



Prefrontal mechanisms in preference and non-preference-based judgments



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ABSTRACT

When we decide between two options, we can make our decision based on what we prefer, (preference-based choice), or we can also choose based on which option we want to avoid more (non-preference-based choice). Most decision making research has examined preference-based choice but has not differentiated it from non-preference-based choice. The decision making process can be decomposed into multiple value-based computational processes, which are shown to be subserved by different regions in the prefrontal cortex (PFC). Here we show that the same decision circuits within the PFC are configured differently depending on whether decisions are made based on preference or non-preference criteria (decision rule). Activation in the dorsolateral PFC changed depending on both the values of the two choice options and decision rule. We also found that activation in the medial and lateral PFC was modulated linearly according to the difference in value between the two items and according to the value of the chosen item, respectively. In the medial and lateral PFC, there were distinct patterns of activation between dorsal and ventral regions: in dorsal regions value-related changes in activation were modulated by the decision rule, whereas in ventral regions activation patterns were not modulated. We propose that preference and non-preference decision rules represented in the dorsal PFC differently configure decision processes, resulting in context-specific significance being attached to the choice values represented in the ventral PFC.

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Introduction

When deciding what to eat, what vacation spot to visit or what course of action to take, we tend to decide based on our “preferences”. It is thought that preference for one choice over another signifies their respective ranks on a common scale (Lebreton et al., 2009). On the surface, liking may appear to be the reverse, or opposite of disliking. However, the way choices are presented can lead to differences in how decisions are made. For example, people tend to avoid risk when a choice is presented to them as a gain, but exhibit risk seeking behavior when it is presented as a loss (known as the ‘framing effect’) (De Martino et al., 2006; Tversky and Kahneman, 1981). It has also been observed that positive dimensions of options are given more weight when subjects are asked to select an option, whereas negative dimensions are considered when subjects are asked to reject an option (known as the

compatibility effect) (Meloy and Russo, 2004; Shafir, 1993). These findings suggest that decision processes are modulated by the contexts in which decisions are made. Humans are able to use different criteria or “rules” to make decisions; for example, a person may choose option A because he/she prefers it more than option B, but can also choose option A because he/she dislikes it less than option B.

It is possible to decompose decision making into multiple computational processes such as the representation of a decision problem, valuation of the different choices, and selection of an action based on valuations (Rangel et al., 2008). However, most research has focused on preference-based decision making, leaving it an open question how and at which stage of the decision process non-preference judgments might differ.

It has been shown that distinct regions of the prefrontal cortex (PFC) are involved in different critical computational steps in decision making (Rushworth et al., 2011). The ventral PFC is considered to be involved in valuation processes. While the ventromedial prefrontal cortex (vmPFC) is involved in encoding reward values of stimuli and comparative values of different choice options available, the ventrolateral prefrontal cortex (vlPFC) is thought to be involved in the assignment of reward and error values to specific choices, as well as the encoding of specific stimulus values (Arana et al., 2003; Boorman et al., 2009; McClure et al., 2004; Paulus and Frank, 2003; Plassmann et al., 2007; Rushworth et al.,

Abbreviations: PFC, prefrontal cortex; dlPFC, dorsolateral prefrontal cortex; dmPFC, dorsomedial prefrontal cortex; vlPFC, ventral lateral prefrontal cortex; vmPFC, ventral medial prefrontal cortex; fMRI, functional magnetic resonance imaging; MFG, middle frontal gyrus.

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2011). The dorsal PFC, on the other hand, is considered to be involved in a variety of functions thought to support cognitive control. The dorsomedial prefrontal cortex (dmPFC), including the anterior cingulate cortex (ACC) is shown to be involved in conflict monitoring, selecting actions based on goals, determining final choice and outcome evaluation, placing it as one of the final areas where choice values are represented for use by choice mechanisms (Grabenhorst et al., 2008; Taren et al., 2011; Venkatraman et al., 2009). The dorsolateral prefrontal cortex (dlPFC), by contrast, is shown to be involved in the maintenance of cognitive rules and goal-related information, integration and comparison of various value signals, value computations at the time of choice, and determining behavioral responses based on values, suggesting a role in integrating and organizing decision processes (Camus et al., 2009; Knutson et al., 2007; Plassmann et al., 2007, 2010; Taren et al., 2011).

We thus focused on the PFC and examined how preference- and non-preference-based decision rules affect the representation, comparison, and selection stages of the decision making process. Using functional magnetic resonance imaging (fMRI), we show that each step of the decision process is associated with activation in distinct regions within the PFC, and that while activation in the ventral PFC (vmPFC and vlPFC) changes according to value parameters regardless of the decision rules, activation in the dorsal PFC (dmPFC and dlPFC) is modulated by both value parameters and decision rule. The results suggest that preference and non-preference are not simply equivalent or opposing processes, but differentially affect multiple stages of the decision making process.

Materials and methods

Subjects

Eighteen healthy subjects (11 M/7 F, avg. age: 27.9 years, range 20–47, all right-handed) participated in the experiment. One participant was excluded from analysis due to failure to perform the task correctly. All subjects were asked to refrain from eating for at least 6 h before the experiment was conducted in order to increase saliency of stimuli and control for effects of satiety. Subjects were screened for general food preferences in order to ensure the applicability of stimuli (i.e. subjects were not vegetarian, vegan, and had no religious food restrictions). All the subjects gave written consent prior to the study. The study and procedures were approved by the ethics committee of the Graduate School of Medicine at the University of Tokyo.

Behavioral paradigm

Subjects performed a two-alternative forced choice task for food items. The stimulus set was comprised of pictures of 60 appetitive and 60 unappetitive foods, which were selected from a larger pool of images after being rated by an independent panel of subjects ($n = 8$) in a behavioral pilot study. Based on these ratings, images were selected so that there were approximately equal numbers of appetitive and unappetitive stimuli, and as well distributed as possible in terms of value. As the analysis was based on subjective ratings, the number of ratings was variable to a certain extent, but reflected the true rating of each individual subject as opposed to a predefined value categorized by the experimenter. A variety of foods were presented, ranging from very appetitive (e.g. grilled steak, desserts) to very unappetitive for most subjects (e.g. grilled insects, innards). Visual properties of stimuli were equalized in terms of dimensions, contrast, brightness and resolution. Each trial consisted of a presentation of a condition cue which also served as a fixation point (a green plus sign (+) in the 'Preference' condition, a red minus sign (−) in the 'Non-preference' condition, jittered length 4000–8000 ms) followed by a presentation of a pair of food pictures (6.5° visual angle) to the left and right of the fixation point (1000 ms) (Fig. 1a). Subjects entered their choices on a button box

using their right index or middle finger indicating their choice of the item presented on the left or right. In the Preference condition, subjects responded to the instructions—'Imagine that you have to eat one of the foods. Please choose which one you would rather eat now'. In the Non-preference condition, subjects responded to the instructions—'Please choose which one you would rather not eat now'. Subjects were instructed to strive for a balance in optimizing speed and accuracy of response.

Subjects were scanned during three sessions of 96 trials (48 Preference trials, 48 Non-preference trials). As such, 288 trials were presented, with 2 pictures viewed on each trial, resulting in a total number of 576 pictures being used; each picture appeared multiple times paired with different pictures. The sessions were organized in mini-blocks of 6 consecutive trials (approx. 40 s) with the same trial type in order to minimize the confounding effect of switch cost from trial to trial. Conditions were alternated for four times each session. Each session also included 20 s rest periods after every four mini-blocks. Prior to the scanning session, a short training session (20 trials) was conducted in order to familiarize subjects with the task procedure. After the scan, subjects were given questionnaires asking them to rate each individual picture used during the scan ("Please rate how much you would like to eat this food now.") on a 9 point Likert scale with 1 being "Not at all", 5 being "Neutral" and 9 being "Extremely". These ratings were used to categorize trial types in the fMRI experiment for each individual subject and for creation of parametric regressors for behavioral and fMRI analysis.

Behavioral data analysis

We first examined how the Decision Rule (Preference and Non-preference) affected behavioral response time (RT). We also examined how the congruency between Decision Rule and values of the choice options affected RT. Based on the findings of compatibility effects reported in previous studies (Meloy and Russo, 2004; Shafir, 1993), we expected that in preference-based decisions, choices between appetitive items would take less time than choices between unappetitive items. Likewise, we expected that in non-preference-based decisions, choosing between unappetitive items would take less time than choices between appetitive items.

To test this idea, for each Decision Rule, trials were classified based on the ratings of the food items presented on that trial made by each individual subject. Ratings equal to or larger than '5' were classified as high value and ratings equal to or smaller than '4' were classified as low value. Accordingly, possible combinations of food pairs included two high value (appetitive) items (HH), one high value item and one low value item (Mix) or two low value items (LL). The resulting 2 (Decision Rule: Preference and Non-preference) by 3 (Pair Value: HH, Mix, and LL) factorial design was used to analyze behavioral data using repeated-measures ANOVA. An advantage of this categorization is that it considers the decision type as more than just a parametric value. For example, a preference choice in a LL trial is a decision between two 'low value' stimuli, but is more accurately described as choosing which of two unappetitive/aversive foods to eat (the lesser of two evils). Thus, we were able to test if deciding according to either preference or non-preference caused the trial types to be represented as different decision problems.

Next, we examined the effect of the difference in value (rating) between the pair of the food stimuli (Difference Value) and its interaction with Decision Rule. Difference Value can be taken as a measure of the difficulty of the value comparison process; it was expected that RTs would be longer on trials with smaller Difference Values. The absolute value of the difference between the two options was used in behavioral and fMRI analyses. We also examined the effect of the value of the chosen item (Chosen Value) and its interaction with Decision Rule. Chosen Value was taken to be associated with the selection process. Under both rules we defined the 'Chosen Value' as the value of the item which the

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