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Dominant men are faster in decision-making situations and exhibit a distinct neural signal for promptness

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Abstract

Social dominance, the main organizing principle of social hierarchies, facilitates priority access to resources by dominant individuals. Throughout taxa, individuals are more likely to become dominant if they act first in social situations and acting fast may provide evolutionary advantage; yet whether fast decision-making is a behavioral predisposition of dominant persons outside of social contexts is not known. Following characterization of participants for social dominance motivation, we found that, indeed, men high in social dominance respond faster—without loss of accuracy—than those low in dominance across a variety of decision-making tasks. Both groups did not differ in a simple reaction task. Then, we selected a decision-making task and applied high-density electroencephalography (EEG) to assess temporal dynamics of brain activation through event related potentials. We found that promptness to respond in the choice task in dominant individuals is related to a strikingly amplified brain signal at approximately 240 ms post-stimulus presentation. Source imaging analyses identified higher activity in the left insula and in the cingulate, right inferior temporal and right angular gyri in high than in low dominance participants. Our findings suggest that promptness to respond in choice situations, regardless of social context, is a biomarker for social disposition.

Key words: High-density electroencephalography, Leadership, Reaction time, Social hierarchy

Introduction

Social hierarchies are pervasive across social species (van der Kooij and Sandi 2015). Although individuals' rank in social hierarchies can be reshuffled with changing circumstances (Knight

and Mehta 2017), there are drastic differences in the predisposition of individuals to attain or strive for dominance (Ellyson and Dovidio 1985; Johnson et al. 2012). Socially dominant individuals show consistently elevated motivation and directed behaviors to

control others (Hall et al. 2005). In social encounters, dominant individuals talk more (Schmid Mast 2002), interrupt others frequently (Ferguson 1977; Goldberg 1990), and are more likely to initiate social interactions, a behavior already observed in dominant children (Johnson et al. 2012). Even though humans use also other strategies (e.g., prestige) to navigate their way through social hierarchies (Maner and Case 2016), dominance is a strong predictor of peer ratings of competence (Anderson and Kilduff 2009) even when an individual actually lacks competence (Wiggins 1979; Buss and Craik 1980; Anderson and Kilduff 2009). Dominance is also the trait that most predicts who emerges as the leader in groups (Guinote 2017), even more so than intelligence (Judge et al. 2002).

Current knowledge about dominant people is mainly derived from their behavior in social, particularly competitive, contexts; little is known about their individual traits. Perhaps dominant people present specific traits, not necessarily depending on social contexts—though also manifested in them—that help them gather the referred social influence. In competitive settings, high dominance individuals have been shown to be faster in decision-making than low dominance ones (Santamaría-García et al. 2014, 2015; Balconi and Vanutelli 2016). Here, we hypothesized that a trait of dominant individuals is fast speed of acting as a general cognitive style. Being the fastest to take control of resources or to ensure survival could provide an evolutionary advantage and facilitate the emergence of dominant behaviour. According to the simple leader-follower decision rule “follow the one who moves first” (Van Vugt et al. 2008), being capable of deciding and consequently acting first in relevant social contexts increases the likelihood of becoming dominant and attaining leadership (Rands et al. 2008; King et al. 2009; Johnson et al. 2012). Despite the known evolutionary advantage redeemed by acting fast in social situations, it is not known whether dominant individuals respond faster as a cognitive style during decision-making, regardless of social context.

To test the hypothesis that trait dominance in humans relates to promptness of action, we first characterized individuals' social dominance motivation through the commonly used Personality Research Form dominance subscale [PRF-d (Jackson 1974)]. People who score high on PRF-d frequently attempt to control both, their environment and other people, and are forceful, decisive, authoritative and domineering (Buss and Craik 1980). They also tend to be considered high in leadership by their peers (Bateman and Crant 1993). Our hypothesis was that whereas high dominance individuals would have shorter latencies to respond when taking decisions on tasks involving cognitive challenges, they would not differ from low dominance individuals when performing a simple reaction task (SRT). Given the well-known sex differences in dominance (Helgeson and Fritz 1999; Dykiert et al. 2012), we focused on men. Thus, we set a series of experiments to assess if people scoring high or low in dominance motivation would differ in their promptness to respond across tasks involving different decision-making processes and in a SRT. Finally, we selected experimental conditions revealing group differences in response time to carry out an event related potentials (ERP) study with high-density electroencephalography (EEG) study to analyze potential differences in temporal dynamics of brain activation.

Materials and Methods

Participants

We recruited students from the Swiss Federal Institute of Technology in Lausanne (EPFL) and the University of Lausanne

(UNIL). Two-hundred and forty male participants were assigned to one of five different experiments included in the study. Participants were classified as either high or low in social dominance, depending on whether their score in the PRF-d (see Personality measurements) was below (low dominance) or above (high dominance) PRF-d = 9 (the median PRF-d score obtained from 412 students to the questionnaire). All participants were in good physical health with no current medical illnesses and had no neurological or psychiatric history. In addition, participants were tested for ocular dominance and completed a standardized handedness questionnaire (Oldfield 1971). We verified that all participants had good visual acuity of at least 1.0, as measured by the Freiburg Visual Acuity Test using both eyes (Bach 1996). Group characteristics and statistical analysis comparing demographic information between the five experiments as well as between the two dominance groups within each experiment are presented in Table 1. Participants gave informed written consent prior to the experiment, after receiving detailed written information. They obtained financial compensation of 20 CHF per hour. Experimental sessions were scheduled between 1 PM and 7 PM. All procedures complied with the Declaration of Helsinki. The Brain Mind Institute Ethics Committee for human behavior approved experiments 1-4, and the Cantonal Ethics Committee from Canton de Vaud the EEG experiment. The experimenters were male and were blind to the participants' personality scores.

Personality measurements

Social dominance motivation was assessed using the Personality Research Form dominance subscale [PRF-d (Jackson 1974)] through an online questionnaire (www.qualtrics.com) that was administered individually to participants several days before the experiment. The PRF-d is a 16-item true/false questionnaire that asserts motivation for social dominance with positive and negative items such as “The ability to be a leader is very important to me” and “I am not very insistent in an argument,” respectively. PRF-d scores are strongly and positively correlated with the frequency of self-reported prototypical social dominance acts such as “issuing orders that got the group organized” (Buss and Craik 1980) and with peer-nominations for leadership (Bateman and Crant 1993).

Spielberger's State-Trait Anxiety Inventory (STAI) (Spielberger et al. 1983) has two components designed to measure trait (STAI-T; e.g., “I worry too much over something that really doesn't matter”) and state (STAI-S; e.g., “I am presently worrying over possible misfortunes”) anxiety, independently. Each questionnaire includes 20-items to which participants respond on a 4-point Likert-type scale from 1 – completely disagree to 4 – completely agree. Scores range from 20 (very low anxiety) to 80 (very high anxiety). Since trait anxiety can correlate with social dominance and predict behavioral outcomes, we assessed STAI-T to control for this variable in statistical analyses.

Behavioral Experiments

We assessed the impact of dominance motivation on latency to respond in three choice tasks involving different cognitive processes and demands and a fourth one consisting of a simple reaction time (RT).

Custom-made E-prime scripts (version 2.0; Psychology Software Tools, Pittsburgh, PA) were used to program the behavioral experiments. In all experiments, participants sat comfortably with their heads approximately 50 cm apart from a

Table 1. Summary of participants' personal information

| | Experiment 1 | Experiment 2 | Experiment 3 | Experiment 4 | Experiment 5 | Between Experiments Analyses |
|--------------------------|----------------------------|----------------------------|----------------------------|----------------------------|-------------------------------|-------------------------------|
| Number of Participants | | | | | | |
| High Dominance | 16 | 20 | 45 | 26 | 13 | |
| Low Dominance | 16 | 20 | 45 | 26 | 13 | |
| High Dominance | 21.19 ± 2.26 | 20.55 ± 2.24 | 20.29 ± 2.61 | 21.35 ± 2.37 | 21.15 ± 2.30 | |
| Age ± SD | | | | | | |
| Low Dominance | 21.38 ± 2.99 | 21.40 ± 1.79 | 21.31 ± 2.60 | 20.85 ± 1.93 | 21.92 ± 3.95 | $F_{4,235} = 0.548, p = .701$ |
| Analysis | $t(30) = 0.200, p = .843$ | $t(38) = 1.328, p = .192$ | $t(88) = 1.862, p = .066$ | $t(50) = 0.835, p = .408$ | $t(24) = 0.607, p = .550$ | |
| High Dominance | 12.50 ± 2.00 | 12.85 ± 1.60 | 11.64 ± 1.63 | 12.58 ± 1.33 | 12.23 ± 1.83 | |
| PRF-d ± SD | | | | | | |
| Low Dominance | 6.00 ± 1.41 | 4.90 ± 1.55 | 5.98 ± 1.75 | 4.73 ± 1.93 | 5.23 ± 2.09 | $F_{4,235} = 0.129, p = .972$ |
| Analysis | $t(30) = 10.614, p < .001$ | $t(38) = 15.955, p < .001$ | $t(88) = 15.906, p < .001$ | $t(50) = 17.062, p < .001$ | $t(24) = 9.085, p < .001$ | |
| High Dominance | 35.19 ± 7.28 | 38.60 ± 37.55 | 39.49 ± 6.91 | 38.27 ± 10.01 | 40.08 ± 10.47 | |
| STAI-T ± SD | | | | | | |
| Low Dominance | 42.63 ± 8.16 | 37.55 ± 8.68 | 41.91 ± 7.97 | 39.23 ± 9.94 | 42.77 ± 11.40 | $F_{4,235} = 1.125, p = .345$ |
| Analysis | $t(30) = 2.720, p = .011$ | $t(38) = 0.404, p = .688$ | $t(88) = 1.541, p = .127$ | $t(50) = 0.348, p = .730$ | $t(24) = 0.627, p = .537$ | |
| Handedness (Right/ Left) | | | | | | |
| High Dominance | | | | | 12/1 | |
| Low Dominance | | | | | 10/3 | |
| Analysis | | | | | $\chi^2(1) = 1.182, p = .277$ | |

Note that handedness was not collected in Experiments 1–4.

computer's screen. In choosing the tasks, we aimed at exploring in a non-parametric manner potential boundaries for findings in response latencies by covering different sensory processing, cognitive load and decision-making processes in each task. We also aimed at including different instructions and time demands across tasks so that in case of finding task-related differences in response latencies, we could explore whether time constraints or lack of them could play a role in our findings.

Experiment 1 involved a facial emotion discrimination task. The stimuli were greyscale pictures of male faces (72 identities) with a frontal profile acquired from the databases FACES (Ebner et al. 2010), Nimstim Set of Facial Expressions (Tottenham et al. 2009), Radboud Faces Database (Langner et al. 2010) and The Karolinska Directed Emotional Faces (Lundqvist et al. 1998). No clothes or jewelry were visible and we took care to avoid features that attracted attention (e.g., scars, moles, facial hair, and unusual haircuts). Adobe Photoshop CS5 software (version 12.0) was used for image adjustment by converting the pictures to greyscale, equalizing contrast, rescaling to 860 × 600 pixels, and then manually standardizing the distance between the eyes and the chin while preserving the original aspect ratio. The picture background was set to grey, and luminance was equalized using the Matlab® Shine Toolbox (Willenbockel et al. 2010). Participants were shown 120 unique pictures: 20 different facial expressions per emotion (anger, happiness or neutral) in their original format and also in their flopped format (obtained by mirror-reversing the original image across the vertical axis). Participants were asked to fixate upon a central cross and to select which of the three emotions were presented by pushing a pre-assigned keyboard key. Participants were asked to be as fast and accurate as possible. The faces were presented in one out of five positions on the screen; either center or 20° or 35° rotated to either side of the center, and appeared for only 80 ms to avoid saccades towards the target. The next face was presented immediately after the participant's response (Fig. 1a). This experiment assessed latency to respond and accuracy in determining facial emotion.

Experiment 2 involved a facial recognition memory task comprising two phases, memorization and recognition. In the first phase, participants were asked to memorize 30 different faces, of which 15 had to be recognized among 15 novel faces in the second phase. We used the same images as in Experiment 1. Faces were displayed for 10 s each. In order to probe different time constraints than in the previous task (in which participants performed under time pressure), in this task participants could progress in the task, to some extent, at their pace. They could pass to the next face by pushing the spacebar in the memorization phase or by answering yes/no in the recognition phase (Fig. 1b). Immediately before the memorization phase, participants were instructed to memorize as many pictures as they could within 90 s and were told that their memory would be tested in the ensuing recognition phase. They were also informed that an average of 3 s per face was allowed because all 30 pictures had to be viewed within 90 s. The latency to pass to the next image was recorded. The second, recognition phase took place within 5 minutes after the memorization phase. Participants were presented with faces and they had to indicate whether they had visualized them during the previous phase. There was no time limit to answer, and participants were instructed to guess in case of doubt. Latency to respond and accuracy were recorded. Due to aberrant response times, data from one participant was removed from the analyses.

Experiment 3 aimed at assessing possible group-related differences in latency to respond in a task essentially different to

the previous ones, not involving faces and intermediate levels of time pressure. We selected a working memory map-based route-learning task, as previously described (Thoresen et al. 2016). This task tests visual working memory by presenting a map trajectory and then presents a test trajectory to which participants must respond as to whether the test trajectory was the same or different. The results presented here are a reanalysis from data reported in (Thoresen et al. 2016), with participants stratified according to the PRF-d questionnaire. For the experiment, 48 maps with similar route densities were created using Google Static Maps API (<https://developers.google.com/maps>). An area of 0.9 km² was shown, and a pixel resolution of 640 × 640 was used. Half the maps were cartographic road maps and half were satellite maps with roads superimposed. Participants viewed animations of a red marker following a set route. Each trial consisted of a learning stimulus and a test stimulus. In the learning stimulus, the marker was animated for approximately 17 s, and participants were instructed to learn the trajectory of the route. After the trajectory finished, the marker remained static for 2 s, and the same trajectory was repeated again. The test stimulus ensued immediately with the question “Is this the same route as before?” appearing in French for 1 s and accompanied by two repetitions of an animation, presented at double speed in a map with a size reduction of 27%. Evenly between trials, in a random order, this would be either the same trajectory as before or one with a subtle difference midcourse. Participants could respond as soon as the second trajectory appeared, but were told that after viewing the repeated trajectory, they would have 4 s to answer (“same” or “different”) using predefined keys of a standard keyboard. Participants were not asked to be fast and would always be able to respond to all trials, regardless of how long they took to respond. The task was preceded by four practice trials for which responses were not recorded. Data from the first block of 24 trials was analyzed for latency to respond and accuracy. A depiction of one trial can be seen in Fig. 1c.

Experiment 4 was a control experiment that assessed participants' performance in a simple reaction time task adapted from a crossed-uncrossed difference task (Fig. 2). At each trial, a grey square appeared either on the left or on the right of a cross displayed at the center of the screen. The inter-trial interval varied randomly between 0.15 and 1.5 s. Participants were asked to push the spacebar of the keyboard as soon as they perceived the square, regardless of the side on which it was presented. After 0.5 s, the stimulus disappeared even if no response had been entered. After a practice block of six trials, a block of 200 stimuli was presented. Breaks were introduced every 50 trials, and the entire task took approximately 10 minutes to complete.

EEG Experiment

Experiment 5 aimed at identifying neural signals related to differences in promptness to respond in high and low dominance participants. To this end, we used an adapted version of the task from Experiment 1. Stimuli included 40 male or female faces with happy, sad, angry, or neutral expressions presented in a randomized fashion. Happy and sad faces were obtained from Ekman and Friesen's Pictures of Facial Affect Series (Ekman and Friesen 1976), while angry and neutral faces were obtained from FACES (Ebner et al. 2010), Radboud Faces Database (Langner et al. 2010) and the Karolinska Directed Emotional Faces (Lundqvist et al. 1998). Using Adobe Photoshop CS5 software (version 12.0), the images were cropped to the

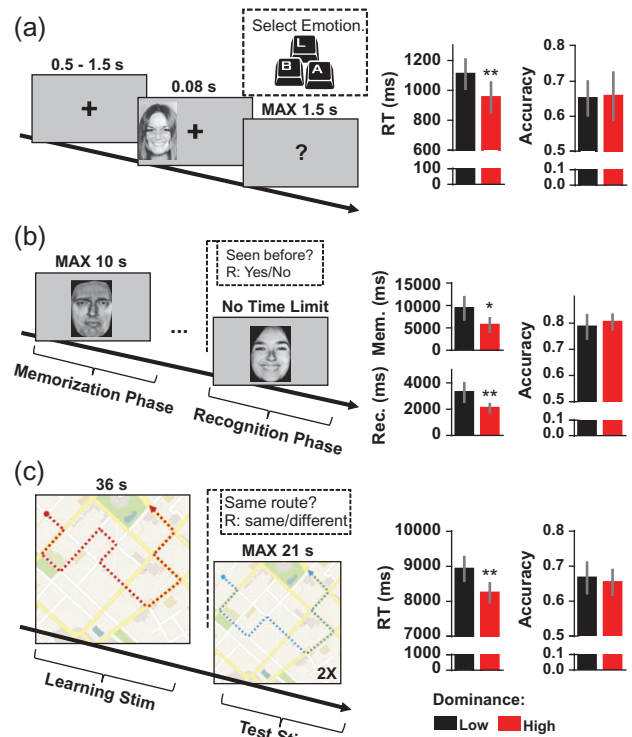


Figure 1. High dominance individuals respond faster but with the same accuracy as low dominance participants in a variety of choice decision-making tests. (a) Schematic representation of the emotion discrimination task included in experiment 1 (left panel) and corresponding RT and accuracy results for high and low dominance participants (right panel). Participants had to indicate the emotion (anger, happiness or neutral) depicted in the presented face, which could appear at different distances from the screen's center. (b) Schematic representation of the facial recognition memory task included in experiment 2 (left panel) and RT for both experimental phases, memorization and recognition, as well as accuracy data for the recognition phase (right panel). Participants learn faces (Mem., memorization phase) and indicated whether phases were familiar (i.e., presented in the memorization phase) or not (Rec., recognition phase) while responding at their own pace. (c) Schematic representation of the map-reading working memory task delivered in experiment 3 (left panel) and corresponding results (right panel). Participants had to indicate whether a route depicted by an animation in the screen was the same or different as the one just presented on a map. Data are presented as mean with 95% CI (* $p < 0.05$, ** $p < 0.01$). See also Table S1 for a summary of the statistical results.

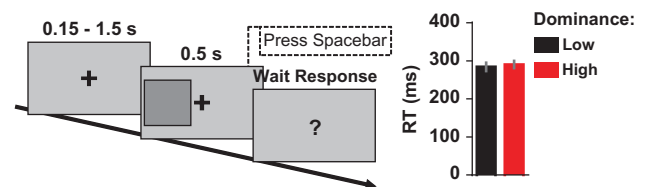


Figure 2. Schematic representation of the simple reaction time task delivered in experiment 4 (left panel) and corresponding results (right panel). Participants had to respond as soon as a grey square appeared on screen. Data are presented as mean with 95% CI (* $p < 0.05$, ** $p < 0.01$).

central portion of the face, regularized for luminosity and contrast, and transformed to the same size (346 × 543 pixels). All stimuli were presented on a grey background (RGB: 192, 192, 192). The images were displayed on an Asus VG248QE monitor with a resolution of 1920 × 1080 pixels and a refresh rate of 144 Hz. Participants sat 50 cm from the monitor in a dimly lit

Faraday cage. Background luminance was below 1 cd/m². Gaze was monitored by an eye tracker (The Eye Tribe ©) throughout the experiment. The head was fixed by a chin rest.

All participants completed two distinct experimental conditions, with the order of the conditions pseudo-randomly assigned to each participant. During the first condition, happy and sad faces (Happy vs. Sad) were used as stimuli, while in the second condition, angry and neutral faces (Angry vs. Neutral) were presented. Each condition began with one practice block with 10 trials followed by four experimental blocks with 80 trials each. Before each condition, participants were presented with onscreen instructions and after the practice block, they were allowed to ask any questions regarding the task. Experimental blocks were separated by a brief interval of 10 s. Participants were instructed to be as fast and accurate as possible, to keep their gaze on a fixation cross in the center of the screen, and to report the perceived emotion by pressing 1 of 2 buttons held in each hand or to guess when they were not sure. The association between response side and valence was counterbalanced across participants evenly within the high dominance and low dominance participants. During each trial, stimuli were presented in the observer's periphery either 26° left or right, during 0.1 s, followed by a 3 s period where the fixation cross was replaced with a question mark, prompting participants to respond. After each response, an inter-trial pause with a random duration from 0.5 to 1.5 s ensued. If a participant failed to respond, a short buzz sounded and the trial was repeated at the end of the presentation stack. For each condition, accuracy was calculated as the percentage of correct responses.

EEG Recording and Processing

Continuous EEG was recorded using a BioSemi Active 2 system (BioSemi) with 192 Ag-AgCl sintered active electrodes referenced to the common mode sense (CMS) electrode. The cap size and placement were adjusted individually: the Cz electrode was positioned halfway between the inion and nasion. The set of electrodes uniformly covered the entire scalp. The electrooculogram (EOG) was recorded with electrodes positioned 1 cm above and below the right eye and 1 cm lateral to the outer canthi. The recording sampling rate was 2048 Hz. Offline data were down sampled to 512 Hz and processed using an automatic pre-processing pipeline (da Cruz et al. 2018) that included the following steps: filtering via a bandpass of 1 – 40 Hz (3rd order Butterworth filter); removal of line-noise (CleanLine; www.nitrc.org/projects/cleanline); re-referencing to the bi-weight estimate of the mean of all channels (Hoaglin et al. 1982); removal and 3D spline interpolation of bad channels; removal of bad epochs; independent component analysis (ICA) to remove eye movement-, muscular- and bad channel-related artefacts; and removal of epoch artefacts. The proportion of interpolated electrodes was less than 5% for each subject. We extracted EEG epochs from 100 ms before stimulus onset (baseline) to 500 ms after stimulus onset. The averaged epochs for each participant were baseline corrected. The percent of rejected epochs was less than 10% for each subject.

Global Field Power Analysis

The global field power (GFP) is an instantaneous reference-independent measure of the neuronal response strength, and it is calculated as the standard deviation of the potentials across all electrodes (Lehmann and Skrandies 1980). To account for

temporal auto-correlation, 10 ms of contiguous significant effects ($p < 0.05$) is considered reliable (Guthrie and Buchwald 1991). The GFP was computed for each participant and each condition separately. Repeated-measures ANOVAs with the factors group (low and high dominance) and condition (Happy vs. Sad, Angry vs. Neutral) were conducted at each time point of the GFPs. Statistics were computed using the Statistical Toolbox for Electrical Neuroimaging (STEN) developed by Jean-François Knebel (<http://www.unil.ch/line/home/menuinst/about-the-line/software-analysis-tools.html>).

Distributed Electrical Source Imaging

Inverse solutions were computed for the time interval corresponding to the significant main effect of group in the GFP to estimate brain regions responsible for the group difference using the Local Auto Regressive Average inverse solution (Grave de Peralta Menendez et al. 2004; Plomp et al. 2010). A source space of 4022 points equally spaced throughout the grey matter of the Montreal Neurological Institute's (MNI) ICBM 152 non-linear atlas template brain (Fonov et al. 2011) was defined, and a model identical to (Plomp et al. 2009, 2010) was used. Source analysis was performed using Cartool software (Brunet et al. 2011). Repeated-measures ANOVAs with the factors group (low and high dominance) and condition (Happy vs. Sad, Angry vs. Neutral) were computed for each solution point on the current densities using STEN. Multiple comparisons for each solution point were partially corrected using the following spatial criterion: the clusters must contain at least 15 neighboring solution points showing significant effects ($p < 0.05$) (Knebel and Murray 2012). Current densities were averaged across the significant region for each cluster for the identification of each activation cluster center of mass (CoM). Activity in the solution point closest to each CoM was used to represent the corresponding brain region.

Salivary Cortisol Analyses

Saliva was collected three times: immediately after each participant had signed the informed consent form, at the beginning of the washout period, and 20 min after the end of the second condition. A sample of approximately 0.8 to 1.4 mL of saliva was obtained at each collection in 10 mL polypropylene tubes and frozen below -20°C until processed. Samples were then centrifuged at 3000 rpm for 15 minutes at room temperature, and salivary cortisol concentrations were measured by enzyme immunoassay according to the manufacturer's instructions (Salimetrics, Newmarket, Suffolk, United Kingdom). The samples were used to analyze cortisol baseline levels and hormonal changes taking place during the experiment. To control for the circadian rhythm of cortisol, all experimental sessions were scheduled between 1 PM and 7 PM. To estimate overall cortisol reactivity, we computed the area under the curve with respect to ground (AUC_g) and with respect to increase (AUC_i) indices (Pruessner et al. 2003). Due to sample contamination, data from 5 subjects had to be excluded resulting in 21 subjects (10 high dominance and 11 low dominance) with complete sets of 3 saliva samples proper for the cortisol AUC_g and AUC_i calculations.

Statistical Analyses

Behavioral data: Trials with latencies to respond values below 200 ms and above the stipulated time limits for each

experiment (c.f., see specific protocols above) were not considered valid and, hence, removed from the raw dataset. Trials with latencies three standard deviations away from each subject's mean latency were excluded (representing less than 5% of trials per subject). The effects of dominance group on latency and on accuracy were tested with ANCOVAs, or mixed-design ANCOVAs if a within-subject variable existed (in Experiment 1, within-subjects variables were used for emotion and difficulty; see Table S1). Accuracy was included as a covariate when latency was a dependent variable to account for possible trade-offs between these two variables (except in experiment 4 that involved a simple RT task in which accuracy is not relevant). Given that trait anxiety can affect individuals' reaction time (Etkin et al. 2004), ANCOVA included trait anxiety (evaluated with the STAI-T) as a covariate on analyses of the dependent variables latency and accuracy. Details concerning models and covariates can be consulted on Table S1. To account for random variation in latency to respond among participants in the EEG experiment, a mixed-effects model was used. The fixed effects were defined as an interaction model of "group" \times "condition" with additional predictors to control for STAI-T and accuracy, as in the previous ANCOVAs. Within-subjects variables differ from experiment 1 to accommodate the changes in the experimental designs: emotion and difficulty were used in experiment 1 while condition was used in experiment 5. Details concerning the fixed effects used in these models can be consulted on Tables S2 and S3. Random effects were the subjective intercept and slope, which respectively account for differences in individual baseline levels of latencies and for different latency changes due to condition. To study the overall effect of the PRF-d score in decision-making tasks' RT, we combined Experiments 1 to 5 in a mixed-effects model with an additional variable encoding decision-making experiments. RTs were standardized (z-scored) for each experiment to avoid comparing responses with different temporal scales. The fixed effects were defined as the interaction between PRF-d and the decision-making encoding variable, with additional predictors to control for STAI-T and accuracy (as done for all previous models). Details concerning the fixed effects used in these models can be consulted on Table S4. Random effects were a random intercept to account for the different experiments and a random slope to account for the two conditions in Experiment 2 (memorization and recognition). Satterthwaite's approximation for the degrees of freedom was used to compute mixed-effects models' p -values with the *lmerTest* package (Kuznetsova et al. 2017). The reported effect size statistics for the ANOVA-based methods were the Eta Square (η^2) for all experiments. Statistical analyses were performed with IBM® SPSS® Statistics Version 21 and in the R programming environment (R Core Team 2014).

Cortisol data: Cortisol AUC_g and AUC_i indices were used as dependent variables in ANOVAs to assess the effect of group on glucocorticoid reactivity in Experiment 5.

EEG data: To assess the effect of the activity in each brain region on RT or accuracy, significant CoM activations were used as independent variables in separate regressions for the dependent variables RT and accuracy. To account for the random variation in RT among participants, a mixed-effect model was used. The fixed effects were the CoM activations and the random effects were, as in the behavioral analysis, the subjective intercept and slope. Satterthwaite's approximation for the degrees of freedom was used to compute p -values. Inter-individual correlations between significant CoM activations were calculated with Pearson partial correlations using the *pcor* package (Kim 2015).

Results

High dominance individuals are faster to respond in choice tasks than low dominance ones

We assessed potential differences between high and low dominance individuals on latency to respond and accuracy in three choice tasks involving different cognitive demands and instructions (Experiments 1–3). We also tested them for latency to respond in a simple reaction time control task (Experiment 4).

In the emotion discrimination task (Experiment 1), high dominance participants had shorter latencies to respond than low dominance ones ($F_{1,28} = 9.06$, $p = 0.005$, $\eta^2 = 0.216$, 95% CI [0.044, 0.414]). The two groups did not differ in accuracy ($F_{1,29} = 0.02$, $p = 0.963$, $\eta^2 < 0.001$, 95% CI [<0.001 , <0.001]; Fig. 1a; Table S1). There were no significant effects for the task-related factors "emotion" and "difficulty", the latter related to the degree of rotation of stimulus presentation from fixation center (except for a significant effect of task difficulty on accuracy; $F_{1,58} = 3.45$, $p = 0.038$, $\eta^2 = 0.105$, 95% CI [0.003, 0.221]). There were no significant interactions between the different factors (see Table S1).

In the facial recognition memory task (Experiment 2; Fig. 1b), high dominance participants had shorter latencies to respond than low dominance ones in both, memorization ($F_{1,35} = 7.28$, $p = 0.011$, $\eta^2 = 0.169$, 95% CI [0.023, 0.333]) and recognition ($F_{1,35} = 9.64$, $p = 0.004$, $\eta^2 = 0.195$, 95% CI [0.043, 0.375]; Fig. 1b; Table S1) phases. In the recognition phase, both groups showed similar accuracy ($F_{1,36} = 0.57$, $p = 0.455$, $\eta^2 = 0.015$, 95% CI [< 0.001 , 0.128]). There was a positive correlation in participant's latencies across the two conditions (memorization and recall) ($r = 0.334$, $n = 40$, $p = 0.035$).

In the map-based route-learning task (Experiment 3; Fig. 1c), high dominance participants responded again faster than low dominance ones ($F_{1,86} = 9.56$, $p = 0.003$, $\eta^2 = 0.097$, 95% CI [0.021, 0.202]; Fig. 1c); Table S1. Here, again, both groups had similar accuracy levels ($F_{1,87} = 0.33$, $p = 0.567$, $\eta^2 = 0.004$, 95% CI [<0.001 , 0.051]).

In the simple reaction time task (Experiment 4), as hypothesized, there were no dominance-related differences in latency to respond ($F_{1,49} = 0.61$, $p = 0.439$, $\eta^2 = 0.012$, 95% CI [<0.001 , 0.101]; Fig. 2). This conclusion was further supported by a one-way Bayesian ANOVA that depicted a Bayesian factor (BF_{10}) for the main effect of group of 0.329 indicating around 3 times more evidence in favor of the null hypothesis (no difference between groups) as compared to the alternative (i.e., that there was a difference between groups).

High dominance individuals show a distinctive EEG signal

To identify brain activations linked with faster latency to respond, we performed an additional experiment (experiment 5) with high-density EEG while participants performed a slightly modified version of the emotion recognition task in experiment 1 (Fig. 3a). First, as in previous experiments, latencies to respond were shorter for high than low dominance participants (Fig. 3b; Table S2; $\beta = 127.57$ ms, SE = 60.88 ms, 95% CI [5.82, 250.89], $t(23.59) = 2.10$, $p = 0.047$). Groups did not differ in accuracy (Fig. 3b; Table S3). We also verified that the observed dominance-related effects on latencies to respond were observed across all performed decision-making experiments when PRF-d scores are considered as a continuous variable instead of using the dichotomous median-split approach used above (Fig. S1; Table S4).

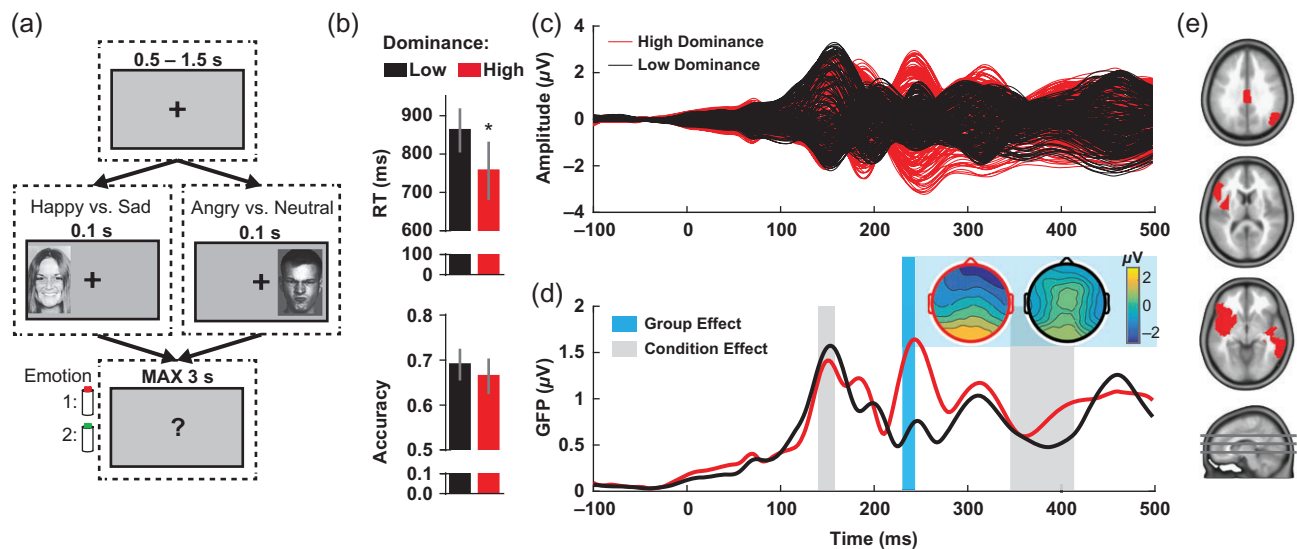


Figure 3. High dominance individuals show a distinctive EEG response related to faster reaction times. (a) Schematic representation of a single experimental trial for the Happy vs. Sad and Angry vs. Neutral conditions included in experiment 5. Following a fixation cross with a random duration from 0.5 to 1.5 s, one of the condition's facial stimuli is presented for 0.1 s. Participants then had 3 s to press the button corresponding to the identified emotion. (b) High dominance individuals performed faster but not less accurate in this task. Data are presented as mean with 95% CI ($p < 0.05$). See also Table S2 and Table S3. (c) Butterfly plots of the grand average ERPs, where each line is the group grand average for a single electrode. (d) GFP, a measure of how much electrode amplitudes deviate from the mean activity and a good indicator of brain activity, is plotted for both dominance groups. GFP showed a large increase in N2/P2 amplitude at approximately 240 ms for high dominance compared to low dominance individuals (cyan region). Topographical maps for each dominance group are also shown for this period. Red contour, high dominance; black contour, low dominance; cyan region $p < 0.05$; first gray regions $p < 0.05$. See also Table S5. (e) EEG source imaging results of the main effect of dominance group from 230 to 243 ms. Regions of significant differences, $p < 0.05$, are indicated in red. High dominance participants showed increased activation of 4 regions: the cingulate gyrus, the right angular gyrus, the left insula, and the right inferior temporal gyrus. See also Fig. S2 and Table S6.

Given previous work indicating that enhanced glucocorticoid levels can affect the activation of neural circuits (Henckens et al. 2011, 2012; Vogel et al. 2016, 2017), we measured salivary cortisol at different time points of the experiment. We found no differences between the groups in cortisol levels throughout the experiment were (AUCg: $F_{1,19} = 0.23$, $p = 0.638$, $\eta^2 = 0.012$, 95% CI [<0.001 , 0.070]; AUCi: $F_{1,19} = 0.24$, $p = 0.633$, $\eta^2 = 0.012$, 95% CI [<0.001 , 0.072]).

EEG event-related potentials (ERP) in high dominance participants showed more prominent deflections, approximately at 210 to 280 ms from stimulus onset, i.e., for the anterior N2 and posterior P2 ERP components (see butterfly plot in Fig. 3c). Repeated measures ANOVA of the global field power (GFP, Materials and Methods for details) showed a significant effect of group between 230 and 243 ms after stimulus onset ($F_{1,24} = 4.87$, $p = 0.037$, $\eta^2 = 0.169$, 95% CI [0.006, 0.370], Fig. 3d). High dominance participants had larger deflections ($M = 2.36 \mu\text{V}$, $SD = 1.26$) than low dominance participants ($M = 1.48 \mu\text{V}$, $SD = 0.68$). There were significant effects for the block condition, but no "group" \times "condition" interaction (for details see Table S5).

During the identified group effect period (230 to 243 ms), EEG source imaging analyses revealed increased activity in the cingulate gyrus, the right angular gyrus, the left insula, and the right inferior temporal gyrus in high dominance participants compared to low dominance participants (Fig. 3e; Fig. S2; Table S6 for Talairach coordinates). In exploratory analyses, we examined the relationship between the cingulate gyrus activity and response latency (Fig. S3), as well as inter-individual correlations between the cingulate gyrus and the right angular gyrus and between the left insula and the right inferior temporal gyrus (see Supplement and Fig. S2).

Discussion

In this study, we show that individuals high in dominance motivation respond faster in a variety of tasks with high cognitive demands, without impairing their accuracy. This dominance-related difference was not observed in a simple, less demanding reaction time task. Importantly, promptness to respond in high dominance individuals is related to a marked brain signal at 240 ms post-stimulus presentation, which is virtually absent in low dominance ones. The neuronal generators of this signal identified several brain regions (i.e., left insula, cingulate gyrus, right inferior temporal gyrus, and right angular gyrus) that showed higher activation in high than in low dominance participants.

Therefore, we found support for our hypothesis that high dominance individuals were consistently faster than low dominance ones even when participants are not in social context. Our strategy was to test participants across several challenges to be able to cover a broad spectrum of situations and, therefore, we did not gather data on parametric manipulations of a specific aspect. This approach allowed us to reveal that promptness of response of high dominance individuals is consistently shown across a variety of tasks that require: i) matching faces to one of 2-3 emotions under a high difficulty level (stimuli presented unpredictably at different locations from the fixation cross for only 80 ms) and trying to be as fast and accurate as possible (Experiments 1 and 5); ii) memorizing faces at own pace with advice to move on every 3 s to allow enough time for the totality of faces (Experiment 2, part 1); iii) recognizing formerly seen vs. unseen faces at own pace, without time limit (Experiment 2, part 2); iv) identifying whether a dynamic

map trajectory was the same as another one just presented before, under slight time pressure (4 s to respond per trial) but no specific instructions to be fast (Experiment 3). Accordingly, high dominance individuals displayed faster latencies to respond in situations ranging from quite high to low degrees of time pressure, and including emotional recognition, facial learning and memory, and a map-reading working memory. Except for the memorization part of Experiment 2 (part 1) in which participants' responses signaled an internal process, in all other cases they had to provide an answer out of 2-3 given choices. Sometimes, the high demanding task conditions, such as in Experiments 1 and 5, participants might have even reacted to some trials by guessing the answer. Importantly, the fact that high dominance subjects did not have an advantage in the SRT (Experiment 4) suggests that their fast responding advantage is not due to a superiority in perception processes or execution of motor actions. Instead, the common factor across tasks in which they show faster responses is a decision-making processes that links choice selection with action.

Previously, a few studies examined performance in participants whose social status was manipulated "artificially" in a competitive setting. When the hierarchy was created before the competitive encounter (i.e., participants were told *a priori* whether they were going to play with a superior or inferior adversary), participants were faster performing a basic visual perceptual decision task than when facing superior players (i.e., when they were made artificially "subordinate") without increasing their error rates and independently of the difficulty level (Santamaría-García et al. 2014). Interestingly, the degree to which their reaction times were reduced when playing with a superior, as compared to an inferior player correlated positively with participants' trait social dominance, suggesting that these individuals are more sensitive to competitive hierarchical cues (Santamaría-García et al. 2015). Social dominance was a combined measure from the behavioral approach reward responsiveness (BAS-R) and drive (BAS-D) scales from the Behavioral Activation System (BAS) questionnaire (Carver and White 1994; Hortensius et al. 2014). The BAS is a motivational system that has been related to feelings of dominance (Gable et al. 2000; Hortensius et al. 2014). When the hierarchy was created during the task, following a first competitive session on a selective attention decision task (i.e., participants were told that their performance in the task immediately before was superior to their competitor, making them artificially "dominant"), participants reduced their latencies to respond in the follow up session though, in this case, their accuracy was also reduced. This effect was specifically observed in individuals that scored high in the BAS questionnaire (Balconi and Vanutelli 2016). These findings suggest a particular sensitivity of individuals high in social dominance to motivate their responses in competitive settings, particularly when competitively challenged or developing a general sense of dominance and superiority than others. However, our study did not involve social competition and we still found lower latencies to respond in choice decision-making tasks in high than in low dominance participants. One possible explanation for this discordance is that the challenge involved in our experimental settings (always involving male experimenters instructed to maintain a behavioral distance with participants) differentially affected the engagement of participants as a function of their dominance motivation. Alternatively, high dominance subjects defined by the BAS questionnaire (used in the studies discussed above) and by the PRF-d questionnaire (used in our study) might not totally overlap. With the PRF-d scale, we might have

captured subjects that show a particularly engaged cognitive style concerning promptness of action in decision-making situations, regardless of the contingent competitive nature. Future studies should include both dominance measurements to cross-validate findings through different studies.

Interestingly, our behavioral findings resonate with a literature in animals that indicates a positive relationship between proactive (bolder and more aggressive than reactive ones) behavioral types and both social dominance and competitive ability (Oortmerssen et al. 1984; David et al. 2011; Riebli et al. 2011). In striking parallelism with our findings in humans, bolder stickleback fish (*Gasterosteus aculeatus*) were found to be faster in the speed of decision-making (time to making a decision) than their shyer conspecifics, though not different in accuracy (Mamuneas et al. 2015). In the wild, bolder fish tend to emerge as leaders and shyer fish as followers (Harcourt et al. 2009; Nakayama et al. 2012).

In humans, dominance is also a strong predictor of leadership (Judge et al. 2002). Therefore, our results might have as well implications for the emergence of leadership. In line with the leader-follower decision rule "follow the one who moves first" that operates in many animal social structures (Van Vugt et al. 2008), the likelihood to become a leader is thought to depend on specific internal or social traits that increases probability of movement initiation (Rands et al. 2008; King and Cowlshaw 2009), what suggest response times to be an indicative psychometric variable in social dominance. Being the fastest to act in situations involving decision-making related to the control of resources or to ensure survival could provide an evolutionary advantage and facilitate the emergence of dominant behavior. The faster cognitive processing in dominant individuals without a speed-accuracy trade-off may help in guiding group decisions without jeopardizing accuracy. Recently, promptness of responding was shown to be related to increased perception of charisma by peers (von Hippel et al. 2015).

Although some studies have highlighted an association between cortisol and social dominance in competitive settings (Mehta et al. 2008; Mehta and Josephs 2010; Turan et al. 2015), high and low dominance groups in our study did not differ in their cortisol levels throughout the experiment. Given that our experiment did not involve competition, and each subject was tested in isolation for their behavioral reactions, the lack of social dominance-related differences in cortisol levels is fully aligned with the literature (Larrieu et al. 2017) indicating that cortisol differences are only revealed by social competitive challenges (Wirth et al. 2006; Mazur et al. 2015; Turan et al. 2015). Therefore, our findings preclude us from relating social dominance-related differences in brain activity with cortisol actions. However, we cannot exclude that other stress-related systems (e.g., brain norepinephrine) known to affect dynamics of brain activation (Hermans et al. 2011) could have been differentially engaged during task performance in the two dominance groups.

Our ERP data identified a time-window between 230-243 ms in which task processing highly differed between the two groups, at which high dominance participants showed large deflections that were virtually absent in the low dominance group. The amplitude modulation of these anterior N2 and posterior P2 components occurred much earlier than motor responses, thus, they do not reflect faster motor executions, as for example, the readiness potential does, but they are a precursor. This N2/P2 component in the EEG may reflect allocation of resources to the detection and categorization of the target stimulus and associated decision-making processes (Mudar

et al. 2016), as well as the intentional effort to carry out the task (Winterer et al. 2002). Therefore, the dominance-related difference in N2/P2 activation may reflect deficits in the mobilization of these resources. As a speculation, the marked increases in N2/P2 responses may be a general marker for social dominance. Intrinsic differences in the identified brain processes at approximately 240 ms may define key differences in cognitive style that, when operating in social contexts, set the basis for the emergence of dominance hierarchies and leader-follower relationships.

In particular, high dominance participants showed increased activations in four brain regions: left insula, cingulate gyrus, right inferior temporal gyrus, and right angular gyrus. Previous studies linked higher activation in the cingulate to faster reaction times (Paus 2001; Hahn et al. 2007; Mulert et al. 2008), particularly when the stimulus location is unpredictable, as in our experiment in which faces were presented either to the left or right of fixation. Cingulate activity was also related to increased efforts performed to excel in tasks (Winterer et al. 2002; Hillman and Bilkey 2012) to motor preparation (Isomura et al. 2003) and to allocation of attention (Winterer et al. 2002). Therefore, the higher activation in the cingulate cortex may reflect the greater ability of dominant individuals to recruit brain resources to facilitate response selection. In addition, high dominance participants showed increased recruitment of regions functionally engaged in the performed task. Specifically, the right inferior temporal gyrus contains the fusiform face area that is involved in face processing (Kanwisher et al. 1997; McCarthy et al. 1997; Gauthier et al. 2000), and activity in the left insula is observed during emotional perception and experience (Duerden et al. 2013).

Group differences in the EEG may have occurred for early, medium, or late components such as the P1, N1, P3 or the lateral readiness potential. Early differences could have been taken as evidence for faster sensory encoding and visual processing. Later difference in the P3 may have been taken as evidence for cognitive difference related to dominance and difference in the readiness potential for faster motor execution. As mentioned, we found only significant and large difference for the medium component indicating that people high in dominance translate sensory evidence faster into decision-making. Our findings raise several questions. First, it will be important to determine whether N2/P2 responses are susceptible to change, for example, when a dominant individual occupies a subordinate role similar to the above mentioned results (Santamaría-García et al. 2014). Second, social hierarchies are already observed in preschool children (Hay et al. 2004). Hence, it will be important to assess during which period of development the increased N2/P2 emerges. Third, it will be important to translate our findings to real life. For example, it will be relevant to assess whether even stronger signals are observed in groups known to be particularly dominant, such as CEOs. In this context, it is important to mention that several functional magnetic resonance imaging (fMRI) and EEG studies have shown a network of activated brain areas in relation to social ranking (Zink et al. 2008; Chiao et al. 2009; Marsh et al. 2009; Santamaría-García et al. 2015; Balconi and Vanutelli 2016; Ligneul et al. 2016). A further key question is whether female participants will show similar behavioral and EEG patterns? Finally, it will be important to determine whether we can find correlates between faster reaction times and increased activity in identified brain areas and everyday life parameters such as income, social status, or sports performance.

Importantly, our results are of correlational nature. Hence, we cannot make any conclusions about causality. For example, whereas faster responses may be beneficial for survival, they might just be an expression of dominance, similar to the observation that the dominant person expresses their opinion first in a group. Likewise, we do not exactly know whether the identified increases in brain activity are causal for faster reaction or just reflect other types of processing relate to dominance. In addition, we cannot exclude the possibility that the feeling of power and superiority, associated with dominance motivation, affects task engagement and, hence, ERPs and latency to respond, in resemblance to the recently discovered effect of artificial rank allocation on response latency and ERPs (Santamaría-García et al. 2014).

Processing speed, revealed through fast responses in laboratory tasks similar to those applied here, has been reported to be a strong predictor of survival (Roberts et al. 2009), and higher ranking individuals exhibit better health (Sapolsky 2005; Marmot 2006). Surprisingly, despite the numerous advantages for health and wellbeing associated with high rank, very little is known regarding the factors that predispose individuals to attain dominance. Our study raises the possibility that differences in promptness to respond in decision-making situations and the associated neural underpinnings are at the core of rank establishment and might link social rank with physical and mental health (Selten et al. 2017).

Supplementary Material

Supplementary material is available at *Cerebral Cortex* online.

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Notes

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