

Orbitofrontal lesion patients show an implicit approach bias to angry faces

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Abstract

2 Damage to the orbitofrontal cortex (OFC) can cause maladaptive social behavior, but the cognitive
3 processes underlying these behavioral changes are still uncertain. Here, we tested whether patients
4 with acquired OFC lesions show altered approach-avoidance tendencies to emotional facial
5 expressions. Thirteen patients with focal OFC lesions and 31 age- and gender-matched healthy controls
6 performed an implicit approach-avoidance task in which they either pushed or pulled a joystick
7 depending on stimulus color. While controls avoided angry faces, OFC patients displayed an
8 incongruent response pattern characterized by both increased approach and reduced avoidance of
9 angry facial expressions. The approach bias was stronger in patients with higher self-reported
10 impulsivity and disinhibition, and in those with larger lesions. Moreover, patients committed more errors
11 in the task, which in turn was correlated with self-rated clinical impairment. We further used linear
12 ballistic accumulator modelling to investigate latent parameters underlying approach-avoidance
13 decisions. Controls displayed negative drift rates when approaching angry faces, whereas OFC lesions
14 abolished this bias. In addition, OFC patients had weaker response drifts than controls during angry
15 face avoidance. Finally, patients showed generally reduced variability in drift rates and shorter non-
16 decision times, indicating impulsive and rigid decision-making. In sum, our findings suggest that OFC
17 damage alters the pace of evidence accumulation in response to threat signals, eliminating a default,
18 protective avoidant bias and facilitating dysfunctional approach behavior.

Significance statement

21 Lesions in the orbitofrontal cortex (OFC) may alter social behavior, rendering individuals irritable or
22 reckless. However, the precise cognitive mechanisms underlying these changes are unknown. We here
23 examined whether OFC damage impacts how persons respond to social signals using a joystick-based
24 task. Contrary to control participants, patients showed both increased approach to, and reduced
25 avoidance of angry facial expressions, i.e. they were quicker to pull angry faces close and slower to
26 push them away. Further analyses of reaction times revealed that OFC patients lack a default tendency
27 against angry face approach, and that they show a slower decision build-up when avoiding angry faces.
28 Thus, our findings suggest that OFC lesions reduce fearful responses to social threat signals.

29 **Introduction**

30 Patients with damage to the orbitofrontal cortex (OFC) often show disruptive social behavior
31 (Barrash et al. 2000; Blair 2004; Beer et al. 2006). OFC lesions typically impact adjacent white matter,
32 thereby hindering OFC-amygdala cross-talk (Folloni et al. 2019) and rendering individuals more
33 emotionally reactive (Motzkin et al. 2015). Consequently, antisocial behavior related to OFC dysfunction
34 has been classically attributed to deficits in emotion regulation (Davidson et al. 2000). However, this
35 view has proven difficult to reconcile with the many other functions ascribed to the OFC, such as
36 subjective value computation (Clithero and Rangel 2014). Recent investigations hence suggest a more
37 general *evaluative* and *generative* role for the OFC (Hiser and Koenigs 2018). According to this view,
38 the OFC codes for the potential hedonic or threatening value of a given stimulus in order to steer the
39 organism towards or away from it (Rudebeck and Rich 2018). In this framework the OFC is assumed to
40 generate cognitive maps of current internal states and external sensory information, enabling the
41 selection of the most appropriate course of action (Wilson et al. 2014; Stalnaker et al. 2015). Such a
42 process has been termed model-based or goal-directed behavior because it operates on the basis of
43 internal representations of oneself and the environment rather than by force of habit (Lucantonio et al.
44 2012).

45 From this rationale, it follows that antisocial behavior after OFC damage could arise from
46 inaccurate assessment and selection processes. More specifically, OFC lesions might impair the ability
47 to correctly predict the consequences of one's own actions in response to social signals (Rudebeck and
48 Murray 2014), e.g., wrongly expecting rewards from approaching potential punishment cues.
49 Nevertheless, evidence to support this tenet is scarce in humans with OFC lesions. One report suggests
50 that OFC-damaged patients display an altered sense of personal distance, e.g., they get closer to
51 strangers (Perry et al. 2016). Comparably, a study showed that persons with OFC lesions judge negative
52 facial expressions (i.e., angry, disgusted, fearful and sad) as *more* approachable (Willis et al. 2010). It
53 remains to be tested, however, whether these tendencies can be attributed to implicit biases during
54 action selection, and whether these putative alterations are linked with actual impairments in daily
55 functioning. Moreover, it is unclear which precise cognitive mechanisms underlie such abnormal
56 behavioral dispositions. These are important steps in understanding how OFC-dependent disturbances
57 in social behavior play out in everyday life.

58 In order to clarify these issues, we investigated whether OFC lesions lead to implicit response
59 biases towards or away from negative, positive, or neutral facial expressions. We used a version of the

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60 approach-avoidance task (AAT) wherein subjects have to either push or pull a joystick depending on
61 the color (e.g. red or green) of a human face (Roelofs et al. 2010). Faces are programmed to grow or
62 shrink in size accordingly, giving the impression that they loom closer or recede upon pulling and
63 pushing, respectively. Hence, the AAT allows measuring implicit response tendencies to task-irrelevant
64 features of the faces such as their emotional expression. A study with this task suggested that
65 psychopaths lack automatic avoidance of angry faces, and that this effect was correlated with
66 aggressiveness (von Borries et al. 2012). Following a similar rationale, we tested whether task scores
67 correlated with patients' daily emotional behavior as measured with validated clinical scales in order to
68 assess the clinical relevance of possible approach-avoidance biases.

69 In addition, we scrutinized the putative cognitive mechanisms underlying altered task
70 performance in OFC patients using Linear Ballistic Accumulator (LBA) modelling on response times
71 (Brown & Heathcote, 2008). LBA modelling assumes that decisions arise from a sequential evidence
72 accumulation process, the speed of which is determined by multiple latent variables (e.g., pre-existing
73 response tendencies or shorter decision latencies) that can be quantified and compared between
74 experimental conditions and/or groups. Previous modelling studies on an explicit version of the AAT
75 reported relatively faster evidence accumulation in healthy subjects when threatening stimuli are to be
76 avoided (Krypotos et al. 2015; Tipples 2019). LBA modelling might hence offer insights not captured by
77 standard methods.

78 **Methods**

79 *Participants*

80 The clinical sample consisted of 13 patients with chronic (> 6 months post-injury or surgery),
81 focal damage to the ventral prefrontal cortex (mean age=50.8 [27-62], 7 women, 12 right-handed).
82 Lesions were predominantly located in ventromedial prefrontal brain regions, with a few lesions
83 extending more dorsally and laterally (Fig. 1A). Etiology of the lesions was either meningioma (n=9),
84 traumatic brain injury (n=2), oligodendrolioma (n=1), or astrocytoma (n=1). The control sample was
85 composed of 31 age- and gender-matched neurologically healthy individuals (mean age=50.1 [43-54],
86 19 women, all right-handed). As previously reported, patients had normal or corrected to normal vision,
87 showed no deficits in standard neuropsychological testing, and had no motor dysfunction of the hands.
88 However, they reported greater difficulties in executive function, metacognition, and behavioral
89 regulation as compared to a separate control sample (see Løvstad et al., 2012 for a complete report).
90 All patients were recruited and measured at Oslo University Hospital and the University of Oslo, whereas

91 the behavioral control sample was recruited and measured at the University of Lübeck. All participants
92 provided informed consent and the study procedures adhered to the Declaration of Helsinki. The study
93 was approved by the ethics committee of the University of Lübeck and the Regional Committee for
94 Medical Research Ethics - South East Norway.

95 *Clinical scales*

96 Patients filled out the self-report form of the Behavior Rating Inventory of Executive Function –
97 Adult version (BRIEF-A; Roth et al., 2005) and the Urgency, Premeditation, Perseverance, Sensation
98 Seeking (UPPS) Impulsive Behavior Scale (Whiteside and Lynam 2001), both ad-hoc translated into
99 Norwegian. The BRIEF-A is a standardized rating scale consisting of 75 items that tap into everyday
100 executive functioning within the past 6 months. Internal consistency and test-retest reliability of the
101 BRIEF-A are reportedly high and construct validity has been established in healthy and clinical
102 populations (Waid-Ebbs et al. 2012). Since we aimed to investigate the neural control of approach-
103 avoidance responses, for the purposes of this study we only considered the scales “Inhibit”, “Emotional
104 Control”, and “Self-Monitor” from the BRIEF-A. The Inhibit scale measures deficits in inhibitory control
105 and impulsivity; the Emotional Control scale assesses a person’s inability to regulate emotional
106 responses; and the Self-Monitor scale evaluates difficulties in social or interpersonal awareness. The
107 UPPS Impulsive Behavior Scale (Whiteside and Lynam 2001) is a 45-item self-report, assessing
108 different facets of impulsivity on four subscales. The UPPS has been shown to display good internal
109 consistency and construct validity (Whiteside et al. 2005). We used the total UPPS score for correlational
110 analyses.

111 *Implicit Approach-Avoidance Task (AAT)*

112 Subjects performed the implicit approach-avoidance task (AAT; Fig. 1B) as previously described
113 (Roelofs et al. 2010; von Borries et al. 2012). Stimuli were photographs (Ekman and Friesen 1976;
114 Lundqvist et al. 1998) showing the face of one out of eight actors (four male and four female) displaying
115 angry, happy or neutral expressions with either direct (straight) or averted (sideways) gaze. Photographs
116 were cut out ovaly and tinted red or green, amounting to a total number of 384 trials. Participants
117 performed 18 practice trials, followed by the experimental trials. After half of the trials, subjects had a
118 break, performed two additional practice trials to recall task demands and completed the second half.
119 Stimuli were presented randomly, with no more than three of the same emotion-response combinations
120 in succession.

121 Pictures were presented at a 1024 x 768 pixels resolution on a computer screen. We placed the
122 joystick (Logitech Attack 3) between subject and screen to allow for comfortable pull and push
123 movements. Participants started each trial by pressing the fire button with the index finger of the
124 dominant hand. A face stimulus appeared in the center of the screen. Participants were instructed to
125 ignore the facial expression and only respond to the color of the face. Half the participants had to push
126 the joystick in response to red and pull in response to green stimuli, the other half had the opposite
127 instruction. To visually emphasize that pull movements meant approach, and push movements meant
128 avoidance, pictures grew or shrank in size following pull or push movements, respectively. Stimuli had
129 a starting size of 9.5° by 13° and could shrink to a minimum of 3.5° by 4.5° when pushing or grow to a
130 maximum of 15.5° by 20° when pulling. In practice trials, pictures remained visible after erroneous
131 responses to allow for response correction, whereas in the task proper stimuli disappeared after they
132 had reached minimal or maximal size. Participants were instructed to respond as quickly and accurately
133 as possible. Importantly, trials could only be initiated once the joystick was placed back in its original
134 centered position.

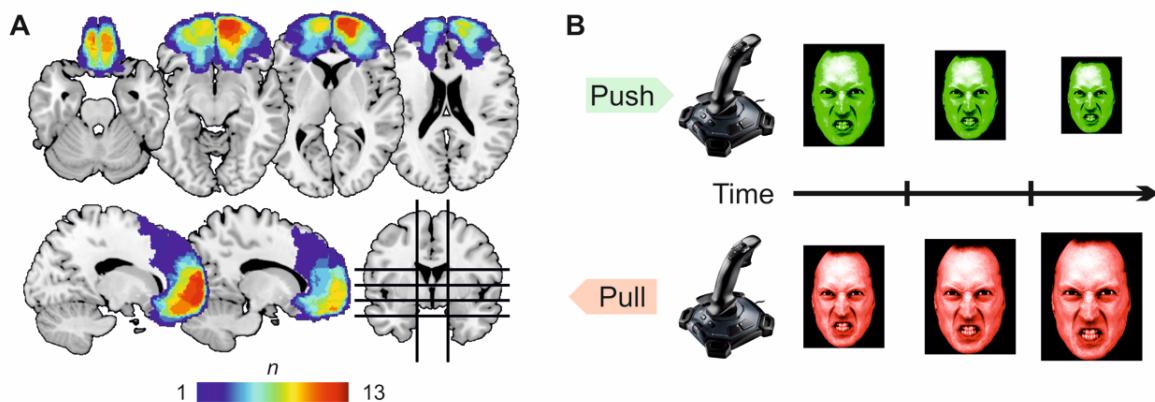


Figure 1. **A)** Lesion overlap. Warmer colors depict more overlap between patients. Peak overlap was located in x=4, y=58, z=-14 (Montreal Neurological Institute space). **B)** Schematic depiction of the implicit Approach Avoidance Task (AAT). Subjects had to either push or pull a joystick in response to the color of the presented face while ignoring its facial expression (angry, happy, or neutral), gaze (direct or averted), gender (male or female), and identity (eight actors). Pushing made faces shrink in size, whereas pulling made them grow larger. The 384 trials were self-paced.

135 *Behavioral data analysis*

136 Reaction times (RT) were recorded as time from stimulus onset until the first joystick movement.
137 We excluded incorrect trials as well as those with RT shorter than 150ms or longer than 1000ms, and
138 extracted mean log-transformed RT per cell (as in Bertsch et al., 2018). We then ran an analysis of
139 variance (ANOVA) on the resulting values with within-subject factors emotion (happy, neutral, angry),
140 actor gender (male, female), gaze (left, right, and direct), movement (pull or push), and the between-

141 subject factor group (OFC vs healthy controls) using the *ez* package (version 4.4-0). We modelled all
142 relevant task factors as in previous studies with the implicit AAT (Roelofs et al. 2010; von Borries et al.
143 2012). In order to control for multiple testing, we applied a False Discovery Rate (FDR) correction as
144 recommended for exploratory ANOVAs (Cramer et al. 2016). Color and condition were counterbalanced
145 across participants (green=pull for one half, green=push for the other half) and are thus controlled for
146 by design. We inspected significant effects with post-hoc t-tests.

147 Due to the relatively low and unevenly distributed number of errors, we simply compared the
148 mean error rate between groups using a Welch's t-test, which is robust to unequal variances and uneven
149 sample sizes (Ruxton, 2006). Subsequently, we computed Pearson correlation coefficients between
150 AAT scores (between-condition differences in RT and overall error rates) and each of the four clinical
151 scales. We assessed the robustness of significant correlations with bootstrap resampling to obtain 95%
152 bias-corrected accelerated confidence intervals (BCa CI) with 10000 iterations using the *bootstrap*
153 package (version 2019.5). We performed all analyses described in this section in R (version 3.6.1)
154 running on R Studio (version 1.1.423).

155 *Linear ballistic accumulator (LBA) modelling of reaction times*

156 We subsequently implemented Linear Ballistic Accumulator (LBA) modelling on reaction time
157 data (Brown and Heathcote 2008). LBA models assume that decisions stem from a sequential evidence
158 accumulation process (Fig. 3A). Evidence for each response option is gathered linearly by a separate
159 accumulator, which races against the other/s until one of them reaches a decision threshold. Evidence
160 accumulation starts after a variable period of non-decision time and its speed is given by the drift rate,
161 which is sampled from a normal distribution. The standard deviation of this distribution constitutes what
162 we here label drift noise, i.e., variability in the pace of evidence accumulation. In addition, the
163 accumulators might begin each trial from a different starting point, which is drawn from a uniform
164 distribution. Therefore, a response option will be taken more quickly if starting point and decision
165 threshold are nearer, if the drift rate is higher and less variable, and if the non-decision time is shorter.
166 LBA models are akin to the now-popular drift diffusion models (DDM), but are simpler and more tractable
167 computationally and thus well-suited for the relatively low amount of trials available in the present
168 dataset (see Heathcote and Hayes, 2012, for a detailed empirical comparison between LBA and DDM).

169 Here, we fitted a series of LBA models with two accumulators (approach and avoidance) and
170 four parameters: decision threshold, starting point, drift rate, and drift noise. We tested a total of 16
171 models in which a given combination of these parameters was allowed to vary between the six

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172 experimental conditions of interest: pull angry, pull happy, pull neutral, push angry, push happy, and
173 push neutral. We could not test for a modulation of experimental condition on non-decision time because
174 models including this effect failed to converge in most subjects. See Table 1 for a summary of all models.
175 We fitted each model on each participant's reaction time data using full information maximum likelihood
176 estimation as implemented in the *glba* package version 0.2. We used raw RT excluding errors and
177 responses quicker than 150ms or slower than 1s. For model comparison and inspected which model
178 yielded the lowest Bayesian Information Criterion (BIC) values across participants. BIC is a standard
179 goodness of fit measure that penalizes for model complexity (Raftery 1995; Burnham and Anderson
180 2004). Our model fitting and comparison approach is highly comparable to that of a recent DDM study
181 on social approach-avoidance decisions (Mennella et al. 2020). Afterwards, we simulated data per group
182 using the *rlba()* function and the average parameter estimates from the winning model. Finally, we
183 compared the parameters of the winning model between groups with independent-samples Welch t-
184 tests. We used R (version 3.6.1) running on R Studio (version 1.1.423) for all analyses in this section.

185 *Neuroimaging data acquisition and analysis*

186 Structural brain volumes were recorded at the Intervention center at Oslo University hospital
187 (Norway) on a Philips Ingenia 3-T scanner. We acquired structural images with a T1-weighted 3D turbo
188 gradient-echo sequence with the following settings: repetition time (TR)=1.900ms, echo time
189 (TE)=2.23ms, flip angle=8°, voxel size=1mm³, field-of-view (FOV)=256x256mm. Members of the team
190 at the University of Oslo, trained in lesion reconstruction, manually delineated lesion masks on each
191 patient's anatomical images. We normalized these masks as recommended for lesioned brains (Ripollés
192 et al. 2012) and created lesion overlap maps using MRIcron (Rorden and Brett 2000). We also inspected
193 whether lesion size was linked with reaction times and error rates in the task. We correlated lesion size
194 with behavioral parameters showing a group difference in the AAT and obtained the 95% bootstrapped
195 CIs with 10000 iterations using the *bootstrap* R package to assess these effects' robustness.

196 **Results**

197 *Approach-Avoidance Task (AAT) results*

198 In our primary analysis of reaction times we observed main effects of group ($F_{1,42}=11.92$,
199 $p=.001$, $pFDR=.013$) and emotion ($F_{2,84}=6.89$, $p=.001$, $pFDR=.010$) which were qualified by an emotion
200 x movement interaction that did not survive multiple comparison correction ($F_{2,84}=4.36$, $p=.015$,
201 $pFDR=.083$), and, crucially, by a group x emotion x movement interaction ($F_{2,84}=12.64$, $p<.001$,
202 $pFDR<.001$). In order to dissect the latter three-way interaction, we computed the difference between

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203 push and pull (i.e., approach minus avoidance) for each emotion and inspected for differences between
204 emotion categories in each group, following previous work (Roelofs et al. 2010; von Borries et al. 2012).
205 As shown in Fig. 2A, OFC patients showed a stronger approach bias toward angry relative to both happy
206 ($t_{12}=3.17$, $p=.008$) and neutral faces ($t_{12}=4.32$, $p<.001$), with no difference between happy and neutral
207 faces ($p=.416$). In comparison (Fig. 2B), controls showed a trend-level avoidant bias for angry relative
208 to neutral faces ($t_{30}=1.75$, $p=.089$), with no further differences between categories (all $p>.272$). Thus,
209 OFC patients were generally slower when pushing angry faces away relative to pulling them close.

210 In order to ascertain whether these effects were predominantly driven by approach or
211 avoidance, we computed the difference in reaction times between emotions separately for push and pull
212 movements in each group. Regarding approach movements, OFC patients were faster to pull angry
213 relative to neutral ($t_{12}=3.66$, $p=.003$) but not happy faces ($p=.107$). Controls showed no between-emotion
214 differences in pull movements (all $p>.278$). For avoidance movements, OFC patients were slower to
215 push angry relative to happy faces ($t_{12}=2.88$, $p=.013$) but comparably fast when pushing angry and
216 neutral ones ($p=.284$). Controls were quicker to push angry as compared to neutral faces ($t_{30}=2.27$,
217 $p=.030$) but not happy ones ($p=.605$). Therefore, controls specifically showed avoidance of angry in
218 comparison with neutral expressions. In contrast, OFC patients showed increased approach of angry
219 relative to neutral faces, and reduced avoidance of angry as compared to happy ones. We used these
220 significant between-emotion differences for later correlation analyses, as they index the increased threat
221 approach (pull angry minus pull neutral) and reduced threat avoidance (push angry minus push happy)
222 demonstrated by OFC patients.

223 Additionally, there was an emotion x gaze interaction across the whole sample ($F_{4,168}=4.63$,
224 $p=.001$, $pFDR=.011$). We computed the difference in reaction times between direct and averted gaze
225 and compared between emotions over all participants to further investigate this effect. The interaction
226 was driven by slower reactions to directly-gazing neutral faces relative to happy ($t_{43}=3.09$, $p=.003$) and,
227 at trend level, angry ones ($t_{43}=1.81$, $p=.077$).

228 We subsequently compared error rates between groups. Although both groups performed the
229 task well, OFC patients committed about twice as many errors ($6.87\pm1.13\%$) than healthy controls
230 ($3.47\pm0.46\%$), $t_{16.14}=2.77$, $p=.013$ (Fig. 1C).

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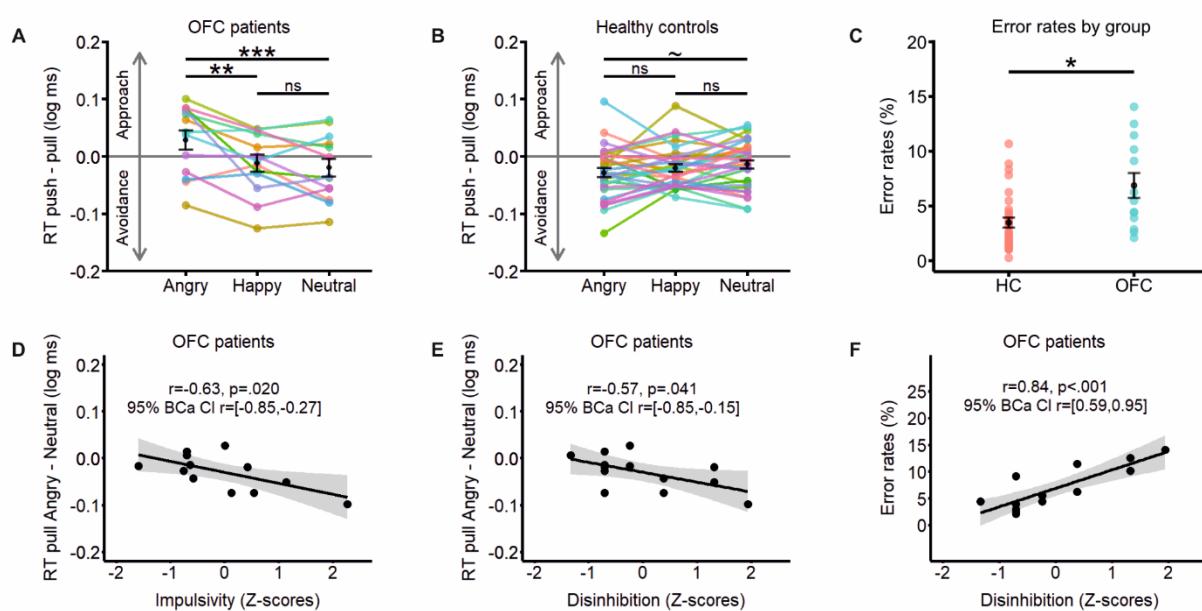


Figure 2. **A**) Patients with orbitofrontal cortex (OFC) lesions showed an approach bias (reaction times [RT] for push minus pull) towards angry relative to happy and neutral faces. **B**) Healthy controls (HC) showed no bias in either direction, with a trend towards avoidance of angry relative to neutral faces. **C**) OFC patients made more errors than HC. **D**) Shorter RT for pull angry minus pull neutral trials were linked with greater self-rated impulsivity in OFC patients. **D**) Shorter RT for pull angry minus pull neutral trials were correlated with greater disinhibition in OFC patients. **F**) Error rates were correlated with all clinical self-reports in OFC patients, including greater self-rated disinhibition. $\sim p < .1$, $* p < .05$, $** p < .01$, $*** p < .001$.

231 Correlations between task scores and clinical scales

232 We then inspected for associations between clinical scales and task-derived scores, with the
 233 aim of testing the clinical relevance of approach-avoidance biases as measured with the AAT. The
 234 approach bias for angry minus neutral faces was linked with increased self-reported impulsivity (Fig. 1D;
 235 $r = -.63, p = .020$, 95% BCa CI $= [-.86, -.28]$), and greater disinhibition (Fig. 1E; $r = -.57, p = .041$, 95% BCa
 236 CI $= [-.85, -.15]$), but there were no correlations with either of the other two clinical scales, or between the
 237 angry push minus happy push difference and any of the scales (all $p > .160$). Error rates were positively
 238 associated with all clinical scales, namely impulsivity ($r = .57, p = .040$, 95% BCa CI $= [.05, .85]$),
 239 disinhibition (Fig. 1F; $r = .84, p < .001$, 95% BCa CI $= [.59, .95]$), emotional control ($r = .59, p = .033$, 95% BCa
 240 CI $= [.23, .78]$), and self-monitoring ($r = .70, p = .007$, 95% BCa CI $= [.25, .90]$).

241 Correlations between lesion size and AAT scores

242 Subsequently, we tested whether task-derived response biases were linked with lesion size.
 243 Patients with larger lesions were quicker to approach angry relative to neutral faces ($r = -.72, p = .004$,
 244 95% BCa CI $= [-.90, -.33]$). Lesion size was not correlated with the push angry minus push happy
 245 difference ($p = .374$) or with error rates ($p > .663$). Lesion extension was thus exclusively associated with
 246 threat approach, but not with the reduced threat avoidance and increased error rates displayed by OFC
 247 patients.

248 *Linear Ballistic Accumulator (LBA) modelling results*

249 Next, we turned to Linear Ballistic Accumulator (LBA) modelling in order to uncover which latent
250 decision parameters might account for OFC patients' response patterns. We provide the complete list
251 of models in Table 1. The winning model assumed that emotional expression and movement modulated
252 drift rates exclusively. This model had the lowest BIC across subjects (median BIC=-646.62, k=10 free
253 parameters) and was the best-fitting model in all 13 OFC patients as well as in 28/31 control participants.
254 According to model-comparison guidelines (Raftery 1995; Burnham and Anderson 2004), the evidence
255 for this model can be considered substantial relative to the two next best-fitting (and slightly more
256 complex) models, one assuming an effect of emotional expression on drift rate and drift noise (median
257 BIC=-629.92, k=15 free parameters), and one in which emotional expression impacted drift rate and
258 decision threshold (median BIC=-629.57, k=15 free parameters). Further, the winning model could
259 reproduce reaction times in pull angry trials with a precision of around ~30-50ms across successive
260 simulations for both OFC patients (example mean simulated data=495ms; mean real data=544ms) and
261 control participants (example mean simulated data=593ms; mean real data=624ms).

Table 1: Summary of Linear Ballistic Accumulator models tested

Modulated parameters in model	K	Median BIC
Threshold, starting point, drift rate, drift noise	25	-546.16
Threshold, starting point, drift rate	20	-575.52
Threshold, starting point, drift noise	20	-75.84
Threshold, drift rate, drift noise	20	-606.32
Starting point, drift rate, drift noise	20	-606.47
Threshold, starting point	15	-117.53
Threshold, drift rate	15	-629.57
Threshold, drift noise	15	-119.90
Starting point, drift rate	15	-624.78
Starting point, drift noise	15	-157.82
Drift rate, drift noise	15	-629.92
Threshold	10	-161.38
Starting point	10	-107.24
Drift rate	10	-646.62
Drift noise	10	-172.87
Null model	5	-169.83

K: number of free parameters; BIC: Bayesian Information Criterion. The model marked in **bold** had the best fit to the data across participants.

262 We subsequently tested whether any of the LBA model parameters differed between groups.
263 Controls had negative response drifts when pulling angry faces close, whereas the mean value for this
264 parameter was centered around zero in OFC patients (Fig. 3B, left; $t_{17.46}=3.51$, $p=.002$). OFC patients
265 also showed lower drift rates than control participants when pushing angry faces away (Fig. 3B, right;
266 $t_{15.56}=2.92$, $p=.010$). Therefore, response drifts in OFC patients were weaker when avoiding angry faces
267 and relatively less negative (i.e. centered around null) when approaching them. OFC patients also had

268 reduced response drifts when pushing happy faces away (Fig. 2C, right; $t_{41.99}=2.29$, $p=.026$), but not
 269 when pulling them close (Fig. 2C, left; $p=.258$). This pattern was also present at trend level for neutral
 270 expressions (Fig. 2D; avoid: $t_{39.10}=1.85$, $p=.070$; approach: $p=.723$). Thus, OFC patients had generally
 271 lower drift rates than controls during avoidance movements, especially for angry faces. Regarding the
 272 remaining parameters, the patient group displayed reduced drift noise (Fig. 2E; $t_{41.11}=3.42$, $p=.001$; HC:
 273 0.18 ± 0.02 , OFC: 0.08 ± 0.01), and non-decision times (Fig. 2F; $t_{13.58}=2.54$, $p=.023$; HC: -1.15 ± 0.10 , OFC:
 274 -1.21 ± 0.40). There were no group differences in decision threshold ($p=.126$) or starting point ($p=.364$).
 275 Hence, evidence accumulation began earlier and was less variable across conditions in OFC patients.

Table 2: Group-wise means and standard errors of free parameters from the winning model

Parameter	HC	OFC
Drift rate pull angry**	$-.24\pm .03$	$.04\pm .07$
Drift rate pull happy	$-.01\pm .009$	$-.001\pm .005$
Drift rate pull neutral	$-.002\pm .008$	$-.005\pm .005$
Drift rate push angry*	$1.46\pm .06$	$.94\pm .16$
Drift rate push happy*	$.04\pm .02$	$-.01\pm .01$
Drift rate push neutral	$.03\pm .02$	$-.01\pm .01$
Drift noise**	$.18\pm .02$	$.08\pm .01$
Starting point	$.13\pm .02$	$.08\pm .03$
Threshold	$.87\pm .14$	$1.56\pm .39$
Non-decision time*	$-.15\pm .10$	$-1.21\pm .40$

HC: healthy controls; OFC: orbitofrontal cortex patients. Asterisks denote significant between-group differences in parameter estimates at * $p<.05$ or ** $p<.01$.

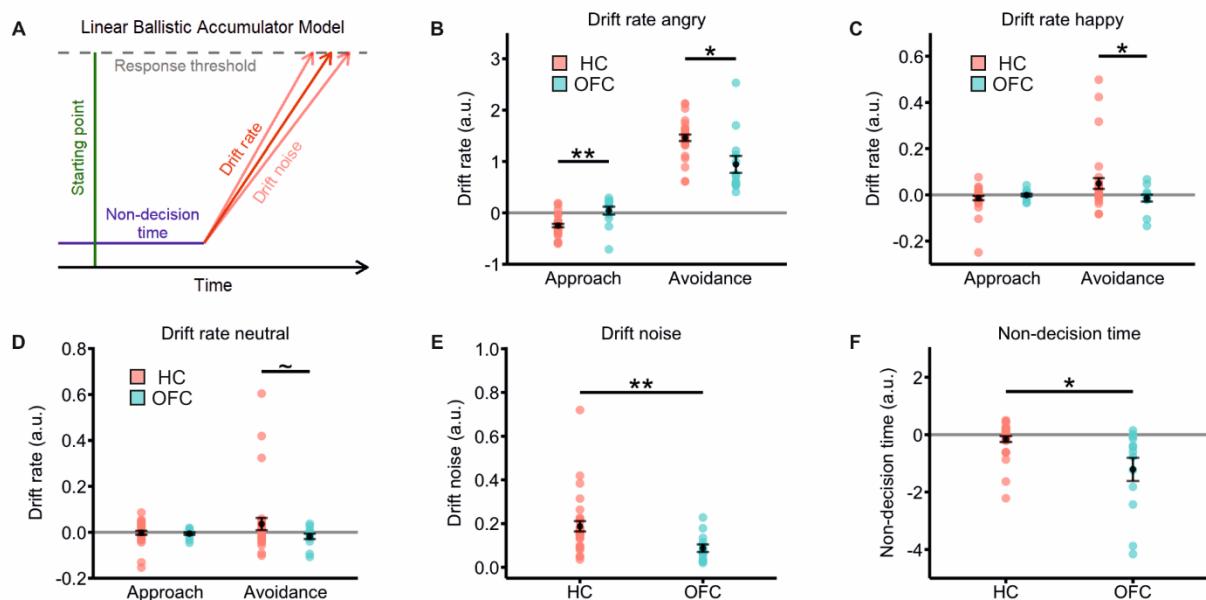


Figure 3. A) Schematic depiction of a Linear Ballistic Accumulator (LBA) model, which operationalizes decisions as the result of a sequential evidence accumulation process. The model assumes separate, competing accumulators for each response option, with faster decisions when the response threshold is lower, starting point is higher, non-decision time is shorter, and the drift towards a given option is stronger and less variable (i.e. higher drift rate and lower drift noise). We estimated the parameters from each participant's reaction time distribution with a maximum likelihood algorithm. **B)** Orbitofrontal cortex (OFC) patients showed less negative (i.e. around zero) drift rates than healthy controls (HC) when pulling angry faces close (left), and lower drift rates when pushing angry faces away (right). **C)** OFC patients had lower drift rates than HC when pushing happy faces away. **D)** OFC patients displayed trend-level lower drift rates than HC when avoiding neutral faces. **E)** OFC patients had lower drift noise. **F)** OFC patients showed shorter non-decision times. A.u.: arbitrary units. ~ $p<.1$, * $p<.05$, ** $p<.01$.

276 In a final exploratory analysis, we tested for associations between LBA parameters and clinical
277 scales in OFC patients as done with reaction times. We limited these analyses to drift rates for threat
278 approach (pull angry minus pull neutral) and threat avoidance (push angry minus push happy), as these
279 were the same contrasts that we computed for correlations with reaction times. There were no
280 associations between either score and any of the clinical scales (all $p > .234$).

281 **Discussion**

282 Maladaptive social behavior is common after orbitofrontal cortex (OFC) damage (Davidson et
283 al. 2000), but the neurocognitive processes underlying these symptoms remain elusive. Here, we tested
284 whether patients with acquired OFC lesions show altered automatic responses to emotional facial
285 expressions. OFC patients displayed both reduced avoidance of, and increased approach to angry
286 faces. Modelling of reaction times revealed relatively slower evidence accumulation when avoiding
287 angry faces in OFC patients relative to controls. Moreover, patients lacked the negative response drifts
288 that controls showed during approach of angry expressions. OFC patients further evinced less variable
289 and earlier-starting evidence accumulation. The approach bias in OFC patients was associated with
290 self-reported clinical measures of impulsive and disinhibited behavior. Patients also committed more
291 errors, which was in turn correlated with greater self-reported impulsivity, disinhibition, problems in
292 emotional control, and worse self-monitoring. Finally, larger lesions were linked with a relatively more
293 pronounced approach bias to angry faces, but not with error rates or avoidance biases. All in all, these
294 findings suggest that OFC damage can precipitate maladaptive behavior by altering the implicit
295 processing of threatening social information during action selection.

296 *OFC lesions increase approach and reduce avoidance of threatening stimuli*

297 Our findings expand on a previous report indicating that OFC-damaged individuals report
298 negative facial expressions to be more approachable (Willis et al. 2010). Here, we showed that this
299 translates into observable, automatic motor behavior, such that OFC patients were quicker to actively
300 approach angry faces (i.e., pull them towards themselves), but slower to avoid them (i.e., push them
301 away). Reduced implicit avoidance of angry faces has been reported in psychopathic offenders (von
302 Borries et al. 2012), who also display dampened physiological reactivity to threatening distractors
303 (Newman et al. 2010). Therefore, both lower threat aversion and enhanced threat approach seem to be
304 at play in populations showing disruptive social behavior.

305 The present results broadly converge with clinical (Blair 2004), volumetric (Chester et al. 2017),
306 and functional (Beyer et al. 2015; Gilam et al. 2015) studies asserting that the OFC is essential for the

307 regulation of aggressive urges. However, our data further indicate that the OFC does not merely
308 suppress automatic impulses but rather directs the course of approach-avoidance reactions, in line with
309 recent proposals (Hiser and Koenigs 2018; Rudebeck and Rich 2018), and with the well-known
310 association between damage to this region and disadvantageous decision-making (Koenigs and Tranel
311 2007). Given that the OFC is involved in the anticipation and evaluation of actions related to certain
312 stimuli (Wilson et al. 2014), we suggest that OFC dysfunction gives rise to an altered processing of
313 threat signals. Specifically, it might be that OFC damage compromises the prediction of behavioral
314 outcomes associated with potentially punishing stimuli, i.e., tagging angry faces as neutral or even
315 potentially rewarding (Rudebeck and Murray 2014). These abnormal value forecasts can in turn enable
316 the impulsive, rule-breaking behavior that characterizes the sequelae of OFC lesions.

317 In line with the latter statement, approach towards angry relative to neutral faces was linked
318 with greater self-reported disinhibition and impulsive behavior. Paralleling our results, it has been
319 reported that patients with borderline personality disorder, who regularly engage in antagonistic and
320 aggressive behavior, also show an approach bias to angry faces (Bertsch et al. 2018) and comparable
321 levels of impulsivity and self-reported anger as those of OFC patients (Berlin et al. 2005). Similarly,
322 healthy individuals with high trait anger are quicker to approach angry relative to happy faces (Veenstra
323 et al. 2017). The current results thus provide further evidence that threat signals might act as appetitive
324 stimuli for individuals with externalizing symptomatology (Chester 2017), and further add that OFC
325 lesions might precipitate such dysfunctional evaluation processes.

326 Of note, the response tendencies observed in OFC patients were independent of gaze direction.
327 This pattern deviates from previous studies reporting group-specific approach-avoidance biases
328 exclusively for directly-gazing angry faces (Roelofs et al. 2010; von Borries et al. 2012). Hence, the
329 present findings tentatively suggest that OFC lesions might be associated with reduced sensitivity to
330 gaze direction. We did find, however, that straight-looking neutral faces were linked with slower reaction
331 times across the whole sample irrespective of movement type. The latter observation insinuates that
332 neutral expressions, due to their inherent ambiguity (Blasi et al. 2009), are more thoroughly evaluated
333 when they are directed to oneself.

334 Importantly, OFC patients performed generally worse in the approach-avoidance task (AAT)
335 than controls. This is largely in line with previous findings on the role of the OFC and lateral frontal pole
336 in controlling social approach-avoidance behavior (Roelofs et al. 2009; Volman et al. 2011). Here,
337 subjects committed more errors than controls in an implicit version of the AAT, which is suggestive of

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338 difficulties in ignoring task-irrelevant stimulus features. This observation concurs with other studies in
339 showing that OFC patients are more susceptible to distraction by to-be-ignored stimulus characteristics
340 (Mäki-Marttunen et al. 2017; Kuusinen et al. 2018), and agrees with the general idea that OFC damage
341 hinders the implementation of goal-directed behavior (Rudebeck and Rich 2018). Moreover, error rates
342 were associated with greater self-reported impulsivity and disinhibition in OFC patients, as well as with
343 worse emotional control and self-monitoring. Such findings speak for the predictive validity of the AAT
344 and support its potential usefulness for assessing emotional dysfunction in neurological patients (Fricke
345 and Vogel 2020).

346 *OFC lesions affect latent decision parameters*

347 We used Linear Ballistic Accumulator (LBA) modelling to delve deeper into the decision
348 processes underlying approach-avoidance responses in OFC patients. These analyses indicated that
349 emotional facial expressions modulated drift rates (i.e., the speed of evidence accumulation after a
350 stimulus appears) but no other parameters. These findings extend previous drift diffusion modelling work
351 using an explicit version of the AAT in which emotional expressions impacted not only drift rates but
352 also response thresholds and non-decision times (Tippl 2019). Hence, the influence of emotional
353 expressions on latent decision variables may be less pronounced when facial expressions are to be
354 ignored. The present data do however fully dovetail previous modelling studies in that response drifts
355 were maximal when threatening stimuli were to be avoided (Krypotos et al. 2015; Tippl 2019). Our
356 results complement these findings by showing that angry faces automatically bias evidence
357 accumulation towards avoidance even in the absence of explicit response contingencies.

358 Between-group comparisons of model parameters revealed profound differences between OFC
359 patients and control participants. OFC patients showed near-zero drift rates when approaching (i.e.,
360 pulling) angry faces, whereas healthy controls showed negative values in this parameter. OFC lesions
361 might thus eliminate a default bias against threat approach. In addition, we observed weaker response
362 drifts during avoidance responses (i.e., push movements) in patients relative to controls. The group
363 difference in this parameter was strongest for angry facial expressions but also present to a lesser extent
364 in happy and neutral trials. Evidence accumulation leading to avoidance decisions is hence more
365 sluggish in OFC patients, and especially so in the presence of angry facial expressions. Therefore, the
366 incongruent approach behavior often observed in OFC patients (Willis et al. 2010; Perry et al. 2016)
367 might be partly attributable to an altered evidence accumulation process in response to threat signals.
368 Specifically, evidence accumulation in OFC patients seems to lack a bias against threat approach and

369 is slower when threatening stimuli are to be avoided. In control participants, in contrast, the positive drift
370 rates when pushing angry faces away might have outweighed the negative drifts when pulling them
371 close, resulting in threat avoidance. These observations agree with the idea that the OFC encodes the
372 currently relevant state-space (Wilson et al. 2014; Stalnaker et al. 2015). Angry facial expressions
373 should, on the basis of previous experience, evoke a representation of possible negative outcomes and
374 thereby facilitate avoidance, as seen in control participants. This negative outcome representation is
375 abolished after OFC lesions, presumably producing the observed alterations in evidence accumulation
376 and the resulting abnormal approach-avoidance tendencies.

377 In addition, OFC patients displayed relatively shorter non-decision times and lower drift rate
378 variability irrespective of experimental condition. This implies that approach-avoidance decision
379 processes start earlier and are more rigid in OFC patients as compared to control participants. The lower
380 non-decision times are in consonance with the generally speeded responding and higher error rates
381 incurred by OFC patients, as well as with the enhanced impulsivity often observed in OFC-damaged
382 individuals (Berlin et al. 2004, 2005). On the other hand, the reduced drift rate variability observed in
383 patients parallels the deficits in goal-directed behavior subsequent to OFC damage, i.e., a failure to
384 update stimulus value resulting in perseverative responses (Rudebeck et al. 2013; Rudebeck and
385 Murray 2014). Importantly, we observed no group differences in starting point or decision threshold,
386 indicating that the approach bias observed in OFC patients is likely due to post-stimulus processing
387 rather than to pre-existing response tendencies. Taken together, LBA results suggest that damage to
388 the OFC might lead to rapid and invariant evidence accumulation, which is in turn slower when avoiding
389 threatening stimuli but relatively faster when approaching these signals.

390 *Limitations*

391 The cross-sectional nature of the design, along with the reduced sample size common in studies
392 with focal lesion patients (Motzkin et al. 2015; Pujara et al. 2016), constrain the generalizability of the
393 present results. Special caution should be exercised regarding the correlations: even though we used
394 bootstrapping to assess their robustness, the ability of the implicit AAT to track interindividual differences
395 is uncertain due to the lack of data on this instrument's reliability (Hedge et al. 2018). In general, effect
396 sizes from discovery studies such as the present one should be assumed to be inflated until replication
397 or follow up studies permit a more precise estimation of the true effect (Wilson et al. 2020). It should
398 also be noted that some lesions affected medial and anterior portions of the prefrontal cortex, and
399 damage in these regions has been linked with reduced punishment sensitivity (Gläscher et al. 2019). In

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400 partial agreement with this finding, we observed that threat approach (but not threat avoidance) was
401 more pronounced in patients with larger lesions. Nonetheless, the strongest lesion overlap was located
402 in ventromedial aspects. Lesion-symptom mapping in larger patient samples is needed to clarify the
403 regional specificity of the observed effects (Gläscher et al. 2019). Finally, due to time constraints, we
404 were not able to measure patients' explicit emotion recognition abilities, which are sometimes (Heberlein
405 et al. 2008) but not always (Willis et al. 2010) impaired in OFC patients. This limitation is minimized by
406 the fact that the task did not require emotion recognition to be performed.

407 *Conclusion*

408 The present study provides insight on how OFC dysfunction impacts the processing of
409 threatening information during approach-avoidance decisions. This was manifested in altered evidence
410 accumulation in response to threatening stimuli in combination with markers of premature and inflexible
411 decision-making. Intervention programs to improve social functioning in OFC patients might therefore
412 benefit from a focus on correctly interpreting and reacting to emotional information as well as on
413 ameliorating impulsivity (Levine et al. 2008). In sum, our study demonstrates that OFC damage can
414 steer individuals towards maladaptive approach behavior by biasing the automatic evaluation of threat
415 signals.

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