

## **Low competitive status elicits aggression in healthy young men: behavioral and neural evidence**

Macià Buades-Rotger<sup>1,2,3\*</sup>, Martin Göttlich<sup>1</sup>, Ronja Weiblen<sup>1,4</sup>,  
Pauline Petereit<sup>1</sup>, Thomas Scheidt<sup>1</sup>, Brian G. Keevil<sup>5</sup>, Ulrike M. Krämer<sup>1,2,6</sup>

<sup>1</sup> Department of Neurology, University of Lübeck, Lübeck, Germany

<sup>2</sup> Department of Psychology, University of Lübeck, Lübeck, Germany

<sup>3</sup> Donders Institute for Brain, Cognition and Behaviour, Radboud University, Nijmegen, The Netherlands

<sup>4</sup> Department of Psychiatry and Psychotherapy, University of Lübeck, Lübeck, Germany

<sup>5</sup> Department of Clinical Biochemistry, University Hospital of South Manchester, Manchester, UK

<sup>6</sup> Center of Brain, Behavior and Metabolism (CBBM), University of Lübeck, Lübeck, Germany

\* Corresponding author:

Macià Buades-Rotger, PhD

Radboud University

Montessorilaan 3

6525 HR Nijmegen

The Netherlands

+24 3655935

[m.buadesrotger@donders.ru.nl](mailto:m.buadesrotger@donders.ru.nl)

ORCID: <http://orcid.org/0000-0003-1219-9216>

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### **Abstract**

Winners are commonly assumed to compete more aggressively than losers. Here, we find overwhelming evidence for the opposite. We first demonstrate that low-ranking teams commit more fouls than they receive in top-tier soccer, ice hockey, and basketball men's leagues. We replicate this effect in the laboratory, showing that male participants deliver louder sound blasts to a rival when placed in a low-status position. Using neuroimaging, we characterize brain activity patterns that encode competitive status as well as those that facilitate status-dependent aggression in healthy young men. These analyses reveal three key findings. First, anterior hippocampus and striatum contain multivariate representations of competitive status. Second, interindividual differences in status-dependent aggression are linked with a sharper status differentiation in the striatum and with greater reactivity to status-enhancing victories in the dorsal anterior cingulate cortex. Third, activity in ventromedial, ventrolateral, and dorsolateral prefrontal cortex is associated with trial-wise increases in status-dependent aggressive behavior. Taken together, our results run counter to narratives glorifying aggression in competitive situations. Rather, we show that those in the lower ranks of skill-based hierarchies are more likely to behave aggressively and identify the potential neural basis of this phenomenon.

Keywords: aggression, status, competition, fMRI, neuroimaging

1           **Introduction**

2           Winners are often taken to be aggressive, not only in sportive environments (Chow *et al.*, 2009;  
3           Trebicky *et al.*, 2013) but in society at large (Waasdorp *et al.*, 2013; Laustsen and Petersen, 2017;  
4           Cheng, 2020; Weick, 2020). Indeed, adjectives such as “aggressive” or “dominant” are frequently casted  
5           in a positive light in competitive contexts (Næss, 2001; Pappas *et al.*, 2004), and leaders perceived to  
6           possess these characteristics are preferred in conflict situations (Kakkar and Sivanathan, 2017). From  
7           this perspective, aggression might serve to both achieve and assert a higher social rank (Lee and  
8           Yeager, 2020). In agreement with this idea, individuals tend to deliver louder sound blasts to a rival they  
9           outperformed than to one who outperformed them (Muller *et al.*, 2012). Contradicting these findings, the  
10          lower sense of control and the frustration occasioned by frequent defeats can fuel aggression in  
11          subordinate competitors (Przybylski *et al.*, 2014; Oxford *et al.*, 2017; Dowsett and Jackson, 2019).  
12          Supporting this notion, a number of studies has shown that individuals are more aggressive towards  
13          persons with high status (Davis and Reyna, 2015; Hu *et al.*, 2016; Saalfeld *et al.*, 2018; Kakkar *et al.*,  
14          2019), as low status might impede goal attainment (Berkowitz, 2012), induce stress (Sapolsky, 2004;  
15          Sapolsky, 2005) and threaten self-image (Horton and Sedikides, 2009). Furthermore, while  
16          accomplished contestants can rely on their ability, less proficient ones might compete more aggressively  
17          to outweigh the skill differential (Kirker *et al.*, 2000; Coulomb-Cabagno and Rasclé, 2006). Hence, those  
18          in the lower ranks of skill-based hierarchies might be more prone to use aggression than those who win  
19          consistently. If that were the case, social narratives emphasizing aggressiveness as a requisite for  
20          competitive success would be misguided. Here, we tested whether competitive status is related to  
21          physical aggression and investigated the neural underpinnings of this association.

22          Status-based hierarchies order social life and are hence imprinted in human neurobiology (Qu  
23          *et al.*, 2017). The rostral aspect of the medial prefrontal cortex (mPFC) has been postulated as a crucial  
24          region for inferring a rival’s dominance during competitive interactions (Ligneul *et al.*, 2016), which might  
25          be partially attributable to this region’s role in encoding stable behavioral traits (Hassabis *et al.*, 2013).  
26          The amygdala and anterior cingulate cortex (ACC), on the other hand, have been suggested to track  
27          moment-to-moment changes in status-based hierarchies (Kumaran *et al.*, 2012; Kumaran *et al.*, 2016).  
28          The ventral striatum (VS) and ventromedial prefrontal cortex (vmPFC) are highly responsive to  
29          competitive outcomes and might thus also contribute to acquire status representations during skill-based  
30          contests (Ligneul *et al.*, 2016). Further, these regions show enhanced reactivity to high- as compared  
31          to low-status individuals during both competitive (Zink *et al.*, 2008) and non-competitive tasks (Zerubavel

32 *et al.*, 2015). In addition, there is evidence suggesting that the hippocampus encodes relational  
33 knowledge of social hierarchies (Kumaran *et al.*, 2012; Schafer and Schiller, 2018; Park *et al.*, 2020),  
34 along with regions involved in social cognition such as the precuneus and the temporoparietal junction  
35 (TPJ) (Muscatell *et al.*, 2012; Tavares *et al.*, 2015; Zerubavel *et al.*, 2015). Thus, the current  
36 neuroscientific evidence permits to formulate a tentative description of how competitive hierarchies are  
37 processed in the human brain. First, regions associated with salience detection (amygdala, ACC)  
38 capture dominance signals and status changes during social interactions. Second, regions involved in  
39 affective valuation (VS, vmPFC) assess an individual's current status and facilitate hierarchy learning  
40 on the basis of victories and defeats. Finally, the *mentalizing network* (precuneus, TPJ, dorsal and rostral  
41 mPFC) and the hippocampus enable the encoding and implementation of status hierarchies during  
42 competitive decision-making. The key question that we addressed here is which role these  
43 neurocognitive processes play in status-dependent aggression. We reasoned that the neural substrate  
44 of status-processing and aggression should show some degree of overlap, be it in subcortical structures  
45 assumed to generate aggressive impulses such as the amygdala (da Cunha-Bang *et al.*, 2017; Buades-  
46 Rotger and Krämer, 2018), in those linked with retaliation such as the VS (Buades-Rotger, Brunlieb,  
47 *et al.*, 2016; Chester and DeWall, 2016), and/or in areas suggested to regulate aggression such as the  
48 vmPFC (Buades-Rotger *et al.*, 2019; Bertsch *et al.*, 2020).

49 A potentially crucial neuromodulator of status-seeking behavior is the steroid hormone  
50 testosterone. Though generally associated with aggression (Geniole *et al.*, 2020), recent evidence  
51 indicates that testosterone can flexibly promote prosocial behavior in order to improve one's social  
52 status (Eisenegger *et al.*, 2011; Terburg and van Honk, 2013; Geniole and Carré, 2018). For instance,  
53 a study showed that endogenous testosterone was positively associated with generosity in low-status  
54 (i.e. junior) rugby players, whereas the relationship was *negative* in high-status (i.e. senior) players  
55 (Inoue *et al.*, 2017). Similarly, men with relatively higher testosterone concentrations punished unfair  
56 offers more severely, but rewarded fair offers more generously (Dreher *et al.*, 2016). Given that high-  
57 testosterone individuals are generally more sensitive to status cues (Josephs *et al.*, 2006; Wagels *et al.*,  
58 2018; Losecaat-Vermeer *et al.*, 2020; Wu *et al.*, 2020; Han *et al.*, 2021), and that competitive situations  
59 inherently invoke the use of aggressive strategies (Waddell and Peng, 2014; Dowsett and Jackson,  
60 2019), testosterone might increase competitive aggression by modulating neural reactivity to status  
61 signals. Specifically, both preparatory and victory-contingent testosterone surges can induce  
62 competitive aggression by activating core neural structures of the threat- and reward-processing

63 systems (i.e., amygdala and VS respectively) (Geniole and Carré, 2018). Importantly, the effect of  
64 testosterone on the neural circuitry of competitive aggression is likely to be more pronounced in men  
65 (Zilioli and Bird, 2017), who show stronger endocrine reactivity to competition (Geniole *et al.*, 2017) as  
66 well as a tighter association between testosterone and aggression (Geniole *et al.*, 2020). The  
67 relationship between status-seeking behavior and testosterone might however be moderated by cortisol,  
68 a stress-related hormone that is thought to partly suppress testosterone's effects (Casto and Edwards,  
69 2016; Dekkers *et al.*, 2019). In the present study, we drew on pre-existing sports data, a behavioral  
70 study and a neuroimaging study to test a) whether competitive status is linked with aggression in healthy  
71 young men, b) whether this is contingent on the neural processing of status signals, and c) whether  
72 testosterone amplifies aggressive and/or neural responses to status cues, either by itself or in interaction  
73 with cortisol.

#### 74 **Correlational study**

75 In a first correlational study, we probed whether competitive status was associated with  
76 aggressive play across seasons in soccer, basketball and ice hockey. This proof-of-principle approach  
77 allowed us to test the link between competitive status and aggression in real-world settings.

#### 78 *Correlational study: data acquisition*

79 We defined competitive status as a team's position at the end of the regular season, with higher  
80 values indicating a lower standing in the rankings. Aggression was operationalized as the number of  
81 fouls (soccer), personal fouls (basketball), or penalty time (ice hockey) incurred relative to received, a  
82 measure that accounts for the reciprocal, "tit-for-tat" character of sports aggression. For basketball and  
83 ice hockey, we determined the position of teams from different divisions on the basis of their win  
84 percentage. We manually extracted data from <http://www.footstats.co.uk> (soccer), <http://www.nba.com>  
85 (basketball), and <http://www.hockey-reference.com> (ice hockey) since the last year in which complete,  
86 correct, data was available onwards (2000-2008 for European football leagues, 2005 for basketball and  
87 hockey). We collapsed these variables separately for the main five European football leagues (England,  
88 Spain, Germany, Italy, and France), the North-American National Basketball Association league (NBA),  
89 and the North-American National Hockey League (NHL) for a total of 2254 observations (i.e. teams in a  
90 given season). By using data aggregated over seasons we minimize the effect of proximal situational  
91 influences (home-field advantage, referee biases, etc.) that might induce fluctuations in the number of  
92 fouls incurred in single games. The correlation between received and committed fouls or penalties was  
93  $r_{1412}=.74$  for football,  $r_{418}=.70$  for basketball and  $r_{418}=.93$  for ice hockey. This indicates that a) aggressive

94 play follows reciprocal, “give-and-take” dynamics so that teams who commit more fouls also tend to  
95 receive more, but b) that the ratio of fouls/penalties committed to received captures some unique  
96 variance in teams’ aggressiveness that is not accounted for by the raw amount of fouls or penalty time  
97 incurred. This is thus a valid measure to assess the degree to which a team engages in sanctioned  
98 aggression.

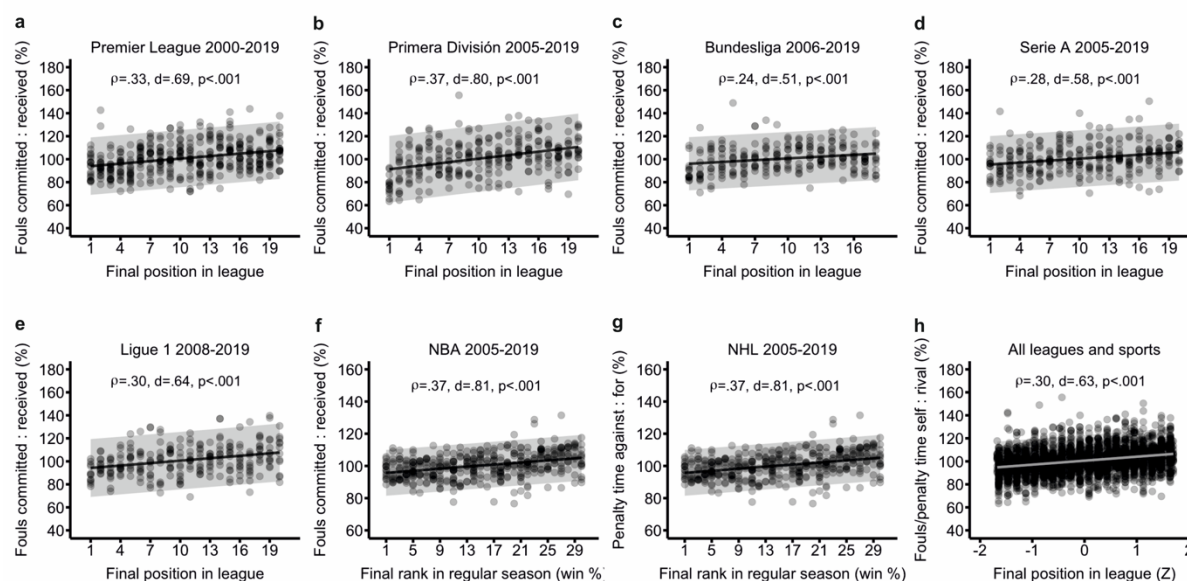
99 *Correlational study: data analysis*

100 Because of the ranked nature of the data, we computed Spearman correlation coefficients  
101 between position and foul ratio. We also tested whether this relationship held across seasons and  
102 leagues and when accounting for the nested data structure. To do so, we ran linear mixed-effects model  
103 analyses with position, season, and league as Z-transformed fixed-effect predictors and team as  
104 grouping factor. Following best-practice recommendations (Barr *et al.*, 2013), we attempted to maximize  
105 the random-effects structure of the model defining by-team random slopes for all fixed effects and  
106 random intercepts for all predictors where possible. The most complex model to converge was one with  
107 random slopes for season and random intercepts for league, position, and team.

108 All analyses were performed in R version 3.6.1 running on R Studio 1.1.423. We used the psych  
109 package (Revelle, 2017) for Spearman correlations and ggplot2 for plotting (Wickham, 2016). For linear  
110 mixed-effects modeling we used the lmerTest package (Kuznetsova *et al.*, 2017). Data and analysis  
111 scripts for this study are available via the Open Science Foundation (<https://osf.io/2jvx4/>).

112 *Correlational study: results*

113 As shown in Fig. 1, low ranking was consistently associated with foul ratio in each individual  
114 league as well as across leagues (mean weighted  $\rho=.30$ ; Cohen’s  $d=.63$ ,  $p<.001$ ). When pooling over  
115 all competitions (Fig. 1h), low-ranking teams (Z-transformed position $>1$ ) showed on average a 9.5%  
116 greater foul ratio (104.68% vs 95.18%) than high-ranking ones (Z-transformed position $<-1$ ). Linear  
117 mixed-effects models revealed that the relationship between rank and foul ratio persisted ( $\beta=.21$ ,  
118  $t_{89}=8.80$ ,  $p<.001$ ) when controlling for league and season, which had no effect and did not interact with  
119 ranking (all  $p>.124$ ; Table 1).



**Fig. 1.** Correlation between competitive status and aggression in elite sports teams. Status was defined as the team's final position at the end of a season. Aggression was defined as the ratio of fouls (soccer), personal fouls (basketball), or penalty time (ice hockey) incurred relative to received, in %. We collapsed data across seasons. We include best-fit lines and 95% prediction intervals. **a**, English Premier League 2000-2019, **b**, Spanish Primera División 2005-2019, **c**, German Bundesliga 2006-2019, **d**, Italian Serie A 2005-2019, **e**, French Ligue 1 2008-2019, **f**, North-American National Basketball Association League 2005-2019, **g**, North-American National Basketball Association League 2005-2019, **h**, All data points collapsed, with position expressed as Z-scores.

Table 1: Results of linear-mixed effects model predicting foul/penalty ratio in sports teams (n=2254)

<i>Predictor</i>	<i>Dependent variable: fouls/penalty time self : rival</i>			
	$\beta$	SE	t	p
<b>Position</b>	<b>0.219</b>	<b>0.025</b>	<b>8.809</b>	<b>&lt;0.001</b>
League	0.016	0.051	0.313	0.762
Season	0.03	0.03	0.995	0.321
Position * League	0.028	0.018	1.537	0.124
Position * Season	0.003	0.022	0.13	0.896
League * Season	0	0.031	0.01	0.992
Position * League * Season	0.032	0.019	1.667	0.096

$\beta$ : regression coefficient, SE: standard error of the regression coefficient, t: t value, p: p-value. Bold values indicate effects significant at p<.001.

## 120 Behavioral study

121 Our analysis of sports data provides consistent -albeit purely correlational- evidence for a link  
 122 between low competitive status and aggression at the level of teams. It is however unclear whether the  
 123 status-aggression relationship can also be observed in individual competitors. Moreover, fouls in sports  
 124 serve a predominantly instrumental function. A more stringent test of our main hypothesis would entail  
 125 manipulating status experimentally during one-to-one contests in which aggression does not strictly fulfil  
 126 a competitive purpose, i.e. it does not directly impact rivals' performance. To that end, we ran a pre-  
 127 registered behavioral study (<https://osf.io/q5qe6>) in order to probe whether individuals would be more  
 128 or less aggressive as a function of their competitive status. In order to investigate the effect of status on  
 129 aggression experimentally, we devised a modified version of the Taylor Aggression Paradigm, a

130 competitive reaction time task in which the winner can choose the volume of a sound blast to punish the  
131 loser (Buades-Rotger, Engelke, *et al.*, 2016). Critically, we manipulated competitive status by  
132 programming the task so that subjects won more often against one rival than against the other.

133 *Behavioral study: participants*

134 As this was an exploratory study, we aimed for a sample size of  $n=30$  in order to have 80%  
135 power to detect a middle-sized within-subject effect ( $d=.5$ ) at a conventional two-sided threshold of  
136  $p<.05$ . After exclusion of three participants (two saw through the status manipulation and one failed to  
137 understand the task, see protocol below), the sample comprised 25 healthy young men (age:  $24\pm 3.1$ ;  
138 height:  $180\pm 5.1$  cm; weight:  $75.96\pm 9$  kg; 23 right-handed, 2 ambidextrous). The study had been  
139 approved by the Ethics Committee of the University of Lübeck. Subjects consented to participate and to  
140 the anonymized dissemination of the data.

141 *Behavioral study: protocol and task*

142 Participants were measured in groups of three and believed they would compete against each  
143 other, but they actually played against the computer. A male confederate filled in for a participant when  
144 an appointment with three subjects was not possible. We first took participants to a computer room in  
145 which they provided informed consent and read the instructions together. Computers were separated  
146 by screen-walls so that participants could not see each other, and they wore headphones throughout.

147 We programmed the task so that participants competed in random order, but not more than  
148 three times in a row, against each opponent. After eight practice trials, the task started (see Fig. 2a for  
149 an outline of the task). Trials began with a decision phase wherein subjects saw the percentage of trials  
150 won by their current opponent and by themselves as separate filled bars, i.e. their competitive status.  
151 During the decision phase, participants set the volume of a sound blast in a 1-8 scale to be later delivered  
152 at their opponent should they win a subsequent reaction time task. The chosen volume was our measure  
153 of aggression. In the reaction time task, they had to be quicker than their rival in pressing any button  
154 when a target appeared (i.e. a bullseye). We manipulated status so that participants lost more frequently  
155 against one rival (66%) than against the other (33%) for a total of 60 trials. To make the setting more  
156 believable, subjects were more likely to lose when they were slower than their own median cumulative  
157 reaction time, and we interspersed shorter (4s) and longer (12s) inter-trial intervals; during the latter, the  
158 opponents allegedly played against each other. Following previous work (Buades-Rotger, Engelke, *et*  
159 *al.*, 2016), we programmed the opponents' punishment selections to increase progressively over time  
160 (i.e. every 20 trials) in order to gradually provoke participants.



161 After the measurement, participants filled out a manipulation check asking how unpleasant they  
162 found the loudest and lowest sound blasts to be with a Likert-type scale ranging from 1 to 8, the  
163 perceived average punishment selection of each opponent (also with a Likert-type 1 to 8 scale), and the  
164 percentage of trials they believed to have won against each opponent. This questionnaire also probed  
165 deception success via three open-end questions: “Did you notice anything special about the behavior  
166 of your fellow players?”, “Did you have a particular strategy for the game?”, and “What do you think was  
167 investigated in this study?”. We excluded participants if they made explicit mention to the task being  
168 preprogrammed (e.g. “The other players were bots”), if they misunderstood the task (e.g. not pressing  
169 any button in the reaction time task), or if they evinced an insufficient knowledge of the German  
170 language. At the end of the experiment, we debriefed participants regarding the goals and methods of  
171 the study.

#### 172 *Behavioral study: data analysis*

173 Average punishment selections show high internal consistency, load onto a single factor  
174 (Chester and Lasko, 2019), and predict real-life aggression (King and Russell, 2019), suggesting that  
175 they are a valid measure of aggression and that they adequately summarize participant’s behavior in  
176 the task. We followed the pre-registered analysis plan (<https://osf.io/q5ge6>) and compared mean  
177 aggression against the high- vs low-status opponent with a paired t-test in R (version 3.6.1) running on  
178 R Studio (version 1.1.423). Data and analysis scripts for this study are freely available via the Open  
179 Science Foundation (<https://osf.io/2jvx4/>).

#### 180 *Behavioral study: results*

181 Post-experimental manipulation checks revealed that they were aware of winning less often  
182 ( $t_{24}=7.55$ ,  $d=1.51$ ,  $p<.001$ ) against the better-performing player ( $34.8\% \pm 2.1\%$  [mean  $\pm$  standard error])  
183 than against the worse one ( $60.5\% \pm 1.9\%$ ). As intended, they did not perceive either rival to be more  
184 aggressive than the other ( $t_{24}=1.58$ ,  $p=.125$ ). Following the pre-registered analysis plan  
185 (<https://osf.io/q5ge6>), we extracted mean punishment selections per condition and compared them with  
186 a paired t-test. Subjects selected louder sound blasts in a low- than in a high-status position ( $t_{24}=2.66$ ,  
187  $d=.54$ ,  $p=.013$ ; Fig. 2b).

#### 188 **Neuroimaging study**

189 In a subsequent neuroimaging study, we used a slightly modified version of the same task to  
190 scrutinize neural responses to status information during a competitive interaction. Further, we tested  
191 whether status-related brain activity was linked with actual aggressive behavior in the task as well as

192 with salivary testosterone and cortisol measured before and after scanning. Unlike the behavioral study,  
193 we programmed opponents' punishments to stay relatively constant over time. We did so in order to  
194 disentangle provocation and status effects and to render trials more comparable throughout the task for  
195 subsequent averaging of brain activity. We hence set the opponents to select punishments in the middle  
196 range (3-6) throughout the task instead of increasing progressively. We also lengthened the task for a  
197 total of 90 trials, divided in 3 runs of 30 trials each (15 per opponent) to increase statistical power. In  
198 this case, the opponents were always confederates of the experimenters who pretended to play against  
199 the participant from computers outside the scanner. To increase the plausibility of this setting,  
200 participants played the eight practice trials together with the confederates in the same computer room  
201 where the pilot measurements had taken place.

202 *Neuroimaging study: participants*

203 We determined the sample size on the basis of a previous study (n=39) in which we observed  
204 middle-sized correlations ( $r \approx .4$ ) between endogenous testosterone, aggression, and brain activity using  
205 a similar task (Buades-Rotger, Engelke, *et al.*, 2016). We thus aimed for a sample size of 50, which  
206 yields ~80% power to detect effects of  $r = .4$  or larger with a two-sided threshold of  $p < .05$ . After exclusion  
207 of six subjects due to non-deception (n=4) and failure to understand the task (n=2), the final sample  
208 comprised 47 men aged  $24 \pm 3.8$  (height:  $182 \pm 6.6$  cm; weight:  $79.90 \pm 11$  kg; 37 right-handed, 7 left-  
209 handed, 3 ambidextrous) who were reportedly free of current psychiatric, neurological, and endocrine  
210 diseases except for one participant with treated hypothyroidism. We included left-handed participants  
211 because we did not have specific hypotheses regarding lateralization of the effects and because  
212 subjects used both hands to perform the task. This study had also been approved by the Ethics  
213 Committee of the University of Lübeck. Subjects provided informed consent for participation and  
214 anonymized dissemination of the data. We used the same post-experimental questionnaire as in the  
215 behavioral study and we debriefed them regarding the goals and methods of the study. Measurements  
216 began between 12 and 15 PM in order to minimize circadian fluctuations in hormonal levels, with the  
217 exception of two measurements (17 and 18 PM) that could not be scheduled otherwise.

218 *Neuroimaging study: acquisition of testosterone and cortisol data*

219 Subjects provided saliva samples in plastic vials (SafeSeal micro tube 2ml from Sarstedt) with  
220 the passive drooling technique before and after scanning. We froze the samples at  $-20^{\circ}\text{C}$  and shipped  
221 them in dry ice to author BGK's laboratory in Manchester (UK) for analysis once study was completed.  
222 Free testosterone and cortisol concentrations were estimated with liquid chromatography tandem mass

223 spectrometry (LC-MS/MS) as described elsewhere (Perogamvros *et al.*, 2009; Keevil *et al.*, 2013).  
224 Coefficients of variation (CV) with this technique have been reported to be 5.3% for testosterone and  
225 8.7% for cortisol, whereas mean inter-assay CV were 9% for testosterone and 7.8% for cortisol  
226 (Perogamvros *et al.*, 2009; Keevil *et al.*, 2013). The lower limits of quantification (LLOQ) were 5 pmol/L  
227 for testosterone and 0.8 nmol/L for cortisol.

228 *Neuroimaging study: acquisition of fMRI data*

229 We acquired all scans with a 64-channel head-coil mounted on a 3-T Siemens Magnetom Skyra  
230 scanner at the Center for Brain, Behavior and Metabolism (CBBM) at the University of Lübeck. For  
231 functional volumes we applied a single-shot gradient-recalled echo-planar imaging (GRE-EPI)  
232 sequence sensitive to blood oxygen level dependent (BOLD) contrast (TR=1060 ms; TE=30 ms; flip  
233 angle=60°; 60 transversal slices; slice thickness 3 mm; in-plane voxel size=3×3 mm<sup>2</sup>; field-of-view  
234 [FOV]=210×210 mm<sup>2</sup>, simultaneous multi-slice factor=4; full-brain coverage). We acquired 570 volumes  
235 per run for a total of three runs (≈30 minutes). Before and after the task we acquired two magnetic field  
236 measurements (2D double-echo gradient-echo sequence; TE<sub>1</sub>=5,17ms; TE<sub>2</sub>=7.63ms; TR=554ms; flip  
237 angle=60°; 50 transversal slices; slice thickness 3 mm; in-plane voxel size=3×3 mm<sup>2</sup>; FOV=240×240  
238 mm<sup>2</sup>) for subsequent offline distortion correction as well as two 6.5 minutes eyes-closed resting-state  
239 runs not analyzed for the present manuscript. We further acquired an anatomical scan at the start of  
240 each measurement applying a 3D T1-weighted Magnetization Prepared-Rapid Gradient Echo (MP-  
241 RAGE) sequence (TR=2300 ms; TE=2.94 ms; TI=900 ms; flip angle=9°; voxel size=1×1×1 mm<sup>3</sup>;  
242 FOV=320×320mm<sup>2</sup>).

243 *Neuroimaging study: analysis of behavioral and hormonal data*

244 For the analysis of behavioral data, we first ran a paired t-test comparing mean aggression  
245 against in the low- vs high-status condition as we had done in the behavioral study. Additionally, we ran  
246 linear mixed-effects models on participants' aggressive behavior, decision latencies, and reaction times.  
247 We specifically tested for effects of opponent status (high or low), trial number (1 to 45), and outcome  
248 of the previous trial (won or lost). These three variables were defined as fixed effects whereas subject  
249 was defined as random effect. We included by-participant slopes for all fixed effects and random  
250 intercepts for all predictors where possible, adhering to standard guidelines for linear mixed-effects  
251 modeling (Barr *et al.*, 2013). Models with random slopes for outcome failed to converge, just as those  
252 with random intercepts for status and outcome. Therefore, all models included random intercepts for  
253 subject and trial as well as random by-participant slopes for status and trial. We performed these

254 analyses using the lmerTest package (Kuznetsova *et al.*, 2017) in R (version 3.6.1) running on R Studio  
255 (version 1.1.423).

256 For testosterone and cortisol, we compared the pre- and post-scan log-transformed values  
257 using paired t-tests in order to inspect for state changes in hormonal concentrations. Two pre-scan  
258 testosterone samples had to be discarded because the amount of saliva did not suffice for reliable  
259 quantification. We then tested whether mean aggression against the high- minus the low-status  
260 opponent was associated with baseline testosterone, cortisol, the testosterone-to-cortisol ratio, and/or  
261 pre-post changes in either hormone using Pearson correlation coefficients. For paired t-tests, we report  
262 Cohen's  $d_m$ , which accounts for the correlation between repeated measurements (Lakens, 2013). For  
263 correlation and regression coefficients, we converted the corresponding  $r$  and  $t$ -values to Cohen's  $d$   
264 using the *psych* package's functions `t2d` and `r2d` respectively (Revelle, 2017). We used `ggplot2` to plot  
265 results (Wickham, 2016).

266 *Neuroimaging study: analysis of fMRI data*

267 We performed the pre-processing and analysis of neuroimaging data using Statistical  
268 Parametric Mapping 12 (SPM12; <https://www.fil.ion.ucl.ac.uk/spm/>) running on Matlab 2019b. We used  
269 a standard pre-processing pipeline that involved, in this order, slice-timing correction to the four middle  
270 slices (i.e. those acquired at 485ms) with a 4<sup>th</sup> degree spline interpolation, realignment to the first  
271 functional volume, coregistration of mean functional and anatomical images, segmentation of the  
272 anatomical images based on default tissue probability maps, normalization to the Montreal Neurological  
273 Institute (MNI) template and smoothing with an 8mm full-width at half-maximum Gaussian kernel.  
274 Additionally, we performed distortion correction using the FieldMap toolbox, except in seven participants  
275 for which this procedure failed or worsened image quality. We excluded one imaging run in three  
276 subjects due to excessive head movements (>3mm or 3° in any direction).

277 First-level models comprised two regressors for the decision phase (high- or low-status  
278 opponent; 4s) and four for the outcome phase (won or lost vs high- or low-status; 4s). We also included  
279 the absolute distance in status between subject and opponent in percentage as a covariate in the  
280 decision phase to control for momentary fluctuations in status. As regressors of no interest, we modelled  
281 the warning sign, target, and motor responses in the reaction time task as well as the sound at the end  
282 of the outcome phase as delta functions with null duration. We further included the six movement  
283 parameters estimated from realignment (x, y, z, pitch, roll, and yaw). We convolved all regressors  
284 (except for motion parameters) with the canonical hemodynamic response function, implemented a

285 high-pass filter with a 128s cut-off, and applied the standard SPM autoregressive model AR(1) to control  
286 for autocorrelation. In order to inspect for trial-wise changes in activity associated with aggression, we  
287 additionally defined identical first-level models that included trial-wise mean-centered punishment  
288 selections as parametric modulator.

289 We first performed multi-voxel pattern analyses (MVPA) to uncover local activation patterns that  
290 most differentiated between the two opponents in the decision phase. We used the Decoding Toolbox  
291 (Hebart *et al.*, 2015) running on Matlab 2019b to implement a linear support vector machine algorithm  
292 that classifies multivariate activation patterns for each condition and run using a leave-one-out cross  
293 validation procedure on the corresponding beta images. We ran such an analysis within each of eight  
294 regions-of-interest (ROIs) putatively involved in the relational processing of social status (Zerubavel *et*  
295 *al.*, 2015; Qu *et al.*, 2017; Schafer and Schiller, 2018). We defined these ROIs as bilateral anatomical  
296 masks extracted from the Automatic Anatomical Labelling atlas (Maldjian *et al.*, 2003): the amygdala  
297 (merge of left and right “Amygdala” masks), anterior cingulate cortex (“Cingulum\_Ant” mask),  
298 dorsomedial prefrontal cortex (“Frontal\_Sup\_Medial” mask), hippocampus (merge of left and right  
299 “Hippocampus” masks), precuneus (“Precuneus” mask), striatum (merge of “Caudate”, “Putamen”, and  
300 “Pallidum” masks), temporal-parietal junction (merge of “Temporal\_Sup” and “SupraMarginal” masks),  
301 and ventromedial prefrontal cortex (merge of left and right “Rectus” and “Frontal\_Med\_Orb” masks). We  
302 resampled the masks to match the voxel size of the functional data (3mm). For each of these regions,  
303 we extracted the participant-wise area under the curve (AUC) minus chance as a classification  
304 performance measure. Here, AUC expresses the total surface below the receiver operating  
305 characteristic curve, which is obtained by plotting the cumulative true positive rates against the  
306 cumulative false positive rates. Hence, higher AUC values indicate a greater capacity to classify  
307 between categories. While standard accuracy measures treat all classifications equally, AUC also takes  
308 into account the “confidence” (i.e. the distance to the decision boundary) that the classifier has regarding  
309 the membership of specific items (Hebart *et al.*, 2015). In order to assess statistically which ROIs  
310 distinguished between conditions, we computed the bootstrapped 95% bias-corrected accelerated  
311 confidence intervals (BCa CI) confidence intervals of the average AUC for each ROI. ROIs whose CI  
312 did not include zero were considered to classify between the high- and low-status rival at an above-  
313 chance level. In order to more precisely localize the observed effects, we performed a post-hoc  
314 searchlight analysis (9-voxel radius sphere) within each ROI showing above-chance classification.  
315 These analyses were thresholded at  $p < .05$ ,  $k > 50$  uncorrected.

316 We subsequently sought for associations between neural reactivity to status signals and  
317 aggression on a within-subject basis. We did so by comparing the parametric modulator for punishment  
318 selections in the low- versus the high-status condition using a paired t-test. This analysis tests for brain  
319 areas showing transient increases in activity as a function of participants' trial-wise aggression levels  
320 against one opponent relative to the other. Five participants had to be excluded from this analysis due  
321 to lack of variability in behavior (i.e. they chose the same punishment in all trials). Given that we had no  
322 a priori hypotheses for these analyses, we applied a threshold of  $p < .001$  at the voxel level with a  $p < .05$   
323 family-wise error (FWE) correction at the cluster level.

324 In the outcome phase, we tested whether wins and losses were differentially processed  
325 depending on status using a flexible factorial analysis. First, we tested the main effects of won vs lost in  
326 order to reproduce the VS and vmPFC activity commonly observed during competitive victories.  
327 Because subjects lost more often against one of the two opponents, status and outcome were not  
328 orthogonal. We therefore did not inspect the main effect of status. Rather, we directly tested the  
329 interaction between the two factors, namely the contrast  $[won\ high + lost\ low] > [lost\ high + won\ low]$   
330 and its opposite using paired t-tests (see Table S1 in Supplementary Material), and post-hoc plotted the  
331 resulting parameter estimates. For these contrasts we also set a voxel-level  $p < .001$  threshold with a  
332 cluster-wise  $pFWE < .05$  correction, as the effect of competitive outcomes on the targeted valuation areas  
333 is usually detectable in whole-brain analyses (Votinov *et al.*, 2015; Ligneul *et al.*, 2016).

334 Finally, we probed whether interindividual differences in status-based aggression were  
335 associated with the neural processing of status signals. We used MarsBaR  
336 (<http://marsbar.sourceforge.net/>) to extract subject-wise parameter estimates from ROIs showing  
337 above-chance classification in the MVPA analyses (whole ROI) and from clusters showing significant  
338 activity in the outcome by status interaction (6 mm sphere around peak coordinate). We computed the  
339 correlation coefficients between activity in each ROI/cluster and mean aggression against the high-  
340 minus the low-status opponent. We also computed the 95% bootstrapped confidence intervals for the  
341 correlation coefficients of significant associations ( $p < .05$ ) in order to assess their robustness and to  
342 protect against the influence of outlying observations. We performed all bootstrapping analyses using  
343 the *bootstrap* package (version 2019.5) in R (version 3.6.1) running on R Studio (version 1.1.423). We  
344 used ggplot2 to depict all neuroimaging results (Wickham, 2016). Behavioral and ROI data along with  
345 analysis scripts for this study are freely available via the Open Science Foundation (<https://osf.io/2jvx4/>).  
346 Raw and pre-processed neuroimaging data are available upon request.

347 *Neuroimaging study: behavioral results*

348 Participants were 47 healthy young men (age=24 ± 3.8 [mean ± standard deviation]) who  
349 believed to be playing against two other participants. These were actually confederates and the task  
350 was again preprogramed. Here, the status manipulation was also successful, as subjects were aware  
351 of winning less often against the stronger than against the weaker rival ( $t_{46}=10.05$ ,  $d=2.36$ ,  $p<.001$ ).  
352 Subjects overestimated the percent of trials won against both the better (41.1% ± 1.6% [mean ± standard  
353 error] vs 33%,  $t_{46}=4.74$ ,  $d=.69$ ,  $p<.001$ ) and worse opponents (71.9% ± 1.7% vs 66%,  $t_{46}=3.40$ ,  $d=.49$ ,  
354  $p=.001$ ). Again, they did not perceive the stronger opponent to be more aggressive ( $t_{46}=1.26$ ,  $d=.27$ ,  
355  $p=.213$ ). As in the pilot study, subjects selected higher average punishments against when they were in  
356 a low- than in a high-status position ( $t_{46}=3.57$ ,  $d=.57$ ,  $p<.001$ ; Fig. 2c). We thus calculated status-  
357 dependent aggression as the difference in average punishment selections in each condition (low- minus  
358 high-status) to be used in later correlation analyses with neural and hormonal data.

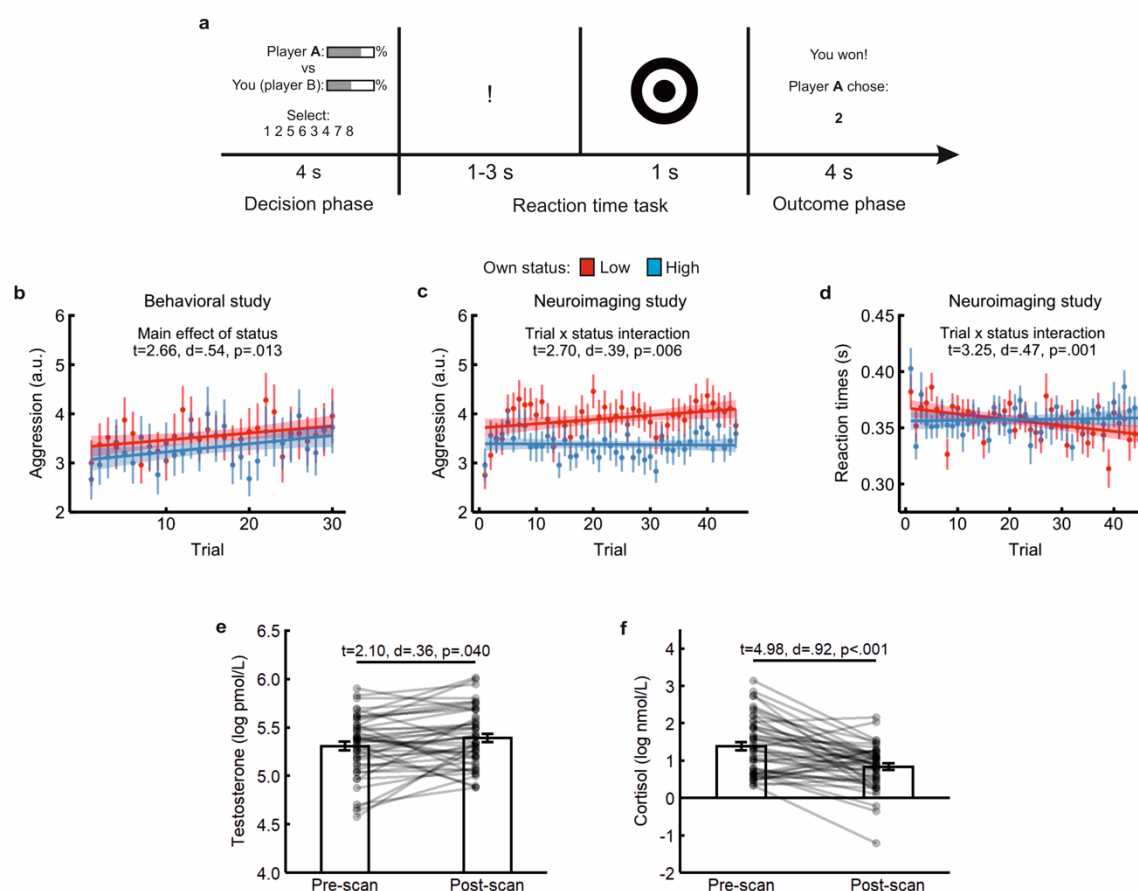
359 We additionally tested whether subjects' behavior changed over time using linear mixed-effects  
360 models (see Methods). Participants selected louder sound blasts over time when they were in a low-  
361 status position, whereas their punishment selections remained unchanged in a high-status one (status  
362 x trial interaction:  $\beta=0.125$ ,  $t_{4062}=2.70$ ,  $p=.006$ ; Fig. 2c; Table 2a). Specifically, they evinced an increase  
363 of around .7 points ( $\approx 8.75\%$  of the scale) in the last (4.09 ± .08 [mean ± standard error]) compared to  
364 the first five trials (3.39 ± .21) when low in status. In contrast, their average aggression levels remained  
365 virtually unchanged as high-status players (first five trials: 3.47 ± .14; last five trials: 3.49 ± .07). Thus,  
366 participants selected stronger punishments in a low rank even when provocation remained constant.

367 Response latency in the decision phase did not vary as a function of status, time, or their  
368 interaction (all  $p>.154$ ; Table 2b). That is, subjects took similarly long to choose the punishment against  
369 either opponent across trials (high-status: 1.32 ± 0.16s; low-status: 1.29 ± 0.12s). Nevertheless, there  
370 was a significant main effect of outcome ( $\beta=0.032 \pm 0.01$ ,  $t_{1073}=2.34$ ,  $p=.019$ ) such that participants  
371 chose about 50ms faster after losing (1.27 ± 0.01ms) than after winning (1.32 ± 0.01s).

372 In the reaction time task, participants became progressively quicker as low-status players  
373 (status-by-trial interaction:  $\beta=0.008$ ,  $t_{4111}=3.25$ ,  $p=.001$ ; Fig. 2d; Table 2c). On average, subjects were  
374 approximately 22ms faster in the last five (3.50 ± 0.03s) relative to the first five trials (3.72 ± 0.06s)  
375 against when they had a low status, whereas they were comparably quick throughout the task in the  
376 high-status condition (first five trials: 3.64 ± 0.12s; last five trials: 3.65 ± 0.06s). This confirms the  
377 motivational relevance of competitive status for participants' performance.

378 *Neuroimaging study: testosterone and cortisol results*

379 Concerning hormonal concentrations, average testosterone levels increased 1.57% after  
380 scanning ( $t_{44}=2.10$ ,  $d=.36$ ,  $p=.040$ ; Fig. 2d) whereas mean cortisol decreased by 39.74%  
381 ( $t_{46}=4.96$ ,  $d=.92$ ,  $p<.001$ ; Fig. 2e). Baseline concentrations of testosterone ( $r_{43}=.08$ ,  $p=.595$ ) or cortisol ( $r_{45}=-.01$ ,  
382  $p=.973$ ) were not associated with aggression, nor was the baseline testosterone-to-cortisol ratio ( $r_{43}=.10$ ,  
383  $p=.497$ ) or the pre-post change in either hormone (testosterone:  $r_{43}=.07$ ,  $p=.627$ ; cortisol:  $r_{45}=.06$ ,  
384  $p=.686$ ). Therefore, we did not use endogenous hormone levels for further analyses.



**Fig. 2.** **a**, outline of the task. Subjects saw the % of victories achieved by the opponent and themselves as a filled bar while choosing the volume of a sound blast to be later directed at their opponent (decision phase). Then, they had to be faster than the rival in pressing a button when a jittered bullseye appeared (reaction time task). In the outcome phase they were informed of whether they won or lost and of the rival's selection. If they lost, they received the sound blast at the end of the trial via headphones. They were consistently worse against one opponent (low-status condition) and better than the other (high-status condition), though both rivals chose equally strong sound blasts on average. **b**, mean punishment selections by trial and participant status in the behavioral study, including best-fit lines and 95% prediction intervals. **c**, mean aggression by trial and participant status in the neuroimaging study, including best-fit lines and 95% prediction intervals. **d**, mean response latency in the reaction time task by trial and participant status in the neuroimaging experiment. **e**, testosterone levels in saliva pre and post-scanning. **f**, cortisol levels in saliva pre- and post-scanning.



Table 2: Results of linear-mixed effects models in the neuroimaging study (n=47)

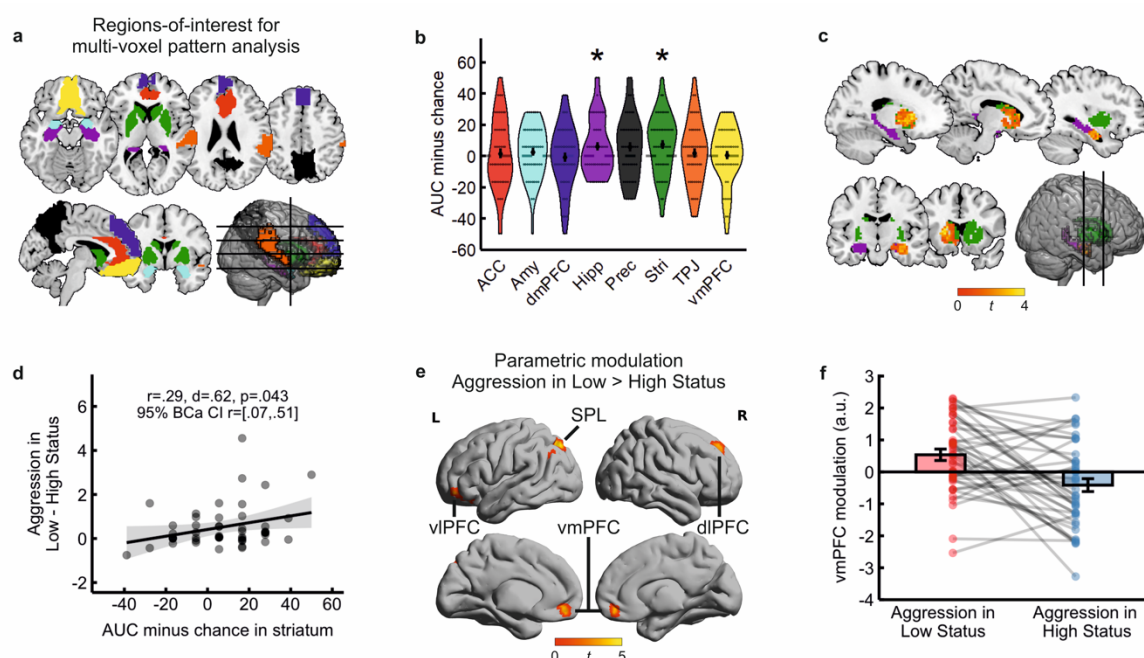
<i>a) Dependent variable: punishment selections</i>				
<i>Predictor</i>	$\beta$	SE	t	p
<b>Status</b>	<b>0.488</b>	<b>0.146</b>	<b>3.347</b>	<b>.002</b>
<b>Trial</b>	<b>0.141</b>	<b>0.059</b>	<b>2.383</b>	<b>.020</b>
Outcome	0.005	0.035	0.132	.895
<b>Status * Trial</b>	<b>0.125</b>	<b>0.046</b>	<b>2.708</b>	<b>.007</b>
Status * Outcome	0.014	0.048	0.288	.773
Trial * Outcome	0.049	0.035	1.394	.164
Status * Trial * Outcome	0.041	0.048	0.85	.395
<i>b) Dependent variable: response latency in decision phase</i>				
Status	0.026	0.018	1.426	.154
Trial	0.020	0.020	0.977	.331
<b>Outcome</b>	<b>0.032</b>	<b>0.013</b>	<b>2.346</b>	<b>.019</b>
Status * Trial	0.023	0.018	1.261	.207
Status * Outcome	0.022	0.019	1.163	.245
Trial * Outcome	0.008	0.014	0.606	.545
Status * Trial * Outcome	0.003	0.019	0.168	.867
<i>c) Dependent variable: response latency in reaction time task</i>				
Status	0.001	0.003	0.591	.554
<b>Trial</b>	<b>0.007</b>	<b>0.002</b>	<b>2.989</b>	<b>.004</b>
Outcome	0.002	0.002	1.097	.273
<b>Status * Trial</b>	<b>0.008</b>	<b>0.002</b>	<b>3.258</b>	<b>.001</b>
Status * Outcome	0.002	0.003	0.656	.512
Trial * Outcome	0.002	0.002	0.821	.412
Status * Trial * Outcome	0.002	0.003	0.737	.461

$\beta$ : regression coefficient, SE=standard error, t: t value, p: p-value. Bold values indicate effects significant at  $p < .05$ .

385 *Neuroimaging study: status-dependent activity patterns during punishment selection*

386 With regards to neuroimaging data, we first tested whether regions-of-interest (ROIs) previously  
 387 linked to the processing of status signals also encode competitive status during decisions to aggress  
 388 (Fig. 3a). To that end, we performed multi-voxel pattern analysis (MVPA) in the decision phase (see  
 389 Methods). This revealed that the striatum and hippocampus distinguished between opponents (Fig. 3b).  
 390 That is, multivariate activity patterns in these regions could classify at an above-chance level whether  
 391 subjects were facing the high- or the low-status opponent. Post-hoc searchlight analyses showed that  
 392 both ventral and dorsal aspects of the left striatum contributed to the effect, whereas in the case of the  
 393 hippocampus classification was most strongly driven by its right anterior portion (Fig. 3c). We then tested  
 394 whether a stronger multivariate differentiation between opponents was linked with status-dependent  
 395 aggression across subjects. To do so, we took classification performance values for the hippocampus  
 396 and striatum and correlated them with mean aggression against the high- minus low-status opponent.  
 397 Although we observed no effects for the hippocampus ( $r_{45} = -.03$ ,  $p = .823$ ), there was an association  
 398 between striatum activity patterns and aggression against the high- minus low-status rival ( $r_{45} = .29$ ,  
 399  $d = .62$ ,  $p = .043$ ; Fig. 3d). In other words, subjects showing a more pronounced differentiation between  
 400 opponents in the striatum showed greater status-contingent aggressive behavior.

401 *Neuroimaging study: trial-by-trial fluctuations in punishment selections*  
 402 We subsequently inquired whether neural reactivity to status cues influenced punishment  
 403 selections on a within-subject basis. We hence performed a parametric modulation analysis comparing  
 404 trial-wise decisions against in each condition (see Methods). As shown in Fig. 3e, greater aggression  
 405 against in a low- compared to a high-status position was associated with *increased* activity in  
 406 ventromedial prefrontal cortex (vmPFC;  $t=4.57$ ,  $k=59$ ,  $x=9$ ,  $y=50$ ,  $z=-10$ ; Fig. 3b), dorsolateral prefrontal  
 407 cortex (dlPFC;  $t=4.11$ ,  $k=57$ ,  $x=21$ ,  $y=44$ ,  $z=41$ ), ventrolateral prefrontal cortex (vlPFC;  $t=4.79$ ,  $k=57$ ,  $x=-$   
 408  $33$ ,  $y=32$ ,  $z=-16$ ) and superior parietal lobe (SPL;  $t=4.80$ ,  $k=88$ ,  $x=-24$ ,  $y=-76$ ,  $z=47$ ). That is, activity in  
 409 these regions co-varied with participants' aggressive behavior in a low- relative to a high-status rank.  
 410 No regions survived in the opposite contrast (high > low).



**Fig. 3.** Neural processing of competitive status during punishment selection (decision phase). **a**, regions-of-interest (ROIs) used in multi-voxel pattern analysis (MVPA) to identify multivariate status representations during punishment selection. **b**, classification performance expressed as area under the curve (AUC) minus chance per each ROI. Each dot shows the AUC value per subject, with higher values indicating better classification between the better- and worse-performing rivals. Asterisks denote ROIs with significant above-chance accuracy according to bootstrap resampling. ACC: anterior cingulate cortex; Amy: amygdala; dmPFC: dorsomedial prefrontal cortex; Hipp: hippocampus; Prec: precuneus; Stri: striatum; TPJ: temporal-parietal junction; vmPFC: ventromedial prefrontal cortex. **c**, results of the post-hoc searchlight MVPA analysis within hippocampus and striatum masks (voxel-level  $p < .05$  uncorrected, cluster size  $k > 50$ ). Higher values indicate a greater contribution to the classification. **d**, correlation between classification performance in the striatum and mean aggression against the high-minus low-status opponent. We include best-fit lines and 95% prediction intervals.  $r$ =Pearson correlation coefficient;  $d$ =Cohen's  $d$ ; 95% BCa CI: 95% bias-corrected accelerated confidence intervals. **e**, parametric modulation in the decision phase (voxel-level  $p < .001$ , cluster-level  $p < .05$  Family Wise-Error [FWE] corrected,  $n=42$ ). Higher values indicate more trial-wise activity as a function of aggression in a low- relative to a high-status position. dlPFC: dorsolateral prefrontal cortex; SPL: superior parietal lobe; vlPFC: ventrolateral prefrontal cortex. **f**, parameter estimates resulting from the parametric modulation in the vmPFC. A.u.: arbitrary units.

411 *Neuroimaging study: neural processing of competitive outcomes as a function of status*

412 In the outcome phase, we observed widespread activation in the contrast won > lost with peaks

413 in the bilateral ventral striatum (VS; Table S1 in Supplementary Material). This is in line with previous

414 results employing competitive tasks (Votinov *et al.*, 2015; Buades-Rotger, Brunnlieb, *et al.*, 2016). More

415 importantly, we tested the interaction between status and outcome in order to inspect whether victories

416 and defeats were differently processed in the low- compared to the high-status condition. The interaction

417 contrast  $[Won\ Low + Lost\ High] > [Lost\ High + Won\ Low]$  revealed activation in left anterior insula (AI),

418 dorsal anterior cingulate cortex (dACC), left dorsolateral prefrontal cortex (dlPFC), left and right

419 temporoparietal junction (TPJ), precuneus, and VS (Fig. 4a-c; see Table S1 in Supplementary Material

420 for complete results). These regions hence reacted more strongly to infrequent, status-incongruent

421 outcomes. However, as becomes apparent from the parameter estimates in the VS and dACC (Fig. 4b-

422 c), the interaction was driven by a stronger effect of the outcome when playing against the high- relative

423 to the low-status opponent. If the effect were merely driven by the infrequency or unpredictability of

424 events, activity should be also increased in lost relative to won trials against the low-status opponent,

425 which was not the case. The opposite contrast, which entailed expectable, status-congruent outcomes,

426 yielded activation in primary visual and inferior temporal cortex as well as a cluster in the brainstem (see

427 Table S1 in the Supplementary Material).

428 We next probed whether the neural processing of victories and defeats was linked with status-

429 dependent aggressive behavior. We therefore extracted parameter estimates from clusters resulting

430 from the  $[Won\ High + Lost\ Low] > [Lost\ High + Won\ Low]$  contrast (dACC, AI, dlPFC, left and right TPJ,

431 precuneus, and VS) and correlated them with the status effect on aggression. Specifically, we extracted

432 the high- minus low-status difference separately for victories and defeats. Because we performed 14

433 correlations (2 values for each of 7 ROIs), we applied a Bonferroni correction to control for multiple

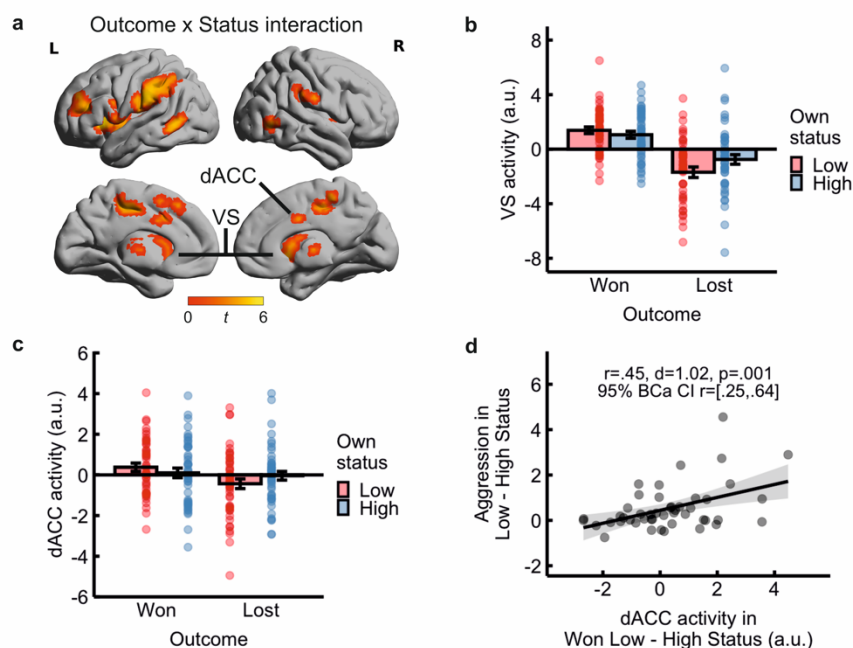
434 comparisons ( $.05/14=.003$ ). Differential reactivity to victories in the dACC was significantly associated

435 with aggression against the high- minus the low-status opponent ( $r_{45}=.45$ ,  $d=1.02$ ,  $p=.001$ ; Fig. 4d).

436 There was no correlation for losses ( $r_{45}=.12$ ,  $p=.394$ ). Activity in the rest of ROIs (AI, dlPFC, left and

437 right TPJ, and VS) was not associated with status-dependent aggression at a corrected level (all  $p>.050$ ;

438 see Table S2 in Supplementary material).



**Fig. 4.** Neural processing of competitive victories and defeats (outcome phase). **a**, regions showing a significant interaction between status and outcome (voxel-level  $p < .001$ , cluster-level  $p < .05$  Family Wise-Error [FWE] corrected). **b**, parameter estimates for the interaction effect in the ventral striatum (VS). **c**, parameter estimates for the interaction effect in the dorsal anterior cingulate cortex (dACC). **d**, correlation between dACC reactivity to victories and aggression in the low- minus high-status condition, including best-fit lines and 95% prediction intervals.  $r$ =Pearson correlation coefficient;  $d$ =Cohen's  $d$ ; 95% BCa CI: 95% bootstrapped bias-corrected accelerated confidence intervals (BCa CI).

439 **Discussion**

440 *Low competitive status is associated with aggression*

441 Aggressiveness is often taken as a requisite for competitive success (Chow *et al.*, 2009;  
 442 Trebicky *et al.*, 2013; Waasdorp *et al.*, 2013; Laustsen and Petersen, 2017; Cheng, 2020; Weick, 2020).  
 443 However, better contenders can rely on their skill, whereas less successful ones may use aggression  
 444 to hamper rivals' progress (Kirker *et al.*, 2000; Coulomb-Cabagno and Rasclé, 2006). Moreover, the  
 445 frustration and loss of control entailed in being repeatedly defeated should facilitate rather than suppress  
 446 aggression in low-status contestants (Przybylski *et al.*, 2014; Yu *et al.*, 2014; Oxford *et al.*, 2017). In a  
 447 correlational analysis and two laboratory experiments we found that low competitive status, measured  
 448 as competitors' relative rank in a hierarchy, was linked with more frequent and intense aggressive  
 449 behavior. Our results replicate and extend previous investigations showing that fouls or penalties are  
 450 associated with worse overall team performance in American football (Hauge, 2012), ice hockey (Coates  
 451 *et al.*, 2012), soccer (Jewell, 2012), and basketball (Berri and Rodenberg, 2012). Unlike these studies,  
 452 however, our measure of aggression (fouls or penalties committed relative to received) captures the  
 453 reciprocal nature of aggressive play and thus provides clearer evidence on the status-aggression  
 454 relationship.

455           The findings from our two experimental studies further show that the link between low status  
456 and aggression holds in competitions between individuals (i.e. not only between teams) and when  
457 aggressive behavior does not directly offer a clear competitive advantage. In addition, in our  
458 neuroimaging experiment subjects became quicker and selected louder sound blasts over time against  
459 in a low-status position, even when the opponents' hostile intent remained constant over time. This  
460 finding further demonstrates that aggression increases as competitive hierarchies emerge and is not a  
461 mere correlate of low performance. Our results also imply that the relationship between competitive  
462 status and aggression is not limited to situations involving face-to-face competition, but also applies to  
463 virtual, indirect contests. In line with this assumption, an online bargaining study showed that individuals  
464 attribute more hostile intentions to higher-status opponents (Saalfeld *et al.*, 2018). Competitive status  
465 thus appears to be a relevant trigger for aggressive behavior in both direct and virtual interactions.

466           Our main finding that participants chose higher punishments when placed in a low rank is  
467 however not entirely expectable. After all, participants might have instead displayed the opposite  
468 pattern, i.e. punishing a weaker rival to assert their dominance while being less aggressive against a  
469 stronger opponent as a conciliatory strategy. Indeed, some studies have shown that participants accept  
470 more unfair offers in experimentally-induced low status (Blue *et al.*, 2016; Hu *et al.*, 2016). Nevertheless,  
471 in these investigations behaving submissively yielded a direct economic benefit. What could explain the  
472 results of the present study, in which there was no money at stake? One possibility is that subjects were  
473 more willing to incur the risk of behaving aggressively when their status was low, as the prospect of  
474 losing increases risk-seeking (Tversky and Kahneman, 1981; Ruggeri *et al.*, 2020). Conversely, being  
475 in a high-status position induces risk aversion, so that subjects might avoid punishing lower-status  
476 individuals due to e.g. reputational concerns (Dreber *et al.*, 2008). Put otherwise, subjects had less to  
477 lose in a low-status position, which facilitates risk-taking. In addition, inducing a low-status mindset  
478 threatens self-worth and increases hostility (Davis and Reyna, 2015), which might have further  
479 exacerbated status-dependent aggression in the present study. Future studies should disambiguate  
480 these putative mechanisms underlying status-based aggression.

#### 481           *Changes in testosterone and cortisol concentrations*

482           We also observed a post-task increase in testosterone concentrations. This surge occurred  
483 instead of the decline that could be expected due to the hormone's circadian rhythm (Keevil *et al.*, 2013;  
484 Buades-Rotger, Engelke, *et al.*, 2016). In men, testosterone tends to rise after winning (Geniole *et al.*,  
485 2017) and when achieving a higher status in skill-based hierarchies (Cheng *et al.*, 2018). Although

486 subjects in the present study only won half of the trials on average, they did clearly defeat one opponent  
487 and overestimated the percentage of trials won against both rivals. Indeed, elevations in testosterone  
488 levels have been linked to more positive self-appraisals of competitive performance (Casto *et al.*, 2017).  
489 However, our data do not allow to determine whether the changes we observed here were purely driven  
490 by competition itself, the resulting outcomes, or other factors. Cortisol concentrations on the other hand  
491 showed a steep decline after the task. This effect, which we have previously observed (Buades-Rotger,  
492 Engelke, *et al.*, 2016), is likely due to anticipatory arousal, circadian decline, and/or relaxation in the  
493 scanner; the latter might have been heightened by the post-task resting-state measurement.  
494 Nonetheless, contrary to prior studies (Carré and Olmstead, 2015), neither endogenous testosterone  
495 nor cortisol were linked with status-dependent aggressive behavior. Our results are also in partial  
496 disagreement with the finding that competition-related surges in testosterone facilitate further  
497 antagonistic behavior (Mehta and Josephs, 2006; Carré *et al.*, 2013), although in the present study  
498 aggression was measured *during* competition rather than after it. Many experimental studies on the  
499 topic subject participants to rigged competitions in which they are clear winners or losers (Geniole *et al.*,  
500 2017). In contrast, the task employed here entailed a sequence of wins and losses, which might have  
501 had mutually cancelling effects on testosterone dynamics and subsequent aggressive impulses.  
502 Furthermore, testosterone increases are stronger when measured more than 10 minutes before  
503 competition (Geniole *et al.*, 2017). Our design might have hence missed out on the preparatory  
504 testosterone rush posited to foster competitive aggression in men (Zilioli and Bird, 2017; Geniole and  
505 Carré, 2018). Recent meta-analytic evidence suggests that the association between testosterone and  
506 aggression in humans is small (Geniole *et al.*, 2020). Testosterone-by-cortisol interactions yield even  
507 lower effect sizes across studies, with highly variable estimates and some evidence for publication bias  
508 (Dekkers *et al.*, 2019). Large, pre-registered investigations (Brannon *et al.*, 2019) are necessary to reach  
509 conclusive evidence on the role of testosterone in status-based aggression.

510 *Neural representations of competitive status during punishment selection*

511 At the neural level, we identified a number of brain regions implicated in the processing of  
512 competitive hierarchies and characterized their relevance for status-dependent aggressive behavior.  
513 Multivoxel pattern analyses revealed that the right anterior hippocampus distinguished between the  
514 better and worse rivals during punishment selection. A growing number of studies indicate that the role  
515 of the human anterior hippocampus is not limited to mapping events in time or items in space. Rather,  
516 this structure has been suggested to encode abstract relationships between entities along several

517 dimensions extracted from statistical regularities in the environment, i.e. relational knowledge (Garvert  
518 *et al.*, 2017; Park *et al.*, 2020). Similar mechanisms have been documented in the social domain, so  
519 that the anterior hippocampus tracks changes in an individual's power and affiliation relative to oneself  
520 (Tavares *et al.*, 2015; Kumaran *et al.*, 2016). Our results therefore provide converging evidence that this  
521 region, analogous to the ventral hippocampus in rodents (Fanselow and Dong, 2010), encodes status  
522 relationships and can thereby inform social decision-making.

523         The left ventral and dorsal striatum also displayed multivariate signals distinguishing the high-  
524 and low-status rivals. Furthermore, participants with a stronger differentiation between opponents in the  
525 striatum showed more status-dependent aggression. Paralleling our findings, striatum neurons in the  
526 rhesus macaque brain respond differentially to social cues from dominant and submissive monkeys,  
527 which concurs with a preference to watch faces from higher-status individuals (Klein and Platt, 2013).  
528 The present results thus indicate that the striatum is not only sensitive to status signals (Zink *et al.*,  
529 2008; Zerubavel *et al.*, 2015) and competitive outcomes (Qu *et al.*, 2017), but also differentiates between  
530 individuals differing in status during decisions to aggress. Our findings are in line with the hypothesized  
531 role of the striatum in retaliatory aggression (Chester, 2017; Bertsch *et al.*, 2020), and concur with meta-  
532 analytic findings demonstrating increased striatal activity when individuals deliver harsher punishments  
533 to unfair co-players (Gabay *et al.*, 2014). Therefore, our data bridge animal and human research in  
534 showing that the hippocampus and striatum are involved in the relational processing of social dominance  
535 signals. The present findings additionally suggest that these mechanisms are at play during competitive  
536 interactions and might contribute to the adoption of aggressive strategies.

#### 537         *Trial-wise covariation between brain activity and status-dependent aggression*

538         The ventromedial prefrontal cortex (vmPFC) evinced a status-dependent covariation with  
539 participants' momentary changes in aggressive behavior. Put another way, this region integrated status  
540 information in decisions to aggress on a trial-by-trial level. A number of volumetric and functional studies  
541 indicate that the vmPFC is crucial for the control of aggressive impulses (Beyer *et al.*, 2015; Gilam *et al.*,  
542 2015; Chester *et al.*, 2017), presumably by downregulating amygdala activity (Coccaro *et al.*, 2011;  
543 Motzkin *et al.*, 2015). There are however contradictory findings showing that vmPFC damage is linked  
544 with *increased* cooperative behavior (Wills *et al.*, 2018), or that vmPFC activation *positively* predicts  
545 aggressive decisions (Buades-Rotger *et al.*, 2017; Repple *et al.*, 2017). Here, the status-contingent,  
546 aggression-related elevations in vmPFC activity went along with those of other regions putatively  
547 involved in emotion regulation and social decision-making such as the dorsolateral or ventrolateral

548 prefrontal cortex (Morawetz *et al.*, 2015; Hackel *et al.*, 2020). In contrast, there were no positive  
549 associations between brain structures assumed to generate aggressive urges (e.g. amygdala,  
550 periaqueductal grey) (Coccaro *et al.*, 2011; Yu *et al.*, 2014) and punishment selections in the task.  
551 Therefore, we speculate that the observed prefrontal and parietal activity might correspond to deliberate,  
552 intentional aggressive decisions. This assumption is supported by the finding that lost trials led to  
553 subsequently faster decisions but did not influence punishment selections, which were strongly driven  
554 by competitive status. The relatively long and invariant response times during punishment selection (i.e.  
555 around 1300ms throughout the task) are also in consonance with this interpretation. Indeed, there is  
556 evidence that willingness to influence the rival's performance accounts for some variation in average  
557 punishment selections in this task (Chester and Lasko, 2019). Nonetheless, as we did not measure  
558 participants' motives, we cannot determine to which extent the intent behind louder sound blasts was  
559 mostly hostile or instrumental in nature.

560 *Status-dependent reactivity to competitive outcomes*

561 Finally, there was enhanced activation for status-incongruent outcomes in the ventral striatum,  
562 anterior insula, dorsal anterior cingulate cortex (dACC), dorsolateral prefrontal cortex, temporoparietal  
563 junction (TPJ) and precuneus. More specifically, these regions showed a stronger differentiation  
564 between victories and defeats when participants were in a low- relative to a high-status position. Our  
565 results resemble those from a previous study in which subjects competed against rivals varying in status  
566 (Zink *et al.*, 2008), and further implicate the VS in competitive hierarchy learning (Ligneul *et al.*, 2016).  
567 The present findings are also consistent with the observation that brain areas involved in valuation (e.g.  
568 VS) and social cognition (e.g. TPJ, precuneus) display differential sensitivity to a person's position in a  
569 hierarchy (Zerubavel *et al.*, 2015). In addition, dACC reactivity to victories in a low as compared to a  
570 high rank predicted greater aggression in the former relative to the latter. That is, the dACC response  
571 to status-enhancing wins, as compared to status-asserting ones, was correlated with greater status-  
572 dependent aggression. The local maximum observed here was located in the most posterior aspect of  
573 the dACC and lied in the near vicinity (i.e. within 5 mm in the sagittal and axial planes) of a meta-analytic  
574 peak for vicarious pain (Lamm *et al.*, 2011). Concordantly, dACC activity has been linked with retaliatory  
575 behavior (Krämer *et al.*, 2007; Gabay *et al.*, 2014; Beyer *et al.*, 2015). In rodents, this brain region was  
576 reported to encode competitive effort, i.e. the net value of a reward when competition is required to  
577 attain it (Hillman and Bilkey, 2012). It is nonetheless puzzling that the dACC failed to show a clear status  
578 distinction in the decision phase. This insinuates that, in the context of competitive aggression, the dACC



579 is more responsive to *changes* in status than to status cues per se. In consonance with this observation,  
580 the cingulate gyrus has been postulated to track moment-to-moment fluctuations in others' motivation  
581 during social interactions (Apps *et al.*, 2016) as well as in their rank and power within a hierarchy  
582 (Kumaran *et al.*, 2016). Taken together, these results tentatively suggest that status-based aggression  
583 might be particularly pronounced in persons for whom status-enhancing victories are more salient.

#### 584 *Limitations*

585 There are at least three key limitations to our experimental studies. First, both samples were  
586 small and restricted to healthy young men from whom we did not collect ethnicity data. The  
587 generalizability of our findings is thus modest. Second, as commented above, we did not address  
588 participants' strategies or intent in the task. Although reaction time and neuroimaging results may  
589 provide some indirect evidence in this regard, we cannot ultimately ascertain whether subjects'  
590 punishment selections were predominantly driven by spiteful or instrumental motives, nor whether they  
591 were influenced by frustration, threatened self-esteem, or other affective processes. Third, participants  
592 did not face a same-status rival, which would have constituted an ideal control condition and allowed to  
593 answer additional research questions. It should be noted that confederates (five male students aged 20-  
594 30) were not the same in all measurements, but this is unlikely to be a major source of variability because  
595 participants did not know the identity of the other players during the game.

596 The correlational sports data is limited in its correlational nature and in that we did not separately  
597 consider direct encounters between low- and high-status teams. Single-match metrics that model the  
598 distance in rank between opposing teams would more closely parallel the behavioral and neuroimaging  
599 studies. Finally, sports data only included men for consistency with the experimental studies and this  
600 also curtails the extrapolation of the obtained results to other competitions.

#### 601 *Conclusions*

602 In sum, we found that low competitive status consistently evokes aggression in healthy young  
603 men. Our findings refute the notion that successful competitors are the more aggressive ones. Rather,  
604 our results indicate that those in the lower echelons of competitive hierarchies use aggression more  
605 frequently and intensely over the course of successive encounters. Our experimental data shows that  
606 this holds even for situations in which aggression does not directly serve any instrumental function.  
607 Although endogenous testosterone levels increased after a competitive interaction, there were no links  
608 between this hormone and aggression, neither alone nor in interaction with cortisol. The latter finding  
609 questions a strong impact of testosterone on status-driven aggression, in line with recent meta-analytic

610 evidence (Dekkers *et al.*, 2019; Geniole *et al.*, 2019). On a neural level, both anterior hippocampus and  
611 striatum displayed multivariate representations of competitive status. Interindividual differences in  
612 status-dependent aggressive behavior could be predicted by a stronger differentiation between  
613 opponents in the striatum and by neural reactivity to status-enhancing victories in the dACC. On a trial-  
614 by-trial, within-subject basis, the vmPFC together with other prefrontal and parietal regions favored  
615 status-based aggression. Our study thus reveals a consistent association between low competitive  
616 status and aggression, and points toward potential neural mechanisms underlying this relationship.

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