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Taste-acceptance and taste-aversion reflected by behavioral manifestations in man and animals

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ABSTRACT - Sensations and feelings, aroused by sensory stimuli are inaccessible to direct measurements. For collaborative human examinees, above verbal age, psychophysical testing methods can be used, in order to assess stimulus-identification as well as semi-quantitative estimates reflecting on intensity and pleasurability (hedonics) of sensations.Taste- and odor-cues, for both man and animals, are known to be polarized between "pleasant" and "aversive" qualities. These hedonic differences were found to release in man distinct and differential, fixed oral and facial motor-behaviors. Since infants at perinatal age, prior to any food-intake experience, were found to respond differentially to sweet and bitter tastes, these behavioral displays can be seen as innate and probably even inherited competencies of the nervous system. Observations on infants, born with severe developmental malformations of the forebrain revealed identical reactivity to that found in the normal termborn neonate. It is, therefore, evident that taste-induced behaviors are primarily controlled by the brainstem. Further experiments revealed,that odor stimuli too can also trigger differential facial expressive behaviors. These reactions were termed: GUSTOFACIAL- and NASOFACIAL-REFLEXES, respectively. Using a multidisciplinary approach, both psychophysical and facial responses of young healthy human examinees were simultaneously recorded. These studies evinced that taste- and odor-induced facial expressions are as sensitive hedonic indicators as are semiquantitative psycho-physical hedonic estimates. Later studies revealed, that nonhuman primates, (monkeys and apes), as well as other mammals, and some other animal species display taste-induced oral or facial responses, similar and analogous to the human gustofacial reflex.

Events occuring in the external or internal environment of a living organism become relevant sensory stimuli, if and when the organism is, - according to its genetic makeup - equipped with adequate sensory apparatuses to detect such events. Even most delicate changes in different kinds of energy (chemical, thermal, mechanical or radiant) can be detected by receptor cells, specialized for, or tuned-to be excited by such changes. Complex mechanisms are responsible for the transduction of the detected event into electrochemical signals, which then compose a sensory message. This travels along dendrites, axons and synapses.

Messages generated and encoded at the periphal receptor, are transmitted to the central parts of the nervous system, to be decoded and evaluated.

Some of the sensory pathways terminate at lower levels of the central nervous system (CNS) and may release at these levels reflectory, involuntary reactions of both motor- and secretory- types. One may refer to these as to "simulus-dependent somatic manifestations". Some other pathways transmit the incoming message up to cortical levels of the brain, where the information is transformed to sensory experience, evaluated by cognition releasing sensations and feelings, which are psychological processes.

In rather general terms: already at the lower brain-levels the incoming sensory information is evalutaed according to the following criteria: a) quality, b) intensity, c) localisation (in the body or in the external environment) and d) according to its "pleasure-displeasure" (hedonic), motivational tone. Therefore, both stimulus-dependent somatic manifestations as well as the elicited "sensations" or "feelings" are in accordance with these criteria (1).

It should be stressed, that sensations and feelings are taking place in the organism's most private domain. It follows that no direct measuring techniques are applicable to assess in quantitative terms feelings and sensations. Still for the sake of the investigation of sensory processes in man and animals, or for clinical or even industrial or commercial purposes there is often a need to gain insight in the world of sensations of fellow human beings or even in that of animals. In order to meet these needs and requirements a variety of indirect methods were developed, which can indicate feelings and sensations and reflect on them by "semiquantitative" measures. There are several approaches by which one can gain an insight into the world of sensations, it is adventageous to list some of them:

A) Assessements based on verbal report (psychophysical testing-rocedures). In a testing-situation of this kind well defined sensory stimuli are presented to the examinee and verbal reports on the stimulus-dependent cognitive processes are recorded. Such tests may involve verbal labeling ("identification") of the stimulus as well as semiquantitative estimates of the perceived sensation's intensity or hedonics. Such estimates can be requested, using different kind of analog scales. Evidently, all kinds of such psychophysical methods are applicable only when reasonably cooperative human subjects, above verbal age, are tested.

B) Assesement-methods based on observation, documentation and direct measurements expressible in quantitative terms of a variety of stimulus-dependent somatic manifestations (s.a. bioelectrical phenomena, stereotyped fixed, reflex-like behaviors of either somato- or visceromotor or even secretory type), occuring within a reasonable span of time after stimulus-application. Such methods are equally applicable in testing human examinees (of all age-groups) as well as in animals.

C) In testing ingestive behavior, aiming in particular the assessement of preference for one kind of food over another, consumatory behavior can be determined, by measuring food or beverage items consumed over a fixed span of time in choice situation.

Investigating human reactivity to sensory stimuli one may find a multidisciplinary approach of special interest. This should be based on simultaneous recording of psychophysical responses and that of stimulus-dependent somatic reactions. An approach of this kind can prove as a tool, providing multiple information for a better insight to the "sealed" world of human sensations and feelings.

As to the "hedonic" (pleasure / displeasure) aspect of the incoming sensory information, it should be emphasized that all sensory stimuli have a certain hedonic aspect; still it seems that chemical ones, in general, and those of gustation and olfaction, in particular, carry much more accentuated hedonic note than visual, acoustic, thermic or tactile ones. Moreover, it should be stressed, that taste and smell stimuli are hedonically polarized. This means that there are tastes and odors which are hedonically positive irrespective of their concentration (strength); others are hedonically negative in all concentrations. Between these two extremes there is an interim category of chemostimulants which have from the pleasure aspect a note of "neutrality" or "indifference" (2, 3).

This polarity among tastes and odors is most impressively reflected by the widely spread methaphoric use of the words "sweet", "honey", "savory", on the one hand and that of "bitter", "acid", "putrid" "stinky" on the other, found in almost all human languages. By the metaphoric use of labels, originally connected to the domains of gustation and olfaction man is able to refer to broad concepts of "good", "pleasant", "desirable", or "benevolent" in contrast to those of "bad" "depressing", "dangerous", "malevolent", "not-wanted". In other words, one may say that there is profound hedonic, motivational and emotional weight by which both gustatory and olfactory experiences are characterized for the sensory sphere of man and most probably also in that of many animal species.

Finally, it should be mentioned that in the psychobiological context the verbal labels "pleasure" and "displeasure" might be somewhat misleading. Therefore it might be more appropriate to differentiate between stimuli which convey a message of "acceptable" or "usable" and those which convey the message of "to be avioded" or "potentialy harmful". Sensory stimuli, which do not induce any particular reaction or response can be labeled as "indifferent" ones. The introduction of these terms here seems to have a particular relevance in order to differentiate most clearly between the concepts of "good" and "bad" in their philosophical, moral or ethical connotations and the use of the verbal labels "good" and "bad" in in a purely biological context, refering to "survival" or to the "maintanence of homeostasis".

As to our experience with behavioral manifestations which indicate acceptance, indifference and aversion to taste- and odor- stimuli it should be mentioned, that when we tested gustatory functions in human

examinees by a rather simple psychophysical procedure (4), we became aware of the fact that intraoral presentation of water, sweet, sour and bitter tasting solutions in different concentrations elicited rather stereotyped fixed facial expressions, which were distinct, and differred primarily according to the quality of the presented stimulants, while concentration of the stimulus was of secondary or even negligable importance. These facial displays were found to be independent of age, sex, ethnic- or cultural- background or health-state of the testees. The most typical features observed, can be summarized as follows:

1) The intraoral presentation of distilled water induced no specific facial expressive movements, except some quick swallows.

2) The presentation of sucrose was always followed by lip-licking or smacking movements, often followed by a fleeting smile and an expression a satisfaction and relaxation appeared typified with a quiet gaze and open eyes.

3) Presentation of citric acid was followed by a rather marked nose-wrinkling, eye-closure, repeated blinking and a marked pursing of the lips (the s.c. Darwin's purse). These features were sometimes followed by slight head-turning movements. This facial display can be characterized as that of mild disgust and aversion.

4) Presentation of the bitter tasting quinine hydrochloride in all five concentrations used (lowest 0.00007 M) induced rather tight closure of the eyes, followed by blinking, depression of mouth-corners, followed by gaping, head turn and even head- shaking. Sometimes retching or drooling of saliva were also observed.

5) Presentation of salt (NaCl) solutions induced two different types of responses. In the near to threshold concentrations the responses were resembling either that of water, or that triggered by the weakest concentration uf sucrose. Higher concentrations induced facial responses resembling those induced by lower concentrations of citric acid. Therefore in the subsequent studies the use of salt solution was excluded.

A cartoon depicting the typical facial displays observed in response to intraoral stimulation with water, sweet sour and bitter are shown in Fig.1.

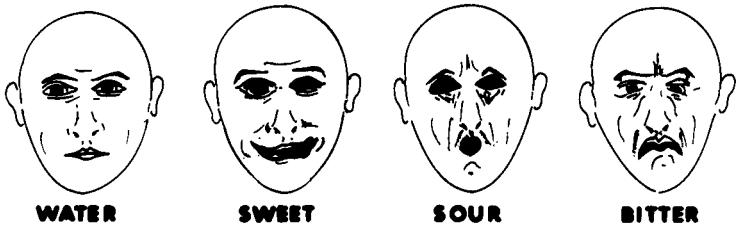

Fig. 1

Impressed by the stereotyped and rather rigid occurance of these facial displays in a rather variegated and large sample of examinees, we assumed that these responses may be innate or probably even inherited sensory-motor coordinations. In order to test this hypothesis we started our experiments on neonate infants. These infant studies, reported in detail (5, 6, 7,) clearly evinced, that the perinatal human infant, tested about 3 -10 hours after birth, prior to any (breast- or bottle-) food-intake experience is, in a most competent manner, able to display the same differential facial features, we have seen in the adult examinees.

Some examples of the neonates' facial displays at rest (1) and in response to water (2), to sweet taste (3) to sour taste (4) and to bitter taste (5) are presented in Fig.2

Having the rare opportunity of testing neonates, born with severe developmental malformations of the brain (anencephalic and

hydronancephalic neonates), also prior to their first feeding experience we could conclude, that the observed facial expressive responses are primarily controlled at brainstem level, not involving cortical structures (5,7). These evidently innate, non-acquired (or learned) responses could, therefore, be named GUSTO-FACIAL REFLEX. Further observations evinced, that this reflectory response does not recede with age, neither is it dependent on positive visual reinforcement or on mental and intellectual development (7).

Since the video-recorded facial displays were found to be easily read and interpreted as expressive signs of acceptance, indifference or aversion respectively, both by trained and untrained observers, a notational-system was developed, to analyze them, according to a list of 25 typical motion-features. It could be concluded, that the facial displays emitted by the neonates in response to different tastes at different intensities,

serve as tools of nonverbal communication between infant and the caretaker adult (8). The gustofacial reflex was later used to demonstrate classical conditioning in the human infant in perinatal age (9).

In further studies, food-related odor stimuli, in addition to gustatory cues were also found to unlock analogous facial displays (6). Since in these experiments too another hydro-anencephalic neonate was tested it could be concluded, that these reactions are also innate, probably inherited ones and primarily controlled by lower brain-structures. The odor induced facial responses were named NASOFACIAL REFLEX. These reflectory, odor-induced differential displays were also found not to recede with age, and independent of visual reinforcement or mental faculties (7).

Based on these and other experiments a multidisciplinary approach was developed, to investigate the correlation between the cognitive, psychophysicl estimates of young, healthy adult examinees with the hedonic ratings ascribed to their taste-and odor-induced facial expressions. This multidisciplinary technique is based on simultaneous recording of psychophysical and somatic responses, with special focus on two types of the latter ones: the facial-expressive responses as well as heart-rate acceleration (10). In these studies a sizable correlation was found between the psychophysical hedonic self-estimates and the mean semiquantitative ratings of the hedonic message conveyed by the examinees facial expressions (scored by two independent evaluators in a double-blind setting). The multidisciplinary approach yielded a comprehensive insight into problems of critical evaluation of odor and taste-hedonics as reported in several studies (11).

Another line of our experiments intended to investigate taste- and odor reactivity in patients affected by different diseases, both somatic and

Fig. 2

psychic or mental ones. Autistic patients are often considered unable to distinguish between pleasant and aversive external stimuli. By their facial displays autistic children and adolescents were found to be able to express their likes and dislikes toward different tastes and odors, in a comparable manner to facial reactions, displayed in response to the same stimuli by their normal, healthy agemates (12). Demented elderly, among them several, diagnosed as having Alzheimer's disease, were also found to display differential facial expressions to tastes and odors, parallel to those observed in their non-demented agemates (13). Patients with affective disorders (depression) were found to display severely reduced facial "acceptance"- responses towards sweet taste, still able to give adequate psychophysical estimates to the same taste-quality (14). Addiction to heroin was found to modulate more the facial expressive responses than the psycho-physical estimates (15). Patients affected by the heredo-degenartive diseases: Usher's syndrome and familial dysautonomia were also tested, and were found to display differential facial behaviors in response to different taste- and odor- qualities (16, 17).

Animal studies evinced, that different species, representing different classes and families of the Animal Kingdom also emit diferential stimulus-dependent sensorimotor reactions, analogous to those of man. The pioneering observations of Grill and Norgren on taste-reactivity in neurologicaly intact as well as in decerebrated and decorticated rats were carried out briefly after the above quoted infant studies have been published (18,19). These findings were not only the first to show that taste-acceptance and taste-aversion are reflected by animals by orofacial motor coordinations, but the brain-ablated animals in these experiments, represent a most relevant model for the reactivity observed by us in neonates, born with severe developmental brain-malformations.

Our own subsequent animal studies evinced differential oral- or facial-motor displays in neonate rats and rabbits, in adult cats as well as in the hetchlings of the domestic chick and even in a sweet-water prawn, (20,21,22,23,24,25). Of very special interest were our findings on the taste-induced facial displays in nonhuman primates. These studies evinced a most striking similarity and analogy between facial behaviors displayed by a variety of monkey- and ape- species and the repertoire of motion-coordinations composing the human gustofacial response (26,27).

In the context of our animal studies it should be noted that in one of our extensive studies gustatory stimuli were found to induce quality-specific arousal responses in the electro-corticogram of the awake rabbit (28). This arousal-reaction was found to be in good correlation with results of a taste-preference study using consumatory-responses. In future studies the correlation between human psychophysical, behavioral and encephalo-graphic responses induced by taste and smell stimuli sholud be nvestigated.

In summary: our studies clearly indicate, that elicitation, documentation and appropriate analysis of innate, non-acquired, most probably even inherited, taste- and odor-induced oral and facial expressive motor coodrinations can be seen as most reliable and valid indicators of taste- and odor- hedonics in human examinees at different ages, and in different health conditions. The experimental setting is a rather simple one, and the procedures can easily be acquired and handled. The simultaneous indication of stimulus-induced, transient heart-rate acceleration, may add a further parameter in sensory-testing of taste- and odor cues. Methods of behavioral testing are applicable to animal-studies as most powerful tools to assess "like" and "dislike" for chemical stimuli in different animal species too.

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