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Research report

Recency gets larger as lesions move from anterior to posterior locations within the ventromedial prefrontal cortex

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ABSTRACT

In the past two decades neuroimaging research has substantiated the important role of the prefrontal cortex (PFC) in decision-making. In the current study, we use the complementary lesion based approach to deepen our knowledge concerning the specific cognitive mechanisms modulated by prefrontal activity. Specifically, we assessed the brain substrates implicated in two decision making dimensions in a sample of prefrontal cortex patients: (a) the tendency to differently weigh recent compared to past experience; and (b) the tendency to differently weigh gains compared to losses. The participants performed the Iowa Gambling Task, a complex experience-based decision-making task [3], which was analyzed with a formal cognitive model (the Expectancy-Valance model; [12]). The results indicated that decisions become influenced by more recent, as opposed to older, events when the damage reaches the posterior sectors of the ventromedial prefrontal cortex (VMPC). Furthermore, the degree of this recency deficit was related to the size of the lesion. These results suggest that the posterior area of the prefrontal cortex directly modulates the capacity to use time-delayed information. In contrast, we did not find similar modulation for the sensitivity to gains versus losses.

1. Introduction

Several studies in the past two decades have demonstrated the important role of the human prefrontal cortex in decision making [3,18,6,45,58,44,48,16,15,34,37,28]. Using functional imaging approaches, neuroscientists have been able to address the question of how the brain encodes the value of various options on a common scale [38], thus suggesting that there may be a common neural "currency" that represents the value of different options. In other experiments, brain regions such as the parietal cortex and anterior cingulate cortex have been shown to be involved in computing the probability or certainty of outcomes predicted by available options [46,25]. Also, some studies have been directed toward understanding how the perceived delay in receiving a reward modulates activity in reward-related brain areas [36], while others have addressed how differences between expected and actual reward contribute to learning [40]. In essence, the field of functional neuroimaging continues to blossom and addresses many of the factors that modulate the "utility" of rewards, and in doing so, affect how these rewards influence decision making.

Although much of this work is well represented in the functional neuroimaging literature, very little work in this area has used the lesion approach. This is historically important since research on the differences between lesion patients and controls has been highly successful in revealing brain functions that support decision making [18]. Therefore, the primary aim of this study is to evaluate in brain damaged patients whether damage to the anterior ventromedial prefrontal cortex (VMPC) shifts decision-making from long-term to short-term outcomes, and whether the degree of this shortsightedness increases as the damage extends more posteriorly to include the more posterior sectors of the VMPC. A further support of this hypothesis would be that the degree of this deficit would depend also on the size of the lesion in the target region. An additional aim of the study is to assess whether the weighting of gains versus losses, which mirrors the difference in response to rewards and penalties, is supported by separate neural subsystems.

The ideas that patients with VMPC lesions have shortened time horizons, and that some of these patients with posterior damage (e.g., including basal forebrain) have some sort of working memory impairment are not new [3,60]. However, the current study is novel in its analysis of behavior and lesion location and size to determine how recency deficits are mapped within the VMPC region on the anterior to posterior axis. Furthermore, the use of these behavioral and anatomical analyses to determine whether gains and losses (reward and punishment) are neurally dissociable within the prefrontal cortex has not been attempted before in

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human lesion studies (for a similar approach in another domain of investigation, see [47]).

The major advancement in the size, complexity, and connectivity of the frontal lobes in humans has occurred in relation to Brodmann area 10, i.e., the frontal pole [49], and not so much to the more posterior areas of the VMPC [50]. Anatomically, the more posterior areas of the VMPC (e.g., Brodmann area 25) 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, while access of more anterior areas is polysynaptic and indirect [43].

Under Bechara and Damasio's [5] framework, the intactness of both posterior and anterior VMPC cortices is important in order for a non-immediate outcome to exert an influence on behavior. If the anterior regions (frontal pole) are damaged, decision-making shifts towards shorter time horizons (i.e., more recent outcomes affect behavior). However, as the damage extends to the more posterior VMPC regions (including the anterior cingulate cortex, basal forebrain, and nucleus accumbens), the shortening of this time horizon (or high recency) becomes more severe [5]. The reason is that damage to anterior sectors shortens the horizon for time somewhat, but more posterior sectors (which are still intact) can still integrate the value of non-immediate outcomes to a certain degree. In contrast, damage to posterior regions isolates the anterior sectors *as well* and impairs their capacity to function and integrate more distant time. Damage to the posterior VMPC impairs the connectivity of the anterior VMPC to the limbic system, rendering the anterior VMPC disconnected and dysfunctional. As a result the time shortening becomes more extreme, and decisions shifts towards attending only to immediately recent or future events.

Empirical evidence for this theoretical framework remains lacking, although there are several clinical observations and studies that are consistent with this notion. The first experimental evidence in support of this notion was found by Fellows and Farah [26], who showed that patients with damage to the VMPC, but not dorsolateral prefrontal cortex (DLPC), demonstrated a severe shortsightedness in their self-defined future. Other studies have shown that these patients also have severe impairments in their prospective feeling-of-knowing judgments [52]. Although time processing has been studied extensively in animal experiments [39], only recently neuroscientists have begun to address this issue in functional neuroimaging [36] and human lesion studies [26,27]. Using a complex decision-making task, such as the Iowa Gambling Task (IGT; [3]), which relies on information of outcomes that occur more recently, or in the distant past, VMPC lesion patients are especially impaired in the "recency" parameter of a cognitive model described below, in that they base their next choice on the most recent outcomes, while neglecting outcomes from earlier trials [62,32]. However, the knowledge so far in this regard has not been sufficient. Thus, the main goal of the current study is to examine how temporal events may be processed across the anterior–posterior axis of the VMPC. While several papers have specifically addressed the cognitive bases of decision-making in the prefrontal cortex [6,27], the current study is a first attempt to evaluate the degree of recency as a function of location (i.e., anterior vs. posterior) and lesion size in the PFC.

In addition to time processing, numerous studies have argued that the right hemisphere plays a dominant role in avoidance behavior, punishment, and negative emotions (which includes loss), whereas the left hemisphere is more important for approach behavior, reward, and positive emotions (which includes gain) [22]. A competing hypothesis has been that punishment and loss (and by inference, avoidance behaviors) is dependent on the lateral areas of the orbitofrontal cortex, including the inferior part of the inferior frontal gyrus, whereas reward and gain (and by inference, approach behaviors) is dependent on the mesial areas of the orbitofrontal cortex [41,34]. Contradictory functional neuroimaging evidence, however, suggests that losses and gains are processed by the same neural system [57]. Using the cognitive model described below, we examine whether the parameter of gain versus loss is affected by one particular lesion, and thus support any of the currently held views just outlined.

Given the assumption that different prefrontal cortex regions may mediate different sub-mechanisms of the overall decision-making process [2,17], and given that lesions studies can establish which specific region may be linked to a specific cognitive mechanism [2], we examined the effects of lesions within the PFC on several parameters of decision-making, namely the weighting of recent compared to past experiences and sensitivity to gains versus losses. In this study, we divided the prefrontal cortex into four sub-regions (bilaterally), and the percentage of each region that was occupied by lesions was calculated for each patient using Brainvox [19,31]. To pinpoint specific cognitive mechanisms which may be related to each region, we used cognitive modeling (e.g., [12,62,32]). The cognitive modeling analysis decomposes the overt behavior in a decision task to the underlying covert cognitive mechanisms.

While several cognitive models exist, we employed the Expectancy-Valance model (EV; [12]), an adaptive learning model which decomposes the behavior in the IGT into three basic mechanisms: (i) a motivational mechanism which captures the tendency to weigh gains and losses differently; (ii) a learning-rate mechanism which captures the tendency to focus on recent outcomes and to ignore past experiences; and (iii) a response mechanism which captures the tendency to respond consistently or in an erratic manner. The model produces quantitative estimations that provide continuous mapping of the decision-makers along the three mechanisms. For example, the recency parameter, which is the most important parameter for examining time discounting, assumes that decision makers form expectancies about the consequences of their choices. When a choice is being made, this expectancy is adjusted, as a function of its previous value and the value of the newly experienced outcome. However, the amount of the adjustment is dependent on the value of the recency parameter, which ranges from 0 to 1. Small parameter values represent less discounting of past experiences, while large values represent strong recency, that is, rapid discounting of past experiences. The model equations appear in the Appendix (for more information about the model, see [12,55,62]). The EV model was used because research shows it captures the essential attention and information-processing mechanisms which underlie experience-based decision tasks such as the IGT [24,61] and because it was found to have better explanatory power than several alternative models [63].

2. Materials and method

2.1. Participants

Fourteen patients with different prefrontal cortex lesions from the Patient Registry of the University of Iowa's Division of Behavioral Neurology & Cognitive Neuroscience participated in the experiment. Nine patients were males (mean age = 49.33, SD = 17.97, range = 21–81) and five females (mean age = 58.6, SD = 11.72, range = 40–70 years old). The participants had, on average, 12 years of education (mean males = 12, SD = 2.34, range = 8–14 years; mean females = 12.1, SD = 3.22, range = 8–18 years), and they were all right-handed. The participants constitute a sub-sample of the patients studied elsewhere [3,6] for whom the extent of the damage to different areas of the prefrontal cortex was mapped and their neuropsychological data was previously collected.[1] The behavioral analyses (EV model) are

[1] Because the main hypothesis in this study involves the association between the location and extent of brain lesions and decision parameters (e.g., recency) we did not study a control group. An analysis of healthy adults' performance in this task as well as the performance of other neuropsychological samples appears elsewhere [5–7].