What might have been? The role of the ventromedial prefrontal cortex and lateral orbitofrontal cortex in counterfactual emotions and choice

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A B S T R A C T

Counterfactual feelings of regret occur when people make comparisons between an actual outcome and a better outcome that would have occurred under a different choice. We investigated the choices of individuals with damage to the ventral medial prefrontal cortex (VMPFC) and the lateral orbital frontal cortex (LOFC) to see whether their emotional responses were sensitive to regret. Participants made choices between gambles, each with monetary outcomes. After every choice, subjects learned the consequences of both gambles and rated their emotional response to the outcome. Normal subjects and lesion control subjects tended to make better choices and reported post-decision emotions that were sensitive to regret comparisons. We suggest the VMPFC is involved in the association between choices and anticipated emotions that guide future choices, while the LOFC is involved in experienced emotions that follow choices, emotions that may signal the need for behavioral change.

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“Let’s not forget that little emotions are the captains of our lives and we obey them without even realizing it.”

Vincent Van Gogh, 1889

1. Introduction

Our emotional responses depend on the lives we live as well as the lives we could have lived. Counterfactual possibilities often serve as reference points against which we evaluate what actually occurred. Two counterfactual comparisons are particularly relevant to risky choice—disappointment and regret. Disappointment refers to the comparison between an actual outcome and a counterfactual one under a different state of the world (i.e., if a coin comes up heads instead of tails) (Bell, 1982; Loomes & Sugden, 1986). Negative comparisons are called regret, and positive ones are called rejoicing.

Research on emotions of pleasure and pain shows that regret comparisons typically have greater impact than disappointment comparisons (Mellers, Schwartz, & Ritov, 1999). Unlike disappointment comparisons, regret comparisons are under the control of the decision maker (i.e., who could have made the other choice) and are likely to be associated with a sense of personal responsibility and remorse. In this way, regret—even more than disappointment—may be beneficial for learning (Roese & Olsen, 1995; Zeelenberg & Pieters, 2007). In this paper, we investigate the unique contributions of the ventromedial prefrontal cortex (VMPFC) and lateral orbitofrontal cortex (LOFC) to risky choice and post-decision emotions indicative of regret comparisons.

The VMPFC has long been implicated in decision making and emotion (see Kringlebch, 2005; Fellows, 2007 for review). Emerging and existing theories claim the VMPFC is involved in the integration of bodily signals that influence decisions (Bechara, Damasio, & Damasio, 2000; Damasio, 1996). The VMPFC is also critical in the representation of stimulus value and the expected value of options (Fellows, 2007). Recent fMRI studies building on connections between VMPFC and decision making (Sommer, Peters, Gläscher, & Büchel, 2009; Lie et al., 2007; Chua, Gonzalez,
Taylor, Welsh, & Liberzon, 2009; Ursu & Carter, 2005) have reported distinct activation patterns in the medial and lateral OFC during periods of regret. Coricelli et al. (2005) for example, found that medial OFC activity increased with both immediate regret and cumulative regret experienced throughout the task, whereas, lateral OFC activity increased only with immediate regret of the outcome. This pattern of neural activity suggests that the medial OFC may be involved in forming associations between an anticipated response and future behavior, whereas the lateral OFC may be involved in the counterfactual comparisons that follow choice.

Collectively the aforementioned results suggest unique roles for the VMPFC and LOFC in post-decision regret; however no human lesion research has compared the effects of VMPFC and LOFC damage on post-decision emotions. Existing work by Gomez Beldarrain, Garcia-Monco, Astigarraga, Gonzalez, and Grafman (2005) showed that ventral prefrontal cortex patients reported fewer spontaneous counterfactual thoughts in response to questions. In addition, in addition, Camille et al. (2004) found that medial OFC patients reported emotions in a gambling task that were insensitive to regret. In neither study was it known whether lesions in the VMPFC extended to the LOFC.

To compare the functions of the VMPFC and LOFC regions, we administered a gambling task to patients with specific VMPFC and LOFC damage. On each trial, participants choose which of two gambles they preferred to play, each gamble having the possibility of a win or loss (Mellers et al., 1999). After making a choice, participants learned their outcome and that of the foregone gamble. Then they rated their pleasure with the outcome on a category rating scale from –50 (“Extremely Unhappy”) to 50 (“Extremely Happy”).

We expected that both the VMPFC and the LOFC group would report emotions that were less sensitive than other groups to regret. Our prediction is derived from past research showing that VMFPC activity increased only with immediate regret of the outcome. This pattern of neural activity suggests that the medial OFC may be involved in forming associations between an anticipated response and future behavior, whereas the lateral OFC may be involved in the counterfactual comparisons that follow choice.

2. Experimental procedures

2.1. Subjects

Neurological patients with focal brain lesions (n = 18) were participants in a gambling task. Lesion patients were recruited from the Patient Registry in the Department of Neurology at the University of Iowa. All patients had focal, stable, adult-onset lesions sustained at least 1 year prior to testing, and had previously undergone extensive screening and evaluation with background measures of neuropsychological function, reported previously in Bechara, Damasio, Tranel, and Anderson (1998), Tranel, Damasio, Denburg, and Bechara (2005) and Bar-On, Tranel, Denburg, and Bechara (2003). A brief survey of the basic neuropsychological functions is presented in Table 1. Exclusion criteria were a history of mental retardation, a learning disability or a psychiatric illness including substance abuse. Patients were selected for eligibility on the basis of neuroanatomical status obtained from an MRI or a computed tomography (CT) scan (see neuroanatomical analysis section subsequently).

Patients in the VMPFC group (n = 7) had bilateral damage in portions of the mesial orbital/ventromedial sector of the prefrontal cortex and/or the frontal pole (Fig. 1). Lesion etiology in the VMPFC group was hemorrhage due to ruptured aneurysm of the anterior communicating artery or tumor resections. Inclusion in the LOFC lesion group (n = 6) was based on unilateral damage (left n = 3, right n = 3) to any part of the ventrolateral sector (including lateral orbital) of the prefrontal cortex, but spared bilateral damage to the mesial orbital/ventromedial prefrontal cortex and frontal pole, albeit in cases the damage extended to the mesial region, but only on one unilateral side (Fig. 2). All lesions were due to either tumor resection or strokes in the overlapping territories of the middle and anterior cerebral arteries.

Although some overlap in the damaged areas cannot be ruled out (i.e., individual lesions from a LOFC group may overlap with a lesion from a VMPFC group or vice versa), the VMPFC and LOFC groups are distinct in terms of lesion location. The area of maximal lesion overlap in the VMPFC group (i.e., the area coded in red color in Fig. 1, slice 3) has no overlap with the area of maximal lesion overlap in the LOFC group (i.e., the area coded in red color in Fig. 2, slice 3).

The non-frontal lesion comparison group (n = 5) had damage in any part of the occipital and or temporal lobes that did not include the hippocampus, entorhinal cortex or amygdala (Fig. 3). These participants had left unilateral (n = 3) or bilateral (n = 2) damage due to strokes or tumor resections.

The three lesion groups were compared to 26 normal age-matched comparison subjects who were recruited through community advertising. Demographic characteristics for all groups are displayed in Table 1. Subjects were paid for their participation and tested in quiet laboratory conditions with task responses recorded via a touch-sensitive monitor. The study was approved by the human subjects committee at the University of Iowa. Before enrollment in the study, written informed consent was acquired in accordance with the Declaration of Helsinki.

2.2. Lesion analysis

Lesion location was confirmed with either an MRI scan or a CT scan if MRI scanning was not possible or available. Two of the seven VMPFC patients had CT scans because of clipped aneurysms (tilt angle was optimized per subject to avoid clip-related artifact (zoom 2.4, field of view 51 cm, fovea 212.5 mm, slice thickness 2–4 mm)). Two of the six LOFC patients had only CT scans, and no MRI scans were available. All patients form the lesion control group had MRI scans. Lesions of individual patients who had MRI scans were transferred manually onto a normal reference brain using the MAP-3 technique (Damasio & Frank, 1992; Damasio, 1995; Frank, Damasio, & Grabowski, 1997) that involved (i) slicing a normal 3D brain in such a way that the slices match those of the MRI scan of the subject with the brain lesion; (ii) transposing the lesion onto the slices of the normal brain, taking into consideration the relation of the lesion and the identified pertinent anatomical landmarks; (iii) rendering each transposed lesion as an ‘object’ that can intersect in space, and thus yield a maximal overlap relative to both surface and depth extension of damage. The few patients with only CT scans were inspected visually and assigned, based on the neuro-radiologist report, as belonging to the VMPFC or LOFC group.

2.3. Stimuli and design

Participants were told that the experiment involved choices between gambles with real monetary wins and losses. Their payments would be the total of their 84 outcomes, making it unlikely that participants would be able to keep track of their payment total during the study. Stimuli were two-outcome gambles, presented on a computer screen, as shown in Fig. 4. Each gamble appeared as a pie chart with colored regions representing the probabilities of different outcomes. Monetary outcomes were specified in or near the region. On each trial, participants selected the gamble they preferred to play.
A box appeared around the chosen gamble. Then spinners appeared in the centers of both gambles and rotated independently. Eventually, the spinners stopped, and participants learned the outcomes. They rated their pleasure or displeasure with their outcome on a category rating scale from 0 (“Extremely Unhappy”) to 50 (“Extremely Happy”).

The experiment consisted of the 21 gamble pairs listed in Table 2. Each pair was presented 4 times. Since the goal of the experiment was to understand post-decision emotions, we slightly adjusted the probabilities on some trials to obtain emotional reactions to more combinations of actual and foregone outcomes. This change was intentional since our goal was to understand emotions that follow from decisions. In previous experiments, Mellers et al. (1999) interviewed subjects after the experiment and learned that no participants were aware of, suspicious of, or concerned about the stated vs. the actual probabilities of outcomes. That is, none were aware that, on some occasions, probabilities were slightly adjusted. For these reasons, we believe the design was ideal for inferences about emotions, though not for learning.

2.4. Statistical analyses

We used regressions to investigate whether reported emotions were predictable from outcomes, disappointment comparisons, and regret comparisons. These predictor variables were weighted according to decision affect theory (Mellers et al., 1999). Outcome
Fig. 2. Lateral OFC lesion group. Overlap of lesions in the LOFC patients. The color bar indicates that warmer colors represent greater degree of overlap across subjects, whereas cooler colors represent less overlap across subjects, with blue reflecting regions in which damage is unique to a participant. On the left side of the brain, red indicates a maximal overlap of lesions from 3 patients with left LOFC lesions, whereas the blue reflects regions in which damage is unique to one patient. The yellow color indicates overlap from 2 lesions. On the right side of the brain, there is only one lesion represented in the figure, which includes LOFC area, but extends to the medial side as well. Two of the lesion patients had only CT scans with smaller lesions that include the ventrolateral prefrontal and lateral orbitofrontal cortex, but spare the mesial orbitofrontal cortex. As can be seen from the color-coding, the area in red is restricted to the lateral OFC, specifically the posterior lateral OFC. By comparing slice 3 from this figure to slice 3 from Fig. 1, it is clear that the areas in red are in distinct anatomical regions, namely the VMPFC (Fig. 1) and LOFC (this figure). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 3. Lesion comparison subject group. Overlap of lesions in the comparison group. The color bar indicates that warmer colors indicate greater degree of overlap across subjects; area in red is the region of maximal overlap indicating overlap from all 5 subjects. Cooler colors indicate less overlap across subjects; areas in blue reflect regions in which damage is unique to a participant. As can be seen from the color-coding, damage is primarily restricted to the occipital cortex with few areas of commonality across participants in this region. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
expected return and higher risk); RA/RS
A (lower expected return and lower risk) vs. risky-and rewarding Gamble B (higher
more risk).
return and lower risk) vs. risk seeking Gamble B (identical expected return and
Gamble B (lower expected return and greater risk); SS/RR
ranged from
Gamble pairs used in the experimental design.
Table 2
Individual trial stimuli were pairs of two-outcome gambles, as illustrated
Fig. 4.

<table>
<thead>
<tr>
<th>Gamble 1</th>
<th>Gamble 2</th>
<th>Gamble type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pair</td>
<td>Out A</td>
<td>Prob A</td>
</tr>
<tr>
<td>1</td>
<td>$8</td>
<td>0.2</td>
</tr>
<tr>
<td>2</td>
<td>–$8</td>
<td>0.5</td>
</tr>
<tr>
<td>3</td>
<td>$8</td>
<td>0.5</td>
</tr>
<tr>
<td>4</td>
<td>$8</td>
<td>0.5</td>
</tr>
<tr>
<td>5</td>
<td>–$8</td>
<td>0.8</td>
</tr>
<tr>
<td>6</td>
<td>$8</td>
<td>0.8</td>
</tr>
<tr>
<td>7</td>
<td>$8</td>
<td>0.8</td>
</tr>
<tr>
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<td>$8</td>
<td>0.2</td>
</tr>
<tr>
<td>9</td>
<td>$32</td>
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<td>10</td>
<td>$32</td>
<td>0.2</td>
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<tr>
<td>11</td>
<td>$8</td>
<td>0.5</td>
</tr>
<tr>
<td>12</td>
<td>–$8</td>
<td>0.8</td>
</tr>
<tr>
<td>13</td>
<td>$8</td>
<td>0.8</td>
</tr>
<tr>
<td>14</td>
<td>$8</td>
<td>0.8</td>
</tr>
<tr>
<td>15</td>
<td>$8</td>
<td>0.2</td>
</tr>
<tr>
<td>16</td>
<td>$32</td>
<td>0.2</td>
</tr>
<tr>
<td>17</td>
<td>$32</td>
<td>0.2</td>
</tr>
<tr>
<td>18</td>
<td>$8</td>
<td>0.5</td>
</tr>
<tr>
<td>19</td>
<td>$32</td>
<td>0.5</td>
</tr>
<tr>
<td>20</td>
<td>$32</td>
<td>0.5</td>
</tr>
<tr>
<td>21</td>
<td>$8</td>
<td>0.8</td>
</tr>
</tbody>
</table>

Note: B/W—better Gamble A (higher expected return and lower risk) vs. worse
Gamble B (lower expected return and greater risk); SS/RR—small-and-safe Gamble A
(lower expected return and lower risk) vs. risky-and rewarding Gamble B (higher
expected return and higher risk); RA/RS—risk averse Gamble A (identical expected
return and lower risk) vs. risk seeking Gamble B (identical expected return and
more risk).

was the monetary value (in dollars) of the amount won or lost and ranged from –32 to +32. Disappointment comparisons were
differences in monetary amounts of the realized and unrealized
outcomes of the chosen gamble multiplied by the surprise
associated with the realized outcome (i.e., one minus the
probability of the obtained outcome). Regret comparisons were
differences in the monetary values of the realized and foregone
outcomes multiplied by the surprise of the joint event (i.e., one
minus the product of the probability of the actual and foregone
outcomes).

To assess whether the emotional responses of normal controls
were influenced by disappointment and regret comparisons, we
conducted statistical tests of relevant coefficients. Each of the 26
normal controls made 84 judgments, but since these judgments
were not independent, we used the number of subjects (26) rather
than the product of responses (26 $ 84) as our degrees of freedom.
In this case, there were three estimated parameters, leaving 23
degrees of freedom.

Comparisons between normal controls and the other three groups
(lesion, ventral medial, and ventral lateral) were also conducted using
regression analyses. These regressions included the same three vari-
ables—outcome, disappointment, and regret—and four new variables. Those were group membership (coded as 0 for normal controls and
1 for the target group) and interactions between group membership
and the three previously mentioned variables. A significant group
effect implies that emotional responses of the target group differ from
those of normal controls in terms of an additive shift. A significant
interaction between group and outcome means that, on average,
emotional reactions are stronger or weaker for the target group when
the coefficient is positive or negative, respectively. A significant
interaction between group and disappointment comparisons means
that the degree of disappointment/elation reflected in reported emo-
tions differs between the target group and normal controls. Similarly, a
significant interaction between group and regret comparisons means
the degree of regret/rejoicing reflected in reported emotional reactions
differs between the target group and normal controls.

Our hypothesis was that VMPPC and LOFC patients would report
emotions with less sensitivity to regret comparisons than the
emotions of normal controls. This hypothesis implies significant
interactions between the target group and regret comparisons (with
negative coefficients). Statistical tests of these hypotheses were based
on the total number of subjects (normal controls plus target subjects)
minus the number of estimated parameters. We estimated 7 coeffi-
cients, and our lesions groups had 5, 7, and 6 for lesion controls,
VMPPC patients, and LOFC patients, respectively. That left us with 24,
26, and 25 degrees of freedom for tests with lesion controls, VMPPC
patients, and LOFC patients, respectively. Our second hypothesis
about the LOFC patients making more financially worse choices is
tested by comparing the percentage of their worse choices to those of
other groups.

3. Results

We present our findings in three sections. The first shows
emotional responses of normal comparison subjects. The second
presents emotional responses of patients (lesion comparisons,
VMPPC and LOFC) relative to those of normal subjects. We also
compare the relative frequencies of counterfactual comparisons
(either disappointment/elation or regret/rejoicing) in patient groups
relative to normal subjects. The third section compares the choices
of patient groups relative to those of normal comparisons.

3.1. Emotions of normal comparison subjects

Previous work by Mellers, Schwartz, Ho, and Ritov (1997, 1999)
demonstrated that emotional reactions to the consequences of
risksy choice depended on outcomes, disappointment (vs. elation)
comparisons, regret (vs. rejoicing) comparisons, and surprise. We
used this framework to evaluate the emotional experiences in this
study. According to decision affect theory, counterfactual compar-
isons of disappointment and regret are weighted by the surprise of
the outcome (or outcomes) that occurred. Disappointment is
weighted by the surprise of the obtained outcome (one minus
the probability of the obtained outcome), and regret is weighted
by the surprise of the actual and foregone outcomes (one minus
the product of the probabilities of the outcomes).

Results of regression analyses for normal controls are shown in
Table 3. The effect of outcome was significant, and disappointment
weighted by surprise was a significant trend (p = 0.06). Participants
reported greater negative emotional reactions when their outcome
was inferior to the other possible outcome of the chosen gamble.
Finally, regret weighted by surprise was significant. Participants
reported greater negative emotional reactions when their outcome
was inferior to the foregone outcome of the gamble not selected.
This model gave a reasonable description of the emotions with a
multiple correlation of 0.71 ($R^2=0.71$, $p<0.001$). Results were generally similar to those obtained by Mellers et al. (1999) using normal undergraduates.

Outcome, disappointment, and regret effects are shown graphically in Figs. 5, 6, and 7, respectively. Normal comparison subjects appear on the left of each figure. Fig. 5 shows outcome effects; gains are reported as more pleasurable than losses. Fig. 6 shows effects due to disappointment comparisons. Emotional reactions are plotted against outcomes of $-8$ and $8$, and $32$. Normal controls and lesion controls do not differ. But outcome effects are significantly greater for the medial and lateral OFC patients.

Fig. 7 shows regret effects, plotted as in Fig. 6, except curves now refer to the foregone outcome of the unselected gamble ($-32$ or $32$) rather than the other outcome of the selected gamble. Regret is seen in terms of the spacing between the lines. Normal controls generally reported greater positive emotional reactions when their outcome was better and greater negative emotional reactions when their outcome was worse.

### 3.2. Emotions of patient groups relative to normal comparison subjects

We compared each lesion group to normal comparison subjects using linear regressions. Table 3 shows the results of these comparison regressions. First, we examine the comparison between normal controls and lesion controls. These subjects did not differ from normal controls; there were no effect of group ($p>0.1$) and no group interactions ($p>0.1$). Emotional responses of the lesion controls and lesion controls. These subjects did not differ from normal controls; there were no effect of group ($p>0.1$) and no group interactions ($p>0.1$). Emotional responses of the lesion.

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**Table 3**

Regression results for normal comparison subjects and comparisons of patient groups with normal comparisons.

<table>
<thead>
<tr>
<th>Normal comparisons</th>
<th>Lesion comparisons</th>
<th>Medial OFC</th>
<th>Lateral OFC</th>
<th>Medial vs. lateral OFC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coefs SE t Stat</td>
<td>Coefs SE t Stat</td>
<td>Coefs SE t Stat</td>
<td>Coefs SE t Stat</td>
<td>Coefs SE t Stat</td>
</tr>
<tr>
<td>Intercept 4.05 0.39 10.37**</td>
<td>4.05 0.39 10.35**</td>
<td>4.05 0.40 10.11**</td>
<td>4.05 0.40 10.22**</td>
<td>4.80 0.82 5.84**</td>
</tr>
<tr>
<td>Outcome 0.47 0.03 14.89**</td>
<td>0.47 0.03 14.76**</td>
<td>0.47 0.03 14.62**</td>
<td>0.47 0.03 14.64**</td>
<td>0.71 0.07 10.77**</td>
</tr>
<tr>
<td>Disapp 0.05 0.03 1.66</td>
<td>0.05 0.03 1.66</td>
<td>0.05 0.03 1.62</td>
<td>0.05 0.03 1.64</td>
<td>0.14 0.06 2.14**</td>
</tr>
<tr>
<td>Group 0.14 0.02 7.35**</td>
<td>0.14 0.02 7.31**</td>
<td>0.14 0.02 7.40**</td>
<td>0.16 0.04 3.74**</td>
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</tr>
<tr>
<td>G × Out 0.78 0.40 1.98</td>
<td>0.75 0.86 0.87</td>
<td>-1.71 0.92 -1.86</td>
<td>-1.46 1.22 -1.02**</td>
<td></td>
</tr>
<tr>
<td>G × Dis 0.03 0.08 0.41</td>
<td>0.09 0.07 1.27</td>
<td>0.01 0.07 0.08</td>
<td>-0.08 0.10 -0.33</td>
<td></td>
</tr>
<tr>
<td>G × Reg 0.00 0.08 0.00</td>
<td>0.01 0.04 0.33</td>
<td>-0.09 0.04 -2.09*</td>
<td>-0.11 0.06 -1.77**</td>
<td></td>
</tr>
</tbody>
</table>

**Note:** The first regression shows normal comparison subjects, and regressions two through four show patient groups relative to normal comparisons. The final regression compares the medial and lateral OFC lesion groups.

* * p < 0.05.

** * p < 0.01.
controls appear in Figs. 5–7. These emotional reactions were sensitive to outcomes (Fig. 5) disappointment comparisons (Fig. 6) and regret comparisons (Fig. 7). Despite the brain damage, these subjects reported emotions that resembled those of normal comparisons.

Next, we examined the relative frequencies of positive or negative counterfactual comparisons in the actual and foregone combinations that each group experienced. Since choices were under the control of participants, the relative frequency of disappointment and regret comparisons might influence emotional ratings. We compared the percentages of disappointing, elating, rejoicing, and regretful outcomes of normal control and lesion control subjects, but found no differences (p’s > 0.1).

Regression comparisons between normal controls and VMPFC patients appear in Table 3. Contrary to our prediction, VMPFC patients reported emotional reactions that were sensitive to regret comparisons. In fact, VMPFC patients reported stronger emotional reactions to outcomes than normal controls, but there were no differences between in sensitivity to disappointment or regret comparisons.

Mean ratings of the reported emotions for VMPFC patients appear in Figs. 5–7. The steeper line in Fig. 5 for VMPFC patients relative to controls shows the greater effect of outcomes, as found in the regression. Greater outcome effects can also be seen in Figs. 6 and 7 with steeper slopes for VMPFC lesion subjects than normal comparison subjects. Reported emotions of VMPFC patients were also sensitive to disappointment and regret comparisons. The spacing between the lines in Figs. 6 and 7 reflects disappointment and regret effects, respectively. VMPFC patients did not differ from normal controls in either of these respects.

The LOFC group also can be seen in Figs. 5–7. LOFC patients reported heightened emotional reactions to outcomes, as found with VMPFC lesion patients (see Table 3). Critically, however, LOFC patients reported emotions that were less sensitive to regret comparisons than those of normal controls, as seen in the decrease in the vertical spacing between the lines in Fig. 7. A separate regression analysis of the LOFC patients alone revealed no effects of disappointment or regret comparisons (p’s > 0.1). An additional regression analysis comparing VMPFC and LOFC patients (shown in Table 3) indicated that the emotional reactions of VMPFC and LOFC patients differed only in terms of regret comparisons. Lateral OFC lesion patients reported emotional reactions that were less sensitive than VMPFC lesion patients to regret comparisons at the level of a trend (t(6) = −1.77, p < 0.07). Our hypothesis about the LOFC group reporting emotions that were less sensitive to regret comparisons was supported.

We wondered whether these differences in disappointment and regret comparisons were due to the relative frequency of experiencing disappointing or regretful outcomes. To find out, we compared the relative frequency of these disappointment and regret comparisons in patients to those of normal controls. These rates were indistinguishable (p’s > 0.1 and p’s > 0.1, correspondingly). Finally to determine whether differences in task payoffs may have influenced the emotional responses of participants, we compared task payoffs (money earned) across groups. Payoff rates were statistically indistinguishable (p’s > 0.1).

To summarize, the emotional responses of lesion comparison subjects and normal comparison subjects did not differ. Contrary to our prediction, the emotional sensitivity of the VMPFC group to regret comparisons did not differ from that of normal controls. However, the emotional sensitivity of the LOFC patients and the normal controls did differ; LOFC patients were less sensitive to regret comparisons.

3.3. Choices of patient groups relative to normal comparison subjects

Next we turn to the choices of patient groups relative to normal controls. We separated gamble pairs into (1) financially better vs. financially worse gambles, (2) safer-and-smaller vs. risky-and-rewarding gambles, and (3) risk averse vs. risk seeking gambles. In the better vs. worse gamble pairs (B/W), better gambles had higher expected returns and less risk. With these pairs, we could examine whether subjects selected made good risk/return tradeoffs. With the safer-and-smaller vs. risky-and-rewarding pairs (SS/RR), we could evaluate preferences for lower expected values and less variance vs. greater return and more variance. With the risk averse vs. risk seeking pairs (RA/RS), we could observe preferences for pure risk holding return (i.e., expected value) constant. There were 9 B/W pairs, and each pair was presented 4 times, so counts were divided by 36 pair presentations. There were 8 (SS/RR) pairs each presented 4 times, or 32 such presentations, and there were 4 (RA/RS) pairs each presented 4 times, for a total of 16 presentations.

Table 4 shows the percentages of better choices, risk-and-rewarding choices, and risk seeking choices for each lesion group relative to normal comparison subjects. Mann–Whitney U tests indicated no differences between normal controls and lesion controls. In addition, there were no differences in preferences for risk (either risk aversion vs. risk seeking preferences or risky-and-rewarding vs. safe-and-smaller preferences) between any patient group and normal comparison subjects.

---

**Table 4**

<table>
<thead>
<tr>
<th>Choice</th>
<th>Normal comp. group (%)</th>
<th>Lesion comp. group (%)</th>
<th>VMPFC group (%)</th>
<th>Lateral OFC group (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Better/worse</td>
<td>77</td>
<td>64</td>
<td>48</td>
<td>66</td>
</tr>
<tr>
<td>Risk seeking/risk averse</td>
<td>62</td>
<td>69</td>
<td>74</td>
<td>56</td>
</tr>
<tr>
<td>Risky-rewarding/smaller-safe</td>
<td>79</td>
<td>81</td>
<td>83</td>
<td>82</td>
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Note: Comp. = comparison. Comparison between lesion groups and normal comparison subjects.

* = p < 0.05.
We predicted that the choices of VMPFC patients would be worse than those of LOFC patients, indicative of VMPFC patients’ lower sensitivity to differences in expected value. As expected, VMPFC patients were less able to identify financially better gambles and selected more financially worse gambles than normal comparison subjects (z = 2.252, p < 0.05). LOFC patients made better gamble choices at a rate that was similar to those of normal comparison subjects. Finally, we compared the percentage of better gamble choices, risk-and-rewarding choices and risk seeking choices of VMPFC and LOFC lesion subjects. VMPFC subjects choose more gambles that were financially worse than normal comparison subjects and (though not predicted), VMPFC patients were also more risk seeking than LOFC patients (z = 1.963, p < 0.05).

To further investigate the choices of VMPFC patients, we plotted the frequency of choosing gamble A as a function of the differences in expected value between options A and B. Fig. 8 shows estimated choice probabilities based on logistic regressions for each group. Probabilities of selecting the better gamble are similar for normal comparison subjects, lesion comparison subjects, and LOFC subjects. VMPFC subjects however exhibit a shallower logistic curve, reflecting a choice pattern indicative of decreased sensitivity to differences in expected value between option A and option B.

4. Discussion

This study examined the role of the medial and lateral OFC in the experience of regret. Participants made choices between risky options with monetary outcomes. After each choice, gambles were resolved and revealed; participants learned both outcomes and rated their pleasure or displeasure with the outcome. This process continued for 84 trials. LOFC patients reported emotional reactions that were less sensitive than normal controls to regret comparisons, as predicted. But contrary to our predictions, VMPFC patients and normal comparison subjects did not differ in their reported sensitivity to regret comparisons. Our prediction that the VMPFC group would select more gambles that were financially worse was supported.

Taken together, the results were surprising. The VMPFC group selected more gambles that were financially worse, but they appeared to experience regret. In contrast, the LOFC group selected more gambles that were financially better, but they appeared to be less sensitive to regret. Less regret did not impair the choices of LOFC patients; their selections resembled those of normal comparison subjects.

This study is the first to compare the effects of VMPFC and LOFC damage on choice and subsequent emotions. The LOFC region of maximal overlap represents an anatomical impairment that is specific to the LOFC group (see slice 3 in Figs. 1 and 2). The VMPFC group region of maximal overlap includes bilateral damage to the medial portions of the PFC. The relatively distinct anatomical damage (albeit some individual lesion overlap) leads us to believe that the VMPFC and LOFC may play distinct roles in choice and emotional reactivity. What might those roles be?

Emotions are critical for learning. Experienced emotions (i.e., those occurring after a choice) are a consequence of choice. They presumably inform anticipated emotions (i.e., those imagined prior to making a choice), and anticipated emotions, in turn, guide future decisions. The VMPFC (as well as the anterior and posterior cingulate) are important to both the formation of associations between choices and outcomes and the encoding of choice values (Rangel & Camerer, 2008; Rushworth & Behrens, 2008; Seo & Lee, 2008). Awareness of the psychological value of a realized outcome is essential for adaptive decision making. There may also be advantages to awareness of the value of options not taken and the consequences that follow; otherwise known as counterfactual outcomes.

Based on our findings that VMPFC lesion participants made financially worse choices, but reported emotions that were sensitive to regret, we propose that the VMPFC is not necessary for the post-decision experience of regret. Rather we support the long held theory that the VMPFC is necessary for representing the anticipated value of choice options. The poor choices of VMPFC lesion subjects, as well as the exaggerated emotional response to gains and losses suggest that VMPFC patients may have been less able to anticipate the value of options, and possibly as a consequence, were surprised by the resulting gains and losses, heightening their emotional responses.

The LOFC however, appears to have a distinct role in experienced emotions. Lateral OFC patients reported emotional reactions not indicative of regret. Regret is a counterfactual comparison between an actual outcome and a foregone outcome under a different choice, so we propose that the LOFC is critical for representing the reward of forgone outcomes that could signal adaptive changes in behavior. A representation of the reward potential of forgone outcome would enable individuals to exploit valuable, otherwise discarded, information in complex environments and allow for more efficient transitions in behavior (i.e., reward potential of forgone option exceeds reward potential of chosen option, presumably changing behavior (Boorman, Behrens, & Rushworth, 2011).

The claim that the LOFC is necessary for representing the reward potential of forgone choices is consistent with evidence that the lateral frontal polar cortex (IFPC), a neighboring anterior region that overlaps slightly with the lateral OFC, contributes to the representation of the forgone outcome. For example, Boorman, Behrens, Woolrich, and Rushworth (2009) showed that, during a
binary choice fMRI task, IFPC activity increased with the reward associated with the option not taken. In addition, a priming lesion study conducted by Noonan et al. (2010) that compared effects of medial and lateral OFC damage in monkeys performing a value-learning task found results that suggested the LOFC codes the value of choices. Noonan and colleagues found that monkeys with medial OFC damage were less able to assess differences in expected values of choice options, whereas monkeys with lateral OFC damage were impaired at assigning post outcome “reward credit” to a choice option.

Individuals with lateral OFC damage may not experience regret because they are unable to conduct a counterfactual comparison between the reward value of the choice taken and the reward value of the forgone choice. The LOFC may guide choices via the comparison of choice options, the integration of context (Beer, Knight, & D'Esposito, 2006), and other changes or shifts in behavior (Kringelbach & Rolls, 2004; Dias, Robbins, & Roberts, 1996), which occur due to sustained representation of the reward value of relevant alternate choices. Future research should clarify anticipated regret on learning, we postulate that individuals with expected value and choose adaptively despite exhibiting less hurtful emotional information. Psychological Science, 17(5), 448–453.


