variability of the OB units and of the MU activity in central sites, the existence of such functional correlations was the most permanent feature in the data.

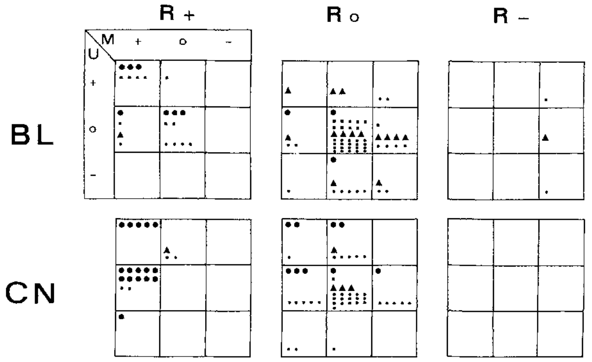

Figure 4. Simultaneous unit (U), multiunit (M) and respiratory responses (R) in behaving rats stimulated by isoamyl acetate (IA) (•) or food odor (F). The F+ (●), F(+) ( ) and F-(▲) symbols correspond to the cases when the pellet was eaten spontaneously, accepted if presented at the mouth or refused actively. The +, 0 and − signs indicate positive, null and negative responses.

The multiunit activity was collected from the mitral cells (BL) or from central areas (CN). As an example, a single stimulation with food odor followed by pellet refusal was accompanied by abated respiration and decreased multiunit activity in the olfactory bulb, while no response could be detected at the unit level.

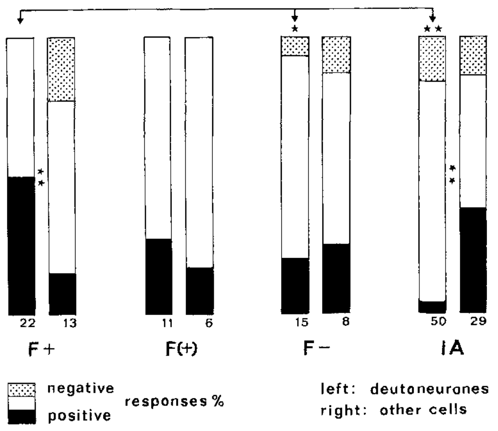

Figure 5. Patterns of unit responses in the OB of behaving rats. The F+, F(+), F− and IA abbreviations are the same as in figure 4. The number of responses is indicated under each column. The stars represent the probability of the difference between two columns: one star = 0.05%, two stars = 0.01%.

Appraisal of the neurophysiological data

At the multiunit level. Since the mitral cell MU activity was selected within the same bandpass as spikes, the common sense interpretation of the MU responses in various internal states is that they correspond to the facilitated processing of the relevant olfactory signals. This supposes that the ascending activity which is coding these signals is integrated to central influxes at the OB level. Histological evidences of specific spatial patterns coding the olfactory information at this stage are obtained on a time-scale compatible with that of the MU records in behaving rats. But the spatial scale is seemingly sharper than the resolving power of the method: the MU signal was summated in $0.02\ \mathrm{mm}^2$ at least, with a time-constant of several hundred milliseconds, smoothing the ascending activity patterns and the centrifugal influences. The MU responses appear as an activation evenly distributed throughout the mitral cell layer. They constitute an instantaneous probe for the prevailing centrifugal effects in the OB, as shown after partial or complete bulb deafferentation.

The MU recording is also adapted to the extraction of spatial invariants at the scale of multistage activated circuits, thus extending functional neuroanatomy to the behaving model. Accordingly, the EEG patterns at the OB surface are unlikely to code the specific olfactory information as such. They could result from an heterogeneous distribution of neuron activity or centrifugal endings in the OB layers. But the successful matching of expected and incoming specific patterns[12] could well trigger propagated oscillations at the wavelength of the beta and gamma EEG activity. The functional unit of this phenomenon should be an extended reverberating loop, and not a glomerule or a column, supposed to be functional units for the OB processing of information.

At the unit level. Part of the high spatial resolution proper to unit data is lost, because the recording methods in behaving animals are not adapted to precise neuron identification. In spite of that, the opposite response patterns obtained in the deutoneuron and granular layers support the initial interpretation of the nutritional modulation: a central suppression of the granular inhibitory influences on the mitral cells[36]. Thus processing the data in 500 ms bins preserved the functional correlates between the MU and unit levels. Moreover, it suggested that the same olfactory information could be processed in the mitral cell layer with the same efficiency, but not necessarily through exactly the same individual cells.

The variability of unit responses in unrestrained animals has been noted by several authors[19,20]. It could be the attribute of neurons with multiple inputs, involved in a complex circuitry. The signal/noise ratio at the relay between two neuronal populations as a whole is possible better than the one effective in a single unit. The spatial OB pattern supposed to code for one olfactory cue should be then defined with some fuzziness at the unit scale.

Another possibility is that the 500 ms resolution confounded the specific olfactory processing to some extent, and that we still have to determine the relevant parameters in the OB neuron discharge. Data from acute preparations in rodents[28] and in fish[30], treated with special attention to the temporal organization of the discharge, underlined its importance in the olfactory processing. The contrast between the mean firing rate of OB units during inspiration and expiration is seemingly a more pertinent feature in the awake restrained rabbit[10] than in the behaving rat. The data processed in 500 ms bins have also been treated with a time resolution equal to one fifth of each respiratory cycle. The results, still to be published, allow the characterization of the activity of each bulb unit by a periodic function involving two intensive and two temporal parameters. They confirm and generalize previous data on the respiratory-olfactory correlations, including discrepant data.

Records from neighboring cells present the mitral cell layer as an anisotropic electrical network, with a linear mesh of two units at least, invaded by steady oscillations of respiratory frequency. The few responses analyzed so far occur as clearcut changes in one or several descriptive parameters; they seem to be reproducible and habituable. In this way, it is possible to separate what is the specific treatment of the olfactory cues, including selective attention, occurring in the first cycles with odor, from the later non-specific activation, triggered back by the stimuli eliciting food consumption. Therefore the resolutive level of single neuron records in the OB is possibly smaller than the functional units for the olfactory coding, and sharper than necessary to study it as a function of space. Nevertheless it is irreplaceable for the necessary interpretation of activity as a function of time.

Functional correlates of the olfactory neuronal activity

In the behaving rabbit, the detection and the complete analysis of an expected olfactory stimulus, up to the decision to act, took place within one respiratory cycle[20]. Most sequences of odor-guided behaviors were considerably longer. From an informational point of view, a sustained electrical activation of OB units and of large neuronal circuits was likely to represent persisting relevant signals, in particular states of behavioral arousal. The activation at the multiunit level, and at the unit scale, in terms of probability, was indeed concomitant with exploratory sniffing and with odor-elicited sniffing; it could be maintained from the orientation towards the dispenser-cup till the pellet was consumed. The nutritional modulation of the OB mitral cell responses had the same time-course as the spontaneous speed of mastication, on a similar nutritional schedule[23]. The time-course was also compatible with that of the prandial release of insulin, a neuroendocrine mechanism elicited by olfactory and other alimentary stimulations[26]. One can mention that periodical increases in the MU activity of the ewe's hypothalamus preceded the release of luteinizing hormone[48]. Thus prolonged electrical activity, observed at any level of organization in heterogeneous neuronal networks, sometimes as propagated oscillations, could be assumed to facilitate both motor and neuroendocrine effectors in odor-guided behaviors.

Concluding remarks

From the above considerations, it appears that the structural organization of the central nervous system, as defined by the anatomy, is not necessarily superposed on the one operating from the neurophysiological point of view, especially in the behaving model. The nested functional units have to be defined in terms of their spatial and temporal dimensions, and to be studied on an accurate scale, which might call for complementary methods. As long as these basic principles are maintained, neuro-behavioral correlates can be observed in various organizational levels of the olfactory system. Moreover, it is possible to understand events at one spatio-temporal degree from what is known about the next degree on the scale. Simply, the events will be observed with some undeterminism, if the recording and analyzing methods are not adjusted accordingly, whenever the resolution of the study is reduced. This character is shared with experimental models in any other field of the sciences.

The consistency of simultaneous neuronal and behavioral events merely illustrates the projection of the same reality onto the parallel planes of physiology and psychology. Finally, one could object that trying to construct bridges between the two phenomenologic levels is reductionism, in one direction, and irrationalism, in the other. In the present state of the art, it seems at least reasonable to predict that the neurophysiology of unpredictable events would progress further, due to the construction of intermediate arcs between the most extreme levels of organization in the behaving subject.

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