NeuroImage 48 (2009) 258–268

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Different representations of relative and absolute subjective value in the human brain

Fabian Grabenhorst [1], Edmund T. Rolls *

University of Oxford, Department of Experimental Psychology, South Parks Road, Oxford OX1 3UD, UK

ARTICLE INFO

Article history:
Received 12 February 2009
Revised 4 June 2009
Accepted 18 June 2009
Available online 25 June 2009

Keywords:
Neuroeconomics
Emotion
Olfaction
Reward
Decision-making
fMRI
Pleasantness
Affect

ABSTRACT

Relative reward value is important for the choice between a set of available rewards, and absolute reward value for stable and consistent economic choice. It is unclear whether in the human brain subjective absolute value representations can be dissociated from relative reward value representations. Using fMRI, we investigated how the subjective pleasantness of an odor is influenced by whether the odor is presented in the context of a relatively more pleasant or less pleasant odor. We delivered two of a set of four odors separated by a delay of 6 s, with the instruction to rate the pleasantness of the second odor, and searched for brain regions where the activations were correlated with the absolute pleasantness rating of the second odor, and for brain regions where the activations were correlated with the difference in pleasantness of the second from the first odor, that is, with relative pleasantness. Activations in the anterolateral orbitofrontal cortex tracked the relative subjective pleasantness, whereas activations in the anterior insula tracked the relative subjective unpleasantness. In contrast, in the medial and midorbitofrontal cortex activations tracked the absolute pleasantness of the stimuli. Thus, both relative and absolute subjective value signals which provide important inputs to decision-making processes about which stimulus to choose are separately and simultaneously represented in the human brain.

Introduction

In economic decision-making, the brain needs to compute the subjective value of different goods in order for choices to be guided by preferences. Reward value is represented in the orbitofrontal cortex and connected areas (Rolls, 2005; Rolls and Grabenhorst, 2008) in that neuronal activity to taste, olfactory, flavor and visual food stimuli decreases as their reward value decreases to zero during feeding to satiety (Critchley and Rolls, 1996; Rolls et al., 1989), in that orbitofrontal cortex neurons are activated from brain-stimulation reward sites (Mora et al., 1980), in that orbitofrontal cortex brain-stimulation reward is decreased by feeding to satiety (Mora et al., 1979), and in that lesions of the orbitofrontal cortex impair reinforcement-related learning (Rolls et al., 1994), the ability to judge emotional and thus reward value (Hornak et al., 1996), and the subjective emotional experience of rewards (Hornak et al., 2003). Further, activations in these areas are correlated with the amount of money won or lost on an individual trial (O'Doherty et al., 2001a), and with the pleasantness (or subjective affective value) ratings made to many classes of stimuli, including taste, olfactory, flavor, thermal and visual stimuli (Grabenhorst and Rolls, 2008; Grabenhorst et al., 2007; Kringelbach et al., 2003; Rolls et al., 2008b). However, different types of value signal may be required for different types of decisions.

Relative reward value is important when choosing between a given set of rewards. A representation of relative reward value takes into account the current reward context in that it is influenced by the value of other rewards that are available. A related psychological phenomenon is positive contrast, in which animals work harder than on average for a high reward value just at the transition between the low and high reward value (Crespi, 1942; Mazur, 1998; Rolls, 2005). One example, investigated here, is that if a pleasant odor is preceded by an unpleasant odor, the pleasant odor may be perceived as more pleasant than usual. It has been shown that neurons in the orbitofrontal cortex encode the relative reward value of a food, responding for example to a symbol that indicates an apple if it was shown in a trial block where the other food was less preferred, and not responding to the apple symbol if it was shown in a trial block with a more preferred reward (Tremblay and Schultz, 1999). In addition, macaque dopamine neurons fire much more when large vs small rewards are given (Fiorillo et al., 2003).

Absolute reward value is important for stable and consistent economic choices (Lee, 2006; Muller et al., 2007; Padoa-Schioppa and Assad, 2008), and such a representation should not be influenced by the value of other available rewards. In a test of whether the absolute value of flavor stimuli is represented in the orbitofrontal cortex, some neurons coded for the value of a food reward independently of the value of the other reward presented on a given trial, and it was suggested that transitivity, a fundamental trait of economic choice, is represented by the neuronal activity (Padoa-Schioppa and Assad, 2008).

* Corresponding author. Oxford Centre for Computational Neuroscience, Oxford, and International Digital Laboratory, University of Warwick, England.
E-mail address: Edmund.Rolls@oxcns.org (E.T. Rolls).
URL: http://www.oxcns.org (E.T. Rolls).
[1] Present address: Department of Psychology and Helen Wills Neuroscience Institute, University of California at Berkeley, Berkeley, California.

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doi:10.1016/j.neuroimage.2009.06.045

It is unclear whether both absolute and relative value signals are expressed in the brain at the same time, and separately. The aim of the present study was to compare brain representations of absolute and relative subjective reward value, to investigate whether both are represented in brain regions such as the orbitofrontal cortex and related regions at the same time, and whether these neural representations are separable. We delivered two of a set of four odors separated by a delay of 6 s, with the instruction to rate the pleasantness of the second odor, and searched for brain regions where the activations were correlated with the absolute pleasantness rating of the second odor, and for brain regions where the activations were correlated with the difference in pleasantness of the second from the first odor, that is, with relative pleasantness.

Methods

Design

We used four odors, two pleasant (citral and vanillin) and two unpleasant (hexanoic acid and isovaleric acid). Two different odors were presented separated by 6 s on each trial, and the participants rated the subjective pleasantness and intensity of the second odor. Every possible combination of odors was presented, so that sometimes a second odor was preceded by an odor of similar pleasantness, and sometimes of different pleasantness. We were then able to show that activations in some brain regions were correlated with the relative pleasantness of the odors (as influenced by the preceding odor), and in other brain regions were related to the absolute value of the pleasantness ratings. Because these analyses were based on how subjective ratings of relative and absolute pleasantness are related to brain activations, this study directly addresses the question of how relative and absolute subjective value are represented in the brain. Contrast analyses were also performed to test whether activations to a given odor were greater if it was more pleasant than the first odor (pos diff) than if it was less pleasant (neg diff). As shown in the Results, from the ratings we were able to show that the pleasantness of a second odor was increased (relative to its average value) if it was preceded by an unpleasant odor vs a pleasant odor. Further, the unpleasantness of a second odor was greater if it was preceded by a pleasant vs an unpleasant odor.

Participants

Twelve healthy volunteers (7 male and 5 female, mean age 27) participated in the study. Ethical approval (Central Oxford Research Ethics Committee) and written informed consent from all subjects were obtained before the experiment.

Stimuli

The set of olfactory stimuli used was selected based on previous fMRI studies on olfaction (Rolls et al., 2003a). The pleasant odors were 1 M citral and 4 M vanillin. The unpleasant odors were hexanoic acid (10% v/v) and isovaleric acid (15%). The odors were made up in propylene glycol.

Stimulus delivery

A purpose-built continuous airflow ten-channel computer-controlled olfactometer was used to allow odor stimuli to be delivered in the MRI scanner (Rolls et al., 2003a). The control and metal components of the system are kept outside the scanner room, and the system is free of any auditory, tactile or thermal shifts that could cue the subject to the onset of odor delivery. The flow of clean medical air is controlled using a pressure regulator and flow meter. The air is directed using solenoid-operated valves controlled by the stimulus computer using TTL pulses to either a clean air wash bottle containing only solvent, propylene glycol, or to one of four other wash bottles each containing one odorant dissolved in the propylene glycol. Each wash bottle is connected by its own Teflon tube (to provide for low adhesion) to a single delivery nozzle placed within 1 cm of the nose to minimize dead space. The delivery nozzle provided two tubes, one for each nostril, to produce birhinal stimulation. The flow rate of the air supply was kept constant at 2 l/min such that the same minimal degree of tactile somatosensory stimulation was delivered throughout. The air line was on continuously by default, and was switched off only when the solenoid directed the clean air supply to another wash bottle so that an odorant could be delivered. This resulted in a system with no perceptible pressure change when the air was replaced during stimulus delivery by an odor for 2 s. This system was used in previous fMRI studies of human olfaction (Rolls et al., 2003a).

Experimental protocol

The experimental protocol consisted of an event-related interleaved design presenting in random permuted sequence the 12 different pairs of olfactory stimuli, which represented all possible combinations of the four olfactory stimuli in which the second and first odors were different. Each trial started at $t=0$ s with the first odor being delivered for 2 s accompanied by a visual label stating "Sniff first stimulus". There was then a 6 s period during which clean air was delivered. In this period at $t=7$ s a visual label was displayed stating "Rate stimulus". At $t=8$ s the second odor was presented for 2 s accompanied by a visual label stating "Sniff Rate stimulus". There was then a 6 s period during which clean air was delivered. At $t=16$ s the subjective ratings were made. The first rating was for the pleasantness of the second odor on a continuous (analogue) visual scale with markers from −2 (very unpleasant), through 0 (neutral), to +2 (very pleasant) at intervals of 1.0. The second rating was for the intensity of the second odor on a scale from 0 (very weak) to 4 (very intense). The ratings were made with a visual rating scale in which the subject moved the bar to the appropriate exact point on the continuous scale using a button box. (The values on this continuous scale were processed with an accuracy of 0.1 divisions on the scale.) There was 4 s for each rating. Subjects were pre-trained outside the scanner in the whole procedure and use of the rating scales. There was an inter-trial interval of 2 s. Each of the odors was presented in the second position 9 times, and the trials were delivered in a random permuted sequence. This general protocol and design have been used successfully in previous studies to investigate activations and their relation to subjective ratings in cortical areas (de Araujo et al., 2005; Grabenhorst et al., 2008a; Grabenhorst et al., 2007; Rolls et al., 2003a,b). These trials were interspersed with other trials in which decision-making was investigated as part of a separate investigation (Rolls et al., 2009b).

fMRI data acquisition

Images were acquired with a 3.0-T VARIAN/SIEMENS whole-body scanner at the Centre for Functional Magnetic Resonance Imaging at Oxford (FMRIB), where 27 T2* weighted EPI coronal slices with in-plane resolution of 3×3 mm and between plane spacing of 4 mm were acquired every 2 s ($TR=2$). We used the techniques that we have developed over a number of years (de Araujo et al., 2003; O'Doherty et al., 2001b), and as described in detail by Wilson et al. (2002) we carefully selected the imaging parameters in order to minimize susceptibility and distortion artefact in the orbitofrontal cortex. The relevant factors include imaging in the coronal plane, minimizing voxel size in the plane of the imaging, as high a gradient switching frequency as possible (960 Hz), a short echo time of 28 ms, and local shimming for the inferior frontal area. The matrix size was 64×64 and the field of view was 192×192 mm. Continuous coverage was