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

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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

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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