NeuroImage 72 (2013) 280–286

Contents lists available at SciVerse ScienceDirect

NeuroImage

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

Processing of time within the prefrontal cortex: Recent time engages posterior areas whereas distant time engages anterior areas

Gilly Koritzky [a,*,1], Qinghua He [a,1], Gui Xue [a,b], Savio Wong [a,c], Lin Xiao [a], Antoine Bechara [a,d]

[a] Brain and Creativity Institute, University of Southern California, USA
[b] National Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, China
[c] Department of Psychological Studies, The Hong Kong Institute of Education, Hong Kong
[d] Department of Neurology, University of Iowa, USA

ARTICLE INFO

Article history:
Accepted 25 January 2013
Available online 4 February 2013

Keywords:
Decision-making
Recency
Cognitive models
Individual differences
Prefrontal cortex
Anterior PFC
Posterior PFC
fMRI
Iowa Gambling Task

ABSTRACT

Studies of prefrontal cortex (PFC) lesion patients suggest that information conveying high immediacy, certainty, or tangibility engages the more posterior part of the PFC, whereas information that is more abstract or complex engages the anterior part. We examined whether the anterior and posterior subdivisions of the PFC have distinct roles in processing temporal information during decision making in healthy individuals. We hypothesized that the more the locus of activation is in the posterior (as opposed to anterior) PFC, the more the decision maker will be affected by recent information at the expense of past outcomes. Participants performed a complex decision task while their PFC activity was monitored using fMRI. Results indicate that individual differences in the effect of recent outcomes correspond to differences in the locus of activation, with elevated recency associated with more posterior loci of activation.

Introduction

An influential contribution to the neuroscience of decision-making has come from research on decision-making in brain lesion patients (e.g., Bechara et al., 1994, 2000; Clark and Manes, 2004; Clark et al., 2004; Damasio, 1994; Kringelbach and Rolls, 2004; Moll et al., 2006; Paulus and Frank, 2003; Rahman et al., 2001; Rogers et al., 1999; Rueckert and Grafman, 1996; Sanfey et al., 2003; Sirigu et al., 1995; Tranel et al., 2002). One of the key neural regions in the neural circuitry sub-serving decision-making is the prefrontal cortex (PFC). Decision-making is affected by numerous factors, and we have proposed a neural framework for how some of these factors may be implemented in the prefrontal cortex (PFC) (Bechara and Damasio, 2005). We have proposed that information conveying high immediacy (or high recency), high certainty, or high tangibility engages the more posterior PFC (including the anterior cingulate cortex (ACC) and basal forebrain), whereas information conveying delay in the future (or distance in the past), low certainty, or less tangibility (i.e., information that is more abstract, hypothetical, or complex) engages the more anterior PFC (i.e., frontal pole) (Bechara and Damasio, 2005). This framework is based on the fact that the major advancement in the size, complexity, and connectivity of the frontal lobes in humans has occurred in relation to Brodmann area (BA) 10, i.e., the frontal pole (Semendeferi et al., 2001), and not so much in relation to the more posterior areas of the PFC (Semendeferi et al., 2002). Anatomically, the more posterior areas of the PFC are directly connected to brain structures involved in triggering (autonomic, neurotransmitter nuclei), or representing (sensory nuclei in the brainstem, insular, and somatosensory cortices) affective states (e.g.,Wong et al., 2007), while access of more anterior areas is polysynaptic and indirect (Öngür and Price, 2000). It follows that coupling of information with representations of somatic states via the posterior PFC is associated with relatively fast, effortless, and strong somatic signals that bias decisions, while signaling via the more anterior PFC is relatively slowed, effortful, and weak.

Consistent with this framework, we proposed that humans have developed a capacity to decide according to outcomes that are far more distant in the future (or rely on more distant information in the past), far less certain, and far less tangible (i.e., more abstract or hypothetical). The role of the PFC in this capacity is evident from studies of lesion patients, animal studies, and imaging studies. In the domain of time, patients with lesions in the medial PFC demonstrate a severe shortening in their personal future time perspective, i.e., short-sightedness in their self-defined future (Fellows and Farah, 2005; Hochman et al., 2010). In a similar fashion, lesion in

* Corresponding author at: Brain and Creativity Institute, University of Southern California, 3641 Watt Way, Los Angeles, CA 90089-2520, USA. Fax: +1 213 740 8565.
E-mail address: koritzky@usc.edu (G. Koritzky).
[1] These authors made equal contribution to this paper.

1053-8119/$ – see front matter © 2013 Published by Elsevier Inc.
http://dx.doi.org/10.1016/j.neuroimage.2013.01.056

the lateral PFC results in impaired time perception in both monkeys (Onoe et al., 2001) and humans (Koch et al., 2003). There is a growing number of studies suggesting that the lateral PFC is important in temporal processing in both animals and humans (see Ivry and Spencer, 2004; Meck et al., 2008; Walsh, 2003 for reviews). Functional MRI studies in human subjects have also shown activation in the general PFC area during temporal processing tasks (see Meck et al., 2008 for a review).

In the domain of tangibility, evidence from primate cellular recording, human functional neuroimaging, and human lesion studies suggest that reward stimuli that are more complex and abstract depend on the more anterior ventromedial PFC, whereas reward stimuli that are more basic or tangible (e.g., food taste) depend on the more posterior ventromedial PFC (e.g., Kringelbach and Rolls, 2004; Sescousse et al., 2010).

Our proposition, namely, that appropriate consideration of intangible information engages the anterior sectors of the PFC, is also consistent with other models of function-specific subdivision of this region. The anterior PFC is thought to be involved in the processing of internally-originated information, which is abstract and imperceptible by nature (for example, reflecting on mental states; see Amodio and Frith, 2006; Beer et al., 2006; Christoff and Gabrieli, 2000; Ramnani and Owen, 2004). It has been suggested that high levels of relational complexity selectively activate the anterior left PFC (Kroger et al., 2002). With regard to deductive reasoning, decreasing dependence on perceptual or concrete information in favor of abstract representation is associated with a shift in neural activity from bilateral posterior regions to more frontal regions (Goel, 2007; Houde and Tzourio-Mazoyer, 2003; Houde et al., 2001).

In this study we focus on the influence of time (recency) on decision-making. Although time processing has been studied extensively in animal experiments (Nichelli, 2002), only in the past decade neuroscientists have begun to address this issue in functional neuroimaging (e.g., McClure et al., 2004) and human lesion studies (e.g., Fellows and Farah, 2005; Hochman et al., 2010). Clinical observations show that patients with damage to the PFC have shortened time horizons, and have been described as having myopia for future consequences (Damasio, 1994). Other studies have shown that these patients also have severe impairments in their prospective feeling-of-knowing judgments (Schnyer et al., 2004).

In their performance of a complex decision-making task such as the Iowa Gambling Task (IGT; Bechara et al., 1994), which requires the processing of information about outcomes that occurred either recently or in the more distant past, PFC lesion patients are generally impaired in the "recency" parameter of a cognitive model described below, in that they base their next choice on the most recent outcomes, as opposed to integrating outcomes from several past trials (Kalidindi and Bowman, 2007; Yechiam et al., 2005). We found that damage to the anterior sector in particular is associated with this shift in decision-making, and that the degree of this shortsightedness increases as the damage extends to include the more posterior sectors of the PFC (Hochman et al., 2010).

Indeed, results from lesion studies support the proposed neural framework, according to which immediate or recent outcomes are represented by more posterior areas of the PFC, while the representation of events more distant in time engages the more anterior areas. Nonetheless, lesion studies are limited in terms of providing evidence for a smooth, gradual shift in anterior–posterior processing of time within the PFC. Furthermore, lesion studies always convey information about neurological patients with impaired decision-making, and the generalization of these mechanisms to the healthy population remains in question. Therefore, the primary objective of this study was to test the applicability of this hypothesis to the general population. This was achieved by examining the PFC activity of healthy individuals while they were performing a complex decision task, which engages the medial and lateral parts of the PFC (e.g., Li et al., 2009). PFC activity during the task was monitored using functional magnetic resonance imaging (fMRI).

Individual differences in recency were assessed using the Expectancy-Valence model (Busemeyer and Stout, 2002), a quantitative model predicting the next choice ahead in complex decision making tasks. According to the model, making repeated choices from a set of alternatives generates a process of learning the expectancies of these alternatives. However, the individual's choice is not a simple function of the actual expectancies (i.e., one does not necessarily select the alternatives with the highest odds of gaining). Rather, *subjective expectancies* are formed, which reflect not only the actual outcomes experienced, but also individual differences in three components of the learning and decision process: (1) a motivational component indicating the subjective weight the individual assigns to gains versus losses; (2) a learning-rate component indicating the degree of prominence given to recent outcomes, compared to past experiences; and (3) a probabilistic component indicating how consistent the decision-maker is between learning and responding. Based on a trial-to-trial analysis of behavior in the decision task, the model extracts three individual parameters corresponding to these components, for each decision maker (Busemeyer and Stout, 2002). We hypothesized that the more the locus of activation is in the posterior (as opposed to anterior) sector of the PFC, the more the decision maker gives prominence to recent outcomes at the expense of past outcomes, i.e., the higher the values of the recency parameter.

The decision task involves making repeated selections between alternatives that yield gains and losses. Each trial consists of two stages: (1) a decision stage, in which the subject selects one of the alternatives; and (2) a feedback stage, in which the amounts won or lost by the selection are displayed. This information is processed by the subject, who updates his or her subjective expectancies (i.e., perceptions on the expected value of each alternative/deck) accordingly. Only after this processing the subject makes a new selection, entering the next decision stage. We predicted that the differences in locus of activation between high- and low-recency subjects will emerge at the feedback stage, when the recently-obtained information is processed, and before another decision is made.

Several studies have examined brain activation related to temporal aspects of decision tasks (Cardinal et al., 2001; Fellows and Farah, 2005; McClure et al., 2004). However, the present study is unique in that it takes an individual difference approach: Rather than focusing on the location of generally invoked responses to temporal cues, we measured how individuals with different loci of activation respond differently to immediate information and information obtained farther in time, consequently displaying individual differences in decision style. As previous studies have shown, such individual differences in recency play a critical role in impaired decision making in and out of the laboratory (Farah et al., 2008; Yechiam et al., 2005, 2008). The present study thus aims to examine the neural mechanism behind these individual differences and test the hypothesis that the anterior and posterior subdivisions of PFC have distinct roles in processing temporal information during decision making in healthy individuals.

Method

Participants

Thirty-four healthy adults participated in this study (18 females and 16 males, on average 20.8 ± 1.8 years of age). All subjects had normal or corrected-to-normal vision. They were free of neurological or psychiatric history, and gave informed consent to the experimental procedure, which was approved by the University of Southern California Institutional Review Board.

The Iowa Gambling Task (IGT; Bechara et al., 1994)

A computerized task in which the participant sees four decks of cards, labeled A, B, C, and D, on the screen. On each trial, the participant

selects a card from any of the four decks. Each card selection yields a gain, but it can also yield a loss. The amounts won and lost are then displayed, and the display also includes the overall cumulative payoff, which is updated with each trial.

Decks A and B yield gains of $100 (in "play money") with every selection. At the same time, Deck A incurs a 0.5 probability of losing $250, and Deck B incurs a 0.1 probability of losing $1250. Therefore choosing from these two decks – referred to as the "disadvantageous" decks – leads to a net loss. Decks C and D yield smaller gains of $50 with every selection. They also incur smaller losses: Deck C incurs a 0.5 probability of losing $50, and Deck B incurs a 0.1 probability of losing $250. Therefore choosing from these two decks – referred to as the "advantageous" decks – leads to a net gain. In each pair of decks, the "disadvantageous" and the "advantageous", both decks have the same expected value, though they differ in the frequency in which losses occur in them, with two decks (B, D) yielding small probability losses.

Participants were given written instructions in which they were told that some decks were worse than others, and that they should avoid these decks in order to succeed in the task. However, no initial information was provided concerning the alternatives' payoff distributions.

Procedure

Participants lay supine on the fMRI scanner bed, and viewed the task back-projected onto a screen through a mirror attached onto the head coil. Foam pads were used to minimize head motion. Stimulus presentation and timing of all stimuli and response events were achieved using Matlab (Mathworks) and Psychtoolbox (www.psychtoolbox.org) on an IBM-compatible PC. Participants' responses were collected online using an MRI-compatible button box.

An event-related design of IGT was used, with standard IGT instructions. Each trial was divided into a decision stage and a feedback stage. At the decision stage, a message ("Pick a Card") was displayed at the center of screen, and participants were asked to choose a card from Decks A, B, C or D by pressing the corresponding button. Response had to be made within 3–7 (mean = 4) s (this interval varied randomly between trials). At the feedback stage, participants were informed how much money they won or lost by their selected card. The feedback stage lasts for 3 s. For win-only trials (no loss), the win feedback ("you win $X") was displayed for 1.5 s, followed by a 1.5-second blank screen. For win-but-loss trials, the win feedback ("you win $X") was displayed for 1.5 s, followed by a 1.5 s display of the loss feedback ("but you also lose $X"). The inter-trial interval, i.e., the time between the 3 s feedback stage and the start of the next trial ("pick a card") varied randomly between 1.1, 2.3, and 3.2 s. The sequence was optimized for design efficiency using an in-house program. In total, participants completed 100 trials and the task lasted for 15 min.

fMRI data acquisition

fMRI imaging was conducted in a 3 T Siemens MAGNETOM Tim/Trio scanner in the Dana and David Dornsife Cognitive Neuroscience Imaging Center at the University of Southern California. Functional scanning used a z-shim gradient echo EPI sequence with PACE (Prospective Acquisition Correction). This specific sequence is dedicated to reduce signal loss in the prefrontal and orbitofrontal areas. The PACE option can help reduce the impact of head motion during data acquisition. The parameters are: TR/TE = 2000/25 ms; flip angle = 90°; 64 × 64 matrix size with resolution 3×3 mm^2. Thirty-one 3.5-mm axial slices were used to cover the whole cerebral cortex and most of the cerebellum with no gap. The slices were tilted about 30° clockwise along the AC–PC plane to obtain better signals in the orbitofrontal cortex. The anatomical T1-weighted structural scan was done using an MPRAGE sequence (TR/TE/TI = 2530/3.1/800 ms; flip angle 10°; 208 sagittal slices; 256 × 256 matrix size with spatial resolution as $1 \times 1 \times 1$ mm^3).

fMRI data analysis

Image preprocessing and statistical analysis were carried out using FEAT (fMRI Expert Analysis Tool), a part of the FSL package (FMRIB software library, www.fmrib.ox.ac.uk/fsl). fMRI images were realigned to compensate for small residual head movements that were not captured by the PACE sequence. Translational movement parameters never exceeded 1 voxel in any direction for any participant. Data were spatially smoothed using a 5-mm full-width-half-maximum (FWHM) Gaussian kernel. The data were filtered in the temporal domain using a nonlinear high pass filter with a 100-second cut-off. A two-step registration procedure was used whereby EPI images were first registered to the MPRAGE structural image, and then into standard MNI space, using affine transformations (Jenkinson and Smith, 2001). Registration from MPRAGE structural image to standard space was further refined using FNIRT nonlinear registration. Statistical analyses were performed in the native image space, with the statistical maps normalized to the standard space prior to higher-level analysis. The data were modeled at the first level using a general linear model within FSL's FILM module. Brain activation in every trial was modeled separately for the decision stage and the feedback stage. The event onsets were convolved with canonical hemodynamic response function (HRF, double-gamma) to generate regressors used in the GLM. Temporal derivatives were included as covariates of no interest to improve statistical sensitivity. Null events were not explicitly modeled, and therefore constituted an implicit baseline.

To test our main hypothesis regarding recency, the location (MNI coordinates in x, y and z) and activation level (% signal change) of the local maxima within the anatomically defined PFC boundary (see Fig. 1 for detail) was recorded for each subject, separately for the decision and feedback stages. The whole-brain assessment of neural activation produces information on the locus of activation in the form of coordinates on a three-axis matrix, which segments the brain along the three dimensions of a Euclidean space: The X axis represents the width, i.e., the left to right dimension; the Y axis represents the depth, i.e., the posterior– anterior dimension; and the Z axis represents that height, i.e., the dorsal–ventral dimension. However, the correspondence of these Euclidean axes to the actual shape of the various brain regions is naturally limited. For instance, the PFC is represented by a range of coordinates that correspond to its curvilinear shape. Particularly, the posterior sector ranges somewhat higher along the Z axis than the anterior sector. Therefore, in order to allow a natural-world representation of the PFC along a single dimension from posterior to anterior, we applied a rotation matrix to the vectors represented by axes Y and Z, rotating them by 45° clockwise.

The X axis remains unchanged. The X coordinates have positive values when located in the right hemisphere and negative values when located in the left hemisphere. In both hemispheres, location shifts from lateral to medial regions as the absolute values of X decrease.

Cognitive modeling of the task's results

We employed the revised Expectancy Valence model (rEV; Busemeyer and Stout, 2002; Yechiam and Ert, 2007), a learning model predicting the next choice ahead in repeated decision making. The model assumes that making repeated choices from a set of alternatives generates a process of learning the expectancies of these alternatives. The individual's choice is based on *subjective expectancies*, namely, an incorporation of the actual experienced outcomes into a learning and

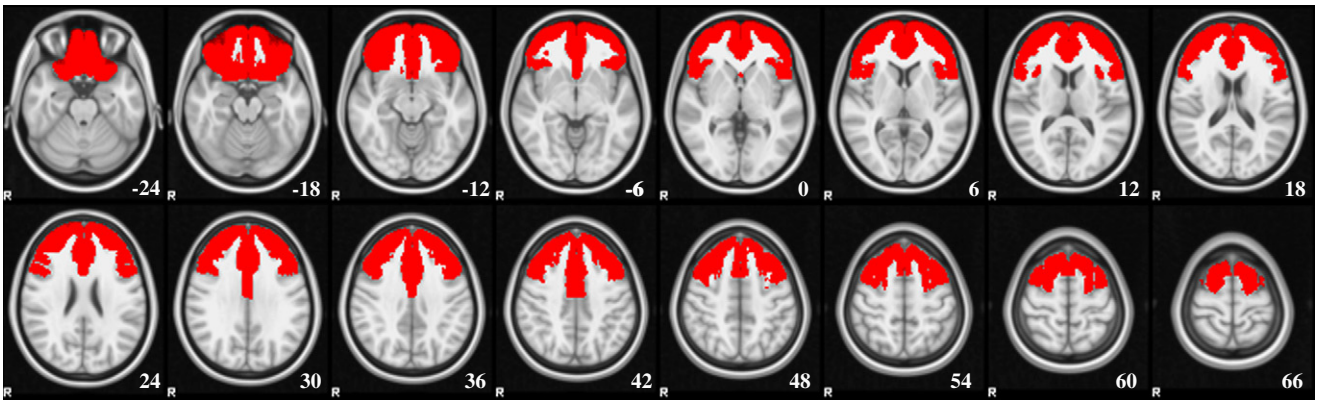

Fig. 1. Explicit mask for PFC was used in this study. To test our hypothesis, the mask covered a broad PFC gray matter area, including bilateral Frontal Pole, Superior Frontal Gyrus, Middle Frontal Gyrus, Inferior Frontal Gyrus (both par triangularis and par opercularis), Frontal Orbital Cortex, Frontal Medial Cortex, Subcallosal Cortex, Anterior Cingulate Cortex, Paracingulate Gyrus, and Frontal Operculum Cortex of the Harvard–Oxford Cortical Structural Atlas provided by FSL package. The outer limits in terms of MNI coordinates are: x = −60 to 60, y = −16 to 74, and z = −30 to 76.

decision process with three components. Each component is represented by a parameter:

1) Relative weight to gains and losses, measured by the attention-weight parameter. The subjective evaluation of the gains and/or losses obtained upon making a choice is called a valence, and denoted $v(t)$. It is calculated as a weighted average of the gains and losses resulting from the chosen option in each trial t.

$$v_j(t) = w \times win(t) - (1-w) \times loss(t),$$

where $win(t)$ and $loss(t)$ are the amounts of money won or lost on trial t; and w is the attention weight parameter ($0 \le w \le 1$).

2) The rate at which recent outcomes are updated, or the relative effect of recent outcomes on the subjective expectancies formed by the decision maker. This is measured by the recency parameter. The outcomes produced by each alternative j are summarized by an expectancy score, denoted $E_j(t)$, and updated as follows:

$$E_j(t) = E_j(t-1) + f \times \left[v(t) - E_j(t-1)\right],$$

where j is the selected alternative. The recency parameter, ϕ, describes the degree to which subjective expectancies reflect the influence of the most recent experience relative to more distant past experiences ($0 \le \phi \le 1$). Higher values of ϕ indicate a greater effect of recent information (at the expense of relying on the full past experience) on the next decision made. Low values of ϕ are generally more optimal.

3) The effect of expectancies on further choice, measured by the choice consistency parameter. The probability of choosing an alternative is a strength ratio of the subjective expectancy of that alternative, relative to all choice options (using Luce's rule):

$$\Pr\left[G_j(t+1)\right] = \frac{e^{\theta(t)\cdot E_j(t)}}{\sum_j e^{\theta(t)\cdot E_j(t)}},$$

where $\Pr[G_j(t)]$ is the probability that alternative j will be selected on trial t. The term $\theta(t)$ controls the consistency of the choice probabilities and the expectancies, where: $\theta(t) = c^5 - 1$, and c is the choice consistency parameter ($0 \le c \le 10$). Higher values of c reflect higher consistency.

Parameters are estimated based on a trial-to-trial analysis of the decision maker's behavior in the task. The accuracy of the model is assessed by comparing its ability to predict the individual's next decision, to a prediction based on the respondent's mean choices (a baseline model). The estimation procedure is described in detail in Busemeyer and Stout (2002). The statistical test used for comparing the fit of the models is the Bayesian Information Criterion (BIC) for log likelihood differences. Positive values of the BIC statistic indicate that the cognitive model performs better than the baseline model.

Results

Task performance

On average, the participants did the task well. The mean proportion of advantageous choice was 57% (SD = 15%), a result significantly higher than 50% ($t_{(33)} = 2.63$, $p = 0.013$). The mean proportion of disadvantageous choice was lower in the last block of 20 trials (mean = 0.37, SD = 0.07) than in the first block (mean = 0.56, SD = 0.02). This difference was significant in a paired t-test ($t_{(33)} = 3.45$, $p = 0.002$), indicating that learning has occurred during the task.

Task performance (proportion of advantageous choice) did not correlate with locus of PFC activation in any of the domains measured.

Modeling results

Descriptive statistics of the EV model's parameters are reported in Table 1. Model fit was adequate (mean = 8.06, SD = 25.45). As can be seen in the table, recency scores were highly skewed. Hence, in further analyses we applied a logarithmic transformation (log 10) to the data.[2]

The relationship between recency and locus of activation

Recency was positively correlated with the overall percentage of activation change in the PFC (as defined by the mask; see Fig. 1), at the feedback stage of each trial ($r_{p(32)} = 0.348$, $p = 0.044$, *Cohen's* $d = 0.742$, denoting a medium effect size). This indicates that individual differences in the weighting of recent outcomes are particularly associated with PFC activation when this information is first encountered and processed. Individuals who behaviorally display a tendency to give prominence to recent outcomes show higher activation levels at this stage.

Table 2 presents the correlations between the rEV Model's three parameters and locus of activation at both decision and feedback stages, along the dimensions of the prefrontal cortex (defined by

[2] Transformations in other bases, such as ln, produced similar results in all the statistical analyses performed in this study.

Table 1
Descriptive statistics of the EV model's parameters in the current sample.

Parameter	Mean	SD	Median	Minimum	Maximum
Sensitivity to gains vs. losses (w)	0.413	0.323	0.338	0	1
Recency (ϕ)	0.108	0.241	0.000002	0	1
Consistency (c)	5.321	4.115	7.211	0.017	10

the mask; see Fig. 1): Left–Right, Posterior–Anterior, Ventral–Dorsal, and Medial–Lateral. As can be seen, the negative association between recency values and locus of activation is significant ($r_{p(32)} = -0.453$, $p<0.01$, *Cohen's d* = 1.013, denoting a large effect size). These results confirm our hypothesis. Fig. 2 presents the recency parameter as a function of the individual's locus of activation at the feedback stage. Parameter values are color coded (Figs. 2A and B), and are plotted along the posterior-to-anterior dimension (Fig. 2C). As can be seen, recency scores are negatively associated with the locus of activation, with high recency largely observed in subjects whose locus of activation is in the dorso-posterior regions of the PFC, and low values of recency largely observed in subjects whose locus of activation is in the ventro-anterior sector.

Apart from the correlation between the recency parameter and activation along the posterior–anterior dimension at the feedback stage, which was the focus of the current paper, two additional significant correlations were observed (see Table 2). The positive correlation between the Consistency parameter and the posterior–anterior dimension can be attributed to the known inverse relationship that exists between the recency and consistency parameters (e.g., in Farah et al., 2008). Although the concepts are not entirely interdependent, in most cases high recency results in making decisions that are inconsistent with the expectancies. In the present case, when recency is controlled for, the correlation diminishes ($r_{p(32)} = -0.065$, $p = 0.718$).

The correlation observed between the gain/loss sensitivity parameter and the ventral–dorsal dimension is harder to interpret, as evidence to reward sensitivity along this domain is mixed (see Fujiwara et al., 2009; Mohr et al., 2010; Xue et al., 2009).

Discussion

We found that high recency, or the effect of recent outcomes on decision making, is associated with increased neural activation of the PFC when the information (feedback) is processed. Our main finding is that individual differences in recency – as measured by behavioral data – correspond to individual differences in the locus of activation: In individuals high in recency, the strongest activation is observed in the posterior sector of the PFC. These results confirm our hypothesis. The differences were pronounced at the feedback stage, namely, when information about the outcome (gain or loss) of one's last choice was encountered and learned, and before further decisions were made. This implies that the locus of activation on the anterior–posterior range corresponds to differences in the extent to which recently obtained information is given a prominent role in the individual's learning processes.

Table 2
Pearson correlation coefficients between the rEV Model's three parameters (gain/loss sensitivity, recency, and consistency) and locus of activation along the dimensions of the prefrontal cortex, at both decision and feedback stages.

		Sensitivity to gains vs. losses	Recency	Consistency
Decision stage	Left–right	0.044	0.069	−0.235
	Posterior–anterior	0.132	−0.101	0.092
	Ventral–dorsal	0.241	−0.106	0.124
	Medial–lateral	−0.002	−0.217	−0.025
Feedback stage	Left–right	0.103	0.034	−0.109
	Posterior–anterior	0.321	−0.452**	0.341*
	Ventral–dorsal	0.381*	−0.252	0.322
	Medial–lateral	0.194	−0.108	0.045

* $p<0.05$.
** $p<0.01$.

The current findings are in accordance with those of Hochman et al. (2010), and extend them from brain-lesion patients to the general population. Although these authors studied patients with lesions that were mostly located in the ventro-medial PFC, recency in these patients was more pronounced as the lesions extended into the more posterior sectors of the PFC. Deficits observed in lesion patients are often associated initially with the specific location of the damage. In the present case, testing the association in the general population, by imaging, confirms that recency is associated with differential patterns of activation across the whole PFC.

Our findings are also consistent with an animal study by Cardinal et al. (2001), which demonstrated that damage to a region included in the posterior prefrontal cortex is associated with choice patterns becoming highly dominated by immediate contingencies. The present study enhances our understanding of this phenomenon by suggesting that the impact of recent outcomes varies between individuals in a continuous fashion, decreasing as the PFC region primarily engaged by the decision process shifts from the posterior to the anterior sector.

Our results contribute to the increasing body of evidence that the anterior PFC is a crucial structure in creating high-level, goal-oriented representations of information (see Bechara, 2005; Beer et al., 2000; Burgess, 2000; Frank and Claus, 2006; Gabrieli et al., 1998). The present study accentuates the necessity of the anterior PFC to proper assimilation of new information in the general population. Moreover, it advances our understanding of how temporal information regarding choice outcomes is mapped within the brain.

It is evident, though, that the brain mapping of temporal information about rewards and penalties goes beyond differences in loci of activation in the PFC alone. For instance, it has been argued that the processing of immediate rewards involves the mesolimbic dopaminergic system (McClure et al., 2004).

Although our predictions were based on a framework which relates the anterior PFC to the processing of information distant in time – either the past or the future (Bechara and Damasio, 2005) – the current study focused on patterns of activation associated with past events alone. Nonetheless, there is evidence to suggest that the anterior PFC is dominant in the representation of the distant future as well. For example, in a neuroimaging study about envisioning emotional future events, D'Argembeau et al. (2008) found that the anterior part of the ventro-medial PFC was more active in envisioning events in the far future than in the near future, whereas the caudate nucleus was engaged in envisioning situations in the near future (D'Argembeau et al., 2008). That common mechanisms function in the learning of, and memory for, both past and future events has been argued repeatedly in the literature (e.g., Addis et al., 2007; Okuda et al., 2003; Szpunar et al., 2007). Taken together, this evidence suggests that individuals are more future-oriented when their locus of activation is in the anterior, rather than posterior, frontal cortex. It is also possible that the locus of PFC activation – from posterior to anterior – represents the extent to which the most readily representable information about (potential or actual) outcomes is given priority over information that is less readily available. This issue should be resolved by future research.

Recency, or being highly affected by recent outcomes, has been shown to correlate with such disruptive behaviors as involvement in violent crime (Yechiam et al., 2008); cannabis and cocaine abuse (Yechiam et al., 2005), or reckless driving (Farah et al., 2008). Linking recency – an aspect cognitive style – to brain functioning can help to illuminate such phenomena. The findings suggest that the locus of

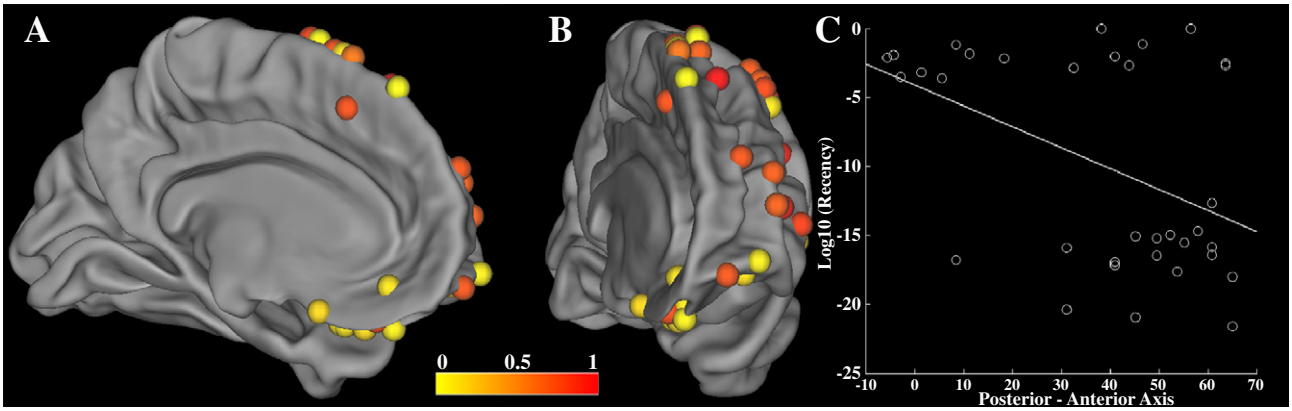

Fig. 2. A) Medial view, and B) anterior view of activation locus in the PFC. Each sphere represents one subject. Sphere colors indicate the value of the recency parameter (see color index bar). C) Scatter plot of the recency parameter as a function of locus of activation on the (rotated) posterior–anterior axis.

prefrontal activation is associated with the likelihood of acting upon recently obtained information in a disadvantageous manner.

In sum, the present study illustrates how information regarding immediate and more distant time points is processed in different locations within the PFC. The notion that the anterior PFC is important to the processing of past outcomes, which emerged from observations in patients with lesions (Hochman et al., 2010), seems to accurately capture the brain functioning of healthy individuals. The study also demonstrates how cognitive models can serve to link behavioral trends to neuro-physiological activation.

Acknowledgments

This research was supported by grants from the National Institute on Drug Abuse (NIDA) R01 DA16708, the National Institute of Neurological Disorders and Strokes (NINDS) P50 NS19632 and National Cancer Institute (NCI) R01 CA152062.We thank Bettina Staschkiewicz, Matthias Brand, Dana Smith, Jaclyn Espinosa, Alex Hollihan and Stephanie Castillo for data collection.

References

Addis, D.R., Wong, A.T., Schacter, D.L., 2007. Remembering the past and imagining the future: common and distinct neural substrates during event construction and elaboration. Neuropsychologia 45, 1363–1377.
Amodio, D.M., Frith, C.D., 2006. Meeting of minds: the medial frontal cortex and social cognition. Nat. Rev. Neurosci. 7, 268–277.
Bechara, A., 2005. Decision making, impulse control and loss of willpower to resist drugs: a neurocognitive perspective. Nat. Neurosci. 8, 1458–1463.
Bechara, A., Damasio, A.R., 2005. The somatic marker hypothesis: a neural theory of economic decision. Games Econ. Behav. 52, 336–372.
Bechara, A., Damasio, A.R., Damasio, H., Anderson, S.W., 1994. Insensitivity to future consequences following damage to human prefrontal cortex. Cognition 50, 7–15.
Bechara, A., Tranel, D., Damasio, H., 2000. Characterization of the decision-making deficit of patients with ventromedial prefrontal cortex lesions. Brain 123, 2189–2202.
Beer, J.S., Shimamura, A.P., Knight, R.T., 2000. Frontal lobe contributions to executive control of cognitive and social behavior. In: Gazzaniga, M.S. (Ed.), The Cognitive Neurosciences. MIT Press, Cambridge, MA, pp. 1091–1106.
Beer, J.S., Mitchell, J.P., Ochsner, K.N., 2006. Special issue: multiple perspectives on the psychological and neural bases of social cognition. Brain Res. 1079, 1–3.
Burgess, P.W., 2000. Strategy application disorder: the role of the frontal lobes in human multitasking. Psychol. Res. 63, 279–288.
Busemeyer, J.R., Stout, J.C., 2002. A contribution of cognitive decision models to clinical assessment: decomposing performance on the Bechara gambling task. Psychol. Assess. 14, 253–262.
Cardinal, R.N., Pennicott, D.R., Sugathapala, C.L., Robbins, T.W., Everitt, B.J., 2001. Impulsive choice induced in rats by lesions of the nucleus accumbens core. Science 292, 2499–2501.
Christoff, K., Gabrieli, J.D.E., 2000. The frontopolar cortex and human cognition: evidence for a rostrocaudal heirarchical organisation within the human prefrontal cortex. Psychobiology 28, 168–186.
Clark, L., Manes, F., 2004. Social and emotional decision-making following frontal lobe injury. Neurocase 10, 398–403.
Clark, L., Cools, R., Robbins, T., 2004. The neuropsychology of ventral prefrontal cortex: decision-making and reversal learning. Brain Cogn. 55, 41–53.
D'Argembeau, A., Xue, G., Lu, Z.-L., Van der Linden, M., Bechara, A., 2008. Neural correlates of envisioning emotional events in the near and far future. NeuroImage 40, 398–407.
Damasio, A.R., 1994. Descartes' Error: Emotion, Reason, and the Human Brain. Putnam Publishing, New York, NY.
Farah, H., Yechiam, E., Bekhor, S., Toledo, T., Polus, A., 2008. Association of risk proneness in overtaking maneuvers with impaired decision making. Transp. Res. 11, 313–323.
Fellows, L.K., Farah, M.J., 2005. Dissociable elements of human foresight: a role for the ventromedial frontal lobes in framing the future, but not in discounting future rewards. Neuropsychologia 43, 1214–1221.
Frank, M.J., Claus, E.D., 2006. Anatomy of a decision: striato–orbitofrontal interactions in reinforcement learning, decision making, and reversal. Psychol. Rev. 113, 300–326.
Fujiwara, J., Tobler, P.N., Taira, M., Iijima, T., Tsutsui, K., 2009. Segregated and integrated coding of reward and punishment in the cingulate cortex. J. Neurophysiol. 101, 3284–3293.
Gabrieli, J.D.E., Poldrack, R.A., Desmond, J.E., 1998. Colloquium paper: the role of left prefrontal cortex in language and memory. Proc. Natl. Acad. Sci. 95, 906–913.
Goel, V., 2007. Anatomy of deductive reasoning. Trends Cogn. Sci. 11, 435–441.
Hochman, G., Yechiam, E., Bechara, A., 2010. Recency gets larger as lesions move from anterior to posterior locations within the ventromedial prefrontal cortex. Behav. Brain Res. 213, 27–34.
Houde, O., Tzourio-Mazoyer, N., 2003. Neural foundations of logical and mathematical cognition. Nat. Rev. Neurosci. 4, 507–514.
Houde, O., Zago, L., Mellet, E., Moutier, S., Pineau, A., Mazoyer, B., Tzourio-Mazoyer, N., 2001. Access to deductive logic depends on a right ventromedial prefrontal area devoted to emotion and feeling: evidence from a training paradigm. NeuroImage 14, 1486–1492.
Ivry, R.B., Spencer, R.M.C., 2004. The neural representation of time. Curr. Opin. Neurobiol. 14, 225–232.
Jenkinson, M., Smith, S., 2001. A global optimisation method for robust affine registration of brain images. Med. Image Anal. 5, 143–156.
Kalidindi, K., Bowman, H., 2007. Using ε-greedy reinforcement learning methods to further understand ventromedial prefrontal patients' deficits on the Iowa Gambling Task. Neural Netw. 20, 676–689.
Koch, G., Oliveri, M., Torriero, S., Caltagirone, C., 2003. Underestimation of time perception after repetitive transcranial magnetic stimulation. Neurology 60, 1844–1846.
Kringelbach, M.L., Rolls, E.T., 2004. The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology. Prog. Neurobiol. 72, 341–372.
Kroger, J.K., Sabb, F.W., Fales, C.L., Bookheimer, S.Y., Cohen, M.S., Holyoak, K.J., 2002. Recruitment of Anterior dorsolateral prefrontal cortex in human reasoning: a parametric study of relational complexity. Cereb. Cortex 12, 477–485.
Li, X., Lu, Z.-L., D'Argembeau, A., Ng, M., Bechara, A., 2009. The Iowa Gambling Task in fMRI images. Hum. Brain Mapp. 31, 410–423.
McClure, S.M., Laibson, D.I., Loewenstein, G., Cohen, J.D., 2004. Separate neural systems value immediate and delayed monetary rewards. Science 306, 503–507.
Meck, W.H., Penney, T.B., Pouthas, V., 2008. Cortico-striatal representation of time in animals and humans. Curr. Opin. Neurobiol. 18, 145–152.

Mohr, P.N.C., Biele, G., Heekeren, H.R., 2010. Neural processing of risk. J. Neurosci. 30, 6613–6619.
Moll, J., Krueger, F., Zahn, R., Pardini, M., de Oliveira-Souza, R., Grafman, J., 2006. Human fronto-mesolimbic networks guide decisions about charitable donation. Proc. Natl. Acad. Sci. U. S. A. 103, 15623–15628.
Nichelli, P., 2002. The processing of temporal information in the frontal lobe. In: Grafman, J. (Ed.), Handbook of Neuropsychology: Frontal Lobes. Elsevier, Amsterdam, pp. 175–193.
Okuda, J., Fujii, T., Ohtake, H., Tsukiura, T., Tanji, K., Suzuki, K., Kawashima, R., Fukuda, H., Itoh, M., Yamadori, A., 2003. Thinking of the future and past: the roles of the frontal pole and the medial temporal lobes. NeuroImage 19, 1369–1380.
Onoe, H., Komori, M., Onoe, K., Takechi, H., Tsukada, H., Watanabe, Y., 2001. Cortical networks recruited for time perception: a monkey positron emission tomography (PET) study. NeuroImage 13, 37–45.
Öngür, D., Price, J.L., 2000. The organization of networks within the orbital and medial prefrontal cortex of rats, monkeys and humans. Cereb. Cortex 10, 206–219.
Paulus, M.P., Frank, L.R., 2003. Ventromedial prefrontal cortex activation is critical for preference judgments. Brain Imaging 14, 1311–1315.
Rahman, S., Sahakian, B.J., Cardinal, R.N., Rogers, R.D., Robbins, T.W., 2001. Decision making and neuropsychiatry. Trends Cogn. Sci. 6, 271–277.
Ramnani, N., Owen, A.M., 2004. Anterior prefrontal cortex: insights into function from anatomy and neuroimaging. Nat. Rev. Neurosci. 5, 184–194.
Rogers, R.D., Everitt, B.J., Baldacchino, A., Blackshaw, A.J., Swainson, R., Wynne, K., Baker, N.B., Hunter, J., Carthy, T., Booker, E., London, M., Deakin, J.F.W., Sahakian, B.J., Robbins, T.W., 1999. Dissociable deficits in the decision-making cognition of chronic amphetamine abusers, opiate abusers, patients with focal damage to prefrontal cortex, and tryptophan-depleted normal volunteers: evidence for monoaminergic mechanisms. Neuropsychopharmacology 20, 322–339.
Rueckert, L., Grafman, J., 1996. Sustained attention deficits in patients with right frontal lesions. Neuropsychologia 10, 953–963.
Sanfey, A., Hastie, R., Colvin, M., Grafman, J., 2003. Phineas Guaged: decision-making and the human prefrontal cortex. Neuropsychologia 41, 1218–1229.
Schnyer, D.M., Verfaellie, M., Alexander, M.P., LaFleche, G., Nicholls, L., Kaszniak, A.W., 2004. A role for the right medial prefrontal cortex in accurate feeling-of-knowing judgments: evidence from patients with lesions to frontal cortex. Neuropsychologia 42, 957–966.
Semendeferi, K., Armstrong, E., Schleicher, A., Zilles, K., Van Hoesen, G.W., 2001. Prefrontal cortex in humans and apes: a comparative study of area 10. Am. J. Phys. Anthropol. 114, 224–241.
Semendeferi, K., Lu, A., Schenker, N., Damasio, H., 2002. Humans and great apes share a large frontal cortex. Nat. Neurosci. 5, 272–276.
Sescousse, G., Redouté, J., Dreher, J.D., 2010. The architecture of reward value coding in the human orbitofrontal cortex. J. Neurosci. 30, 13095–13104.
Sirigu, A., Zalla, T., Pillon, B., Grafman, J., Agid, Y., Dubois, B., 1995. Selective impairments in managerial knowledge following pre-frontal cortex damage. Cortex 31, 301–316.
Szpunar, K.K., Watson, J.M., McDermott, K.B., 2007. Neural substrates of envisioning the future. Proc. Natl. Acad. Sci. U. S. A. 104, 642–647.
Tranel, D., Bechara, A., Denburg, N.L., 2002. Asymmetric functional roles of right and left ventromedial prefrontal cortices in social conduct, decision-making, and emotional processing. Cortex 38, 598–612.
Walsh, V., 2003. A theory of magnitude: common cortical metrics of time, space and quantity. Trends Cogn. Sci. 7, 483–488.
Wong, S.W., Massé, N., Kimmerly, D.S., Menon, R.S., Shoemaker, J.K., 2007. Ventral medial prefrontal cortex and cardiovagal control in conscious humans. NeuroImage 35, 698–708.
Xue, G., Lu, Z., Levin, I.P., Weller, J.A., Li, X., Bechara, A., 2009. Functional dissociations of risk and reward processing in the medial prefrontal cortex. Cereb. Cortex 19, 1019–1027.
Yechiam, E., Ert, E., 2007. Evaluating the reliance on past choices in adaptive learning models. J. Math. Psychol. 51, 75–84.
Yechiam, E., Busemeyer, J.R., Stout, J.C., Bechara, A., 2005. Using cognitive models to map relations between neuropsychological disorders and human decision making deficits. Psychol. Sci. 16, 973–978.
Yechiam, E., Kanz, J., Bechara, A., Stout, J.C., Busemeyer, J.R., Altmaier, E.M., Paulsen, J., 2008. Neurocognitive deficits related to poor decision-making in people behind bars. Psychon. Bull. Rev. 15, 44–51.