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THE PRIMATE AMYGDALA: NEURONAL REPRESENTATIONS OF THE VISCOSITY, FAT TEXTURE, TEMPERATURE, GRITTINESS AND TASTE OF FOODS

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Abstract—The primate amygdala is implicated in the control of behavioral responses to foods and in stimulus-reinforcement learning, but only its taste representation of oral stimuli has been investigated previously. Of 1416 macaque amygdala neurons recorded, 44 (3.1%) responded to oral stimuli. Of the 44 orally responsive neurons, 17 (39%) represent the viscosity of oral stimuli, tested using carboxymethyl-cellulose in the range 1–10,000 cP. Two neurons (5%) responded to fat in the mouth by encoding its texture (shown by the responses of these neurons to a range of fats, and also to non-fat oils such as silicone oil ($(Si(CH_3)_2O)_n$) and mineral oil (pure hydrocarbon), but no or small responses to the cellulose viscosity series or to the fatty acids linoleic acid and lauric acid). Of the 44 neurons, three (7%) responded to gritty texture (produced by microspheres suspended in cellulose). Eighteen neurons (41%) responded to the temperature of liquid in the mouth. Some amygdala neurons responded to capsaicin, and some to fatty acids (but not to fats in the mouth). Some amygdala neurons respond to taste, texture and temperature unimodally, but others combine these inputs. These results provide fundamental evidence about the information channels used to represent the texture and flavor of food in a part of the brain important in appetitive responses to food and in learning associations to reinforcing oral stimuli, and are relevant to understanding the physiological and pathophysiological processes related to food intake, food selection, and the effects of variety of food texture in combination with taste and other inputs on food intake. © 2005 Published by Elsevier Ltd on behalf of IBRO.

Key words: appetitive learning, Pavlovian conditioning, obesity, food intake, reward.

The amygdala is implicated in emotion and motivation by lesion, single neuron recording, and neuroimaging investigations (Sanghera et al., 1979; Nishijo et al., 1988a; Davis, 1994; Francis et al., 1999; Rolls, 1999; Schoenbaum et al., 1999; LeDoux, 2000; Rolls, 2000). Part of the function of the amygdala in motivation and emotion appears to be in associating previously neutral (e.g. auditory or visual) stimuli to primary (unlearned) reinforcers such as taste and somatosensory including painful stimuli (Davis, 1994; Rolls, 1999, 2000; LeDoux, 2000), and in primates, for example, reward devaluation learning depends on the amygdala (Murray et al., 1996). This associative function (Rolls and Treves, 1998) implies a representation of primary reinforcers such as the taste of food, and indeed taste neurons have been described in the amygdala (Sanghera et al., 1979; Nishijo et al., 1988a,b; Scott et al., 1993; Yan and Scott, 1996) and taste responsiveness in the human amygdala (O'Doherty et al., 2001). Almost nothing is known, however, about whether aspects of food other than taste and smell are represented in the amygdala. The texture of food is important in its palatability and acceptability (Bourne, 2002, consider e.g. damp cereal or potato chips), and temperature may also be important (Zellner et al., 1988). We describe here for the first time the responses of primate amygdala neurons to oral texture and temperature stimuli, and show that they are combined in some neurons with responsiveness to the taste of food. The investigation was performed in macaques in order to make it as relevant to understanding the operation of this system in humans as possible, and in the context that the taste system is differently connected in rodents and primates, with taste pathways in primates to the amygdala only after cortical processing (Norgren, 1984; Rolls et al., 2003). Understanding the factors that determine the palatability of food is currently of great interest, given the role of palatability in the control of food intake, and the rapidly increasing incidence of obesity which is accompanied by serious health risks (Berthoud, 2003; Steinberger and Daniels, 2003). The factors investigated included the texture of food as reflected by viscosity (tested parametrically with a viscosity series made with cellulose); oral fat; oral fatty acids which might signal the presence of fat in the mouth if salivary lipase was present (Gilbertson, 1998); oral texture as manipulated by inert microspheres; oral temperature; taste; and the effects of capsaicin, an oral irritant present in a number of foods.

EXPERIMENTAL PROCEDURES

Subjects

The recordings were made in three hemispheres of two rhesus macaques (*Macaca mulatta*; one female weighing 2.6–3.3 kg and one male weighing 6.1–6.7 kg). To ensure that the macaques were willing to ingest the test foods and fluids during the recording sessions, they were on mild food (150 g of nutritionally balanced mash plus fruits, boiled chicken eggs, nuts, seeds and pop corn) and fluid (1 h/day *ad libitum* water) deprivation, in that both were provided after the daily recording session. The monkeys showed steady increases in bodyweight. All procedures, including preparative and subsequent ones, were carried out in accordance with the National Institutes for Health Guide for the Care and Use of Laboratory Animals, and were licensed under the UK Animals (Scientific Procedures) Act, 1986, and were designed to minimize

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Abbreviations: BJ, blackcurrant juice; CMC, carboxymethylcellulose; CO, coconut oil; GR, gritty texture stimulus; LaA, lauric acid; LiA, linoleic acid; MO, mineral oil; SaO, safflower oil; SC, single cream; SiO, silicone oil; VO, vegetable oil.

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the number of animals used and maximize their welfare by adopting, for example, group housing, and environmental enrichments.

Recordings

Recordings were made with epoxylite-coated high impedance (2–10 MΩ at 1 kHz; Frederic Haer & Co., St. Bowdoinham, ME, USA) tungsten microelectrodes from single neurons in the amygdala, which included areas in which taste responses have previously been described (Sanghera et al., 1979; Nishijo et al., 1988a,b; Scott et al., 1993), using neurophysiological methods as described previously (Scott et al., 1986a,b; Rolls et al., 1990, 1999, 2003; Verhagen et al., 2003). The signal-to-noise ratio was typically 3:1 or higher as illustrated in Fig. 4. The data were collected using a Datawave Discovery Inc. (Tucson, AZ, USA) system which digitized the signal (12 bit, 16 kHz) for 8 s after stimulus onset. The spikes were sorted off-line using the cluster cutting method provided with the Datawave system, and this procedure was straightforward as the data were collected with single neuron microelectrodes which typically recorded from only one neuron at a time. To prevent visual associative input from evoking neural activity, we prevented the monkeys from seeing the stimuli and experimenter by a view-obstructing screen.

Localization of recordings

X-radiography was used to determine the position of the microelectrode after each recording track relative to permanent reference electrodes and to the anterior sphenoidal process, followed by microlesions on selected tracks and reconstruction from histological sections of the brain using the methods described by Feigenbaum and Rolls (1991).

Stimuli

The neurons of the amygdala were tested for their responsiveness to the set of taste, viscosity, gritty, oily stimuli, and capsaicin, at room temperature (23 °C), and also the set of temperature stimuli as shown in Table 1. Details of the rationale for the choice of the stimuli are given by Rolls et al. (2003) and Verhagen et al. (2003). Distilled water at 23 °C was one member of the temperature series (T23), and with its viscosity of 1 cP was also one member (V1) of the viscosity series. For an additional comparison, the neuronal responses were tested to 20% blackcurrant juice (BJ; Ribena SmithKline Beecham), because with its complex taste and olfactory components and high palatability it is an effective stimulus when searching for and analyzing the responses of cortical neurons (Rolls et al., 1990). The viscosity series was made with carboxymethylcellulose (CMC; Sigma; high viscosity, Mw 700,000, dialysed, code C5013), a virtually odor- and tasteless thickening agent used widely in the food industry (see Rolls et al., 2003). The gritty stimulus consisted of hard (Mohs scale 5) hollow microspheres (Fillite grade PG, with 87% having a diameter with the range 100–300 μm; Trelleborg Fillite, Runcorn, UK) made up in methylcellulose to have a measured viscosity of 1000 cP (100 g of Fillite PG was added to 4.7 g of CMC in 500 ml of water). To test for and analyze the effects of oral fat on neuronal activity, a set of oils and fat-related stimuli was included. The triglyceride-based oils consisted of vegetable oil (VO; viscosity 55 cP at 23 °C), safflower oil (SaO), and coconut oil (CO). Single cream (SC; 18% fat, viscosity: 12 cP; Coop brand, pasteurized) was used as an exemplar of a natural high fat content food of the type for which we wished to examine the neural representation and sensing mechanisms. Four of the orally responsive neurons were tested with mineral oil (MO), a hydrocarbon mixture with a viscosity of 25 cP. All the neurons with fat-related responses described in this and our earlier study (Rolls et al., 1999) responded well to SC. As Gilbertson (1998) had reported differential effects in isolated taste cells to linoleic and lauric acid (LaA) *in vitro*, suggesting that the gustatory modality might be involved in orally sensing fat, we included (Verhagen et al., 2003) in the stimulus set free linoleic (LiA; 100 μM) and LaA (100 μM) sodium salts (Sigma), as well as oils rich in conjugated LiA (SaO, 68–83%, 50 cP; Aldrich), and LaA (CO, 45–50%, 40 cP; Sigma; Weiss, 1983; Wills et al., 1998). All fatty oils were kept in the dark under N_2 at 4 °C to avoid oxidation.

To investigate whether the neurons responsive to fat-based oils were in some way responding to the somatosensory sensations elicited by the fat, stimuli with a similar mouth feel but non-fat chemical composition were used. These stimuli included paraffin/MO (pure hydrocarbon, viscosity 25 cP at 23 °C, Sigma), and silicone oil (SiO; $Si(CH_3)_2O)_n$, 10, 100 or 280, and 1000 cP (Brookfield viscometer calibration fluid except 280 cP; Aldrich).

The temperature series was provided by water at 10 °C (chosen as the cold stimulus; commercial cold drinks are served at 6 °C), at 42 °C (warm/hot but not noxious), 37 °C (body temperature), and 23 °C (room temperature).

The capsaicin was made up as a 10 μM solution (containing 0.3% ethanol). This is approximately 15 times the human recognition threshold of 0.66 μM (Szolcsanyi, 1990).

The monkeys' preference for the stimuli was measured objectively by an acceptability rating, where +2 indicates that the macaque reached for the stimulus and placed it in the mouth, +1 indicates that the macaque actively opened the mouth to receive and swallow the stimulus, 0 indicates neutrality in which the stimulus was accepted only passively by mouth opening, −1 indicates that the macaque closed the mouth to try to reject the stimulus; and −2 indicates that the macaque used the hand to push away the stimulus from the mouth (Rolls et al., 1977, 1989). This rating scale has been extensively validated by comparison with neuronal activity in the lateral hypothalamus and orbitofrontal cortex in studies of sensory-specific satiety, in the sense that there was a close relation found between the acceptability rating and the neuronal response in these regions, as shown in previously published data (Rolls et al., 1986, 1989; Critchley and Rolls, 1996). The ratings were repeated a total of four (or for one macaque 5) times by two independent investigators, with a high correlation between the ratings given by the two investigators ($r=0.85$, $n=25$, $P<10^{-7}$).

Stimulus delivery

The general method for stimulus delivery and accurate stimulus onset marking (Rolls et al., 1990) was modified by introducing repeater pipettes (Verhagen et al., 2003). For chronic recording in monkeys, a manual method for stimulus delivery is used because it allows for repeated stimulation of a large receptive surface despite different mouth and tongue positions adopted by the monkeys (Scott et al., 1986a,b). The stimulus application volume was 200±10 μl, because this is sufficient to produce large gustatory neuronal responses which are consistent from trial to trial, and yet which do not result in large volumes of fluid being ingested which might, by producing satiety, influence the neuronal responses (Rolls et al., 1989, 1990).

The monkey's mouth was rinsed with 200 μl T23/V1 (water) during the inter-trial interval (which lasted at least 30 s, or until neuronal activity returned to baseline levels) between taste stimuli. Due to the tenacious nature of the oral coating resulting from the delivery of cream or of oil, and also for gritty and capsaicin, four 200 μl-rinses with T23/V1 were given, while allowing the subjects to swallow after each rinse. For V1000 and V10,000, we used two such rinses. All the stimuli shown in Table 1 were delivered in permuted sequences, with the computer specifying the next stimulus to be used by the experimenter. The spontaneous firing rate of the neuron was measured from trials in which no stimulus delivery occurred.

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