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Proc. R. Soc. B 2012 **279**, 2275-2280 first published online 1 February 2012
doi: 10.1098/rspb.2011.2523

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Testosterone disrupts human collaboration by increasing egocentric choices

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Collaboration can provide benefits to the individual and the group across a variety of contexts. Even in simple perceptual tasks, the aggregation of individuals' personal information can enable enhanced group decision-making. However, in certain circumstances such collaboration can worsen performance, or even expose an individual to exploitation in economic tasks, and therefore a balance needs to be struck between a collaborative and a more egocentric disposition. Neurohumoral agents such as oxytocin are known to promote collaborative behaviours in economic tasks, but whether there are opponent agents, and whether these might even affect information aggregation without an economic component, is unknown. Here, we show that an androgen hormone, testosterone, acts as such an agent. Testosterone causally disrupted collaborative decision-making in a perceptual decision task, markedly reducing performance benefit individuals accrued from collaboration while leaving individual decision-making ability unaffected. This effect emerged because testosterone engendered more egocentric choices, manifest in an overweighting of one's own relative to others' judgements during joint decision-making. Our findings show that the biological control of social behaviour is dynamically regulated not only by modulators promoting, but also by those diminishing a propensity to collaborate.

Keywords: collaboration; testosterone; information aggregation; social

1. INTRODUCTION

Collaborative efforts, for example, when lions hunt in prides or human scientists toil together in the laboratory, can provide benefits to the individual and the wider social group [1–3]. In perceptual decisions, human groups can achieve a performance benefit by combining individuals' information [4], and the potential for benefits from such information aggregation by groups is an important concept in disciplines like political science [5]. Similar benefits from collaboration can accrue to groups in tasks assaying intelligence [6], and collaborative efforts also underlie many cooperative behaviours in choices over the division of resources such as food or money [1,7]. However, a tension exists between collaborative and more self-oriented behaviours: for example, while groups may benefit from a collective intelligence [6] they can be subject to problems such as 'group-think' [8]. Previous work on biological factors influencing this balance has identified factors that promote collaboration (e.g. the hormone oxytocin [9] and neural reward mechanisms [10,11]). Instead, here we test whether a candidate agent, the hormone testosterone, can diminish collaboration.

Testosterone is implicated in a variety of social behaviours, and these data point to a potential to diminish collaboration. Higher endogenous testosterone correlates with increased anti-social behaviour in female prisoners [12], higher aggression [13] and more punitive reactions to unfair offers in a bargaining game [14]. Consistent with a potential to disrupt social collaboration, administering exogenous testosterone decreases facial mimicry as measured by facial muscle responses to photographs of emotional faces [15]; decreases the ability to infer emotional states from photographs of eyes [16]; and decreases ratings of trustworthiness in photographs of faces [17]. It has been argued that such findings reflect a more general role for testosterone in increasing a motivation to dominate others (i.e. achieve or maintain social status) [18,19]. Increased status-seeking would in turn predict decreased collaboration in that it entails that individuals, by being more assertive, may be less willing to take account of the opinions of others.

However, when identifying testosterone's effects on social choice, it is important to have a control for testosterone's effects on non-social decision making. In individual choice,

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Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2011.2523 or via http://rspb.royalsocietypublishing.org.

Received 2 December 2011
Accepted 11 January 2012

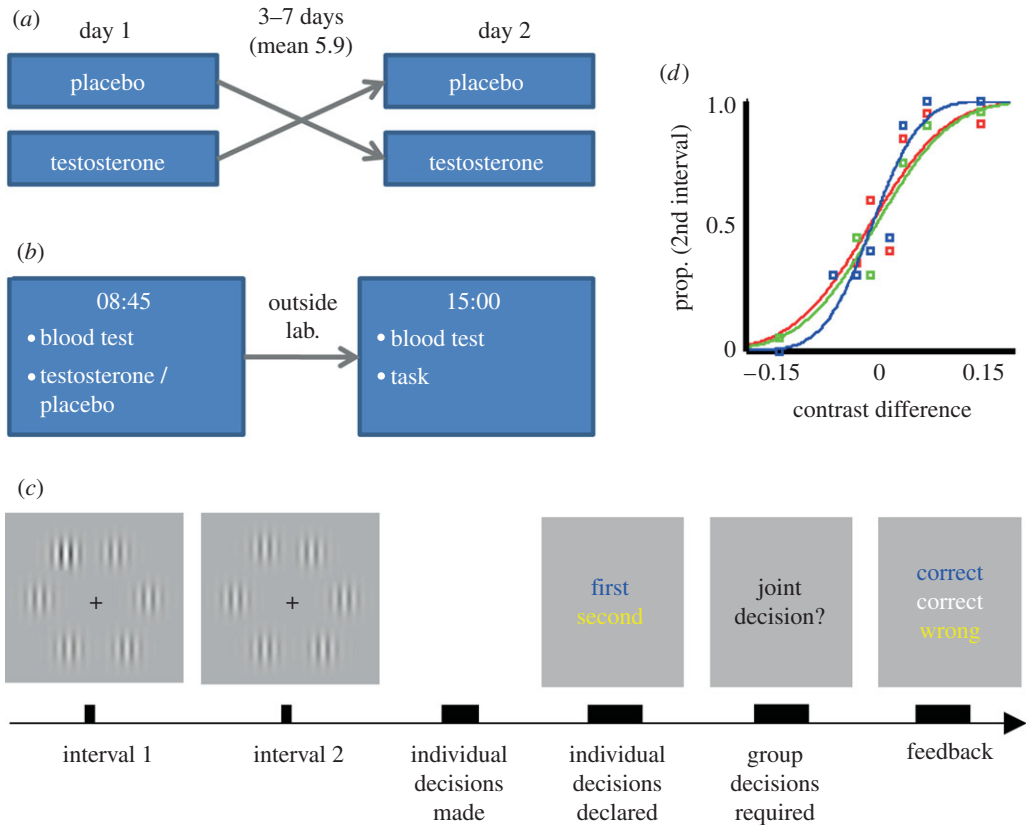

Figure 1. Experimental design. (*a*) Pairs of female participants (dyads) attended on two separate days in a blinded, randomized, placebo-controlled cross-over design. Both dyad members received identical treatment order. (*b*) Participants had blood taken before treatment and testing. (*c*) During testing dyad members sat in the same room viewing separate monitors. In a 2-alternative forced choice, design gratings were presented at two intervals, one containing a target grating with increased contrast. Each participant initially responded without consultation, providing measures of individual decision-making (S_{indiv}). If they disagreed, a joint decision was requested, which provided a measure of collaborative decision-making ($S_{collective}$). (*d*) Example psychometric function for dyad 1 under placebo. Proportion of trials reported as second interval is plotted against target contrast difference. Highly sensitive observers give steep functions with large slope (S). Here individuals (S_{indiv}) are red and green, and the dyad ($S_{collective}$) blue.

endogenous testosterone in men and women has been correlated with psychological variables such as attention [20] and economic variables, such as risk-taking [21]. Administering exogenous testosterone has widespread effects on non-social cognition, for example on working memory [22], spatial memory [23] and reward processing [24]. In particular, testosterone's known associations with reward-related processing [21,24,25] can complicate the interpretation of its effects in traditional economic tasks assaying social choice [26]. These concerns motivate a focus here both on collaborative decision-making without an economic dimension, and also on the need to dissociate testosterone's potential effects on social and individual choice.

To isolate the impact of testosterone on collaborative and individual decision-making, we exploited a task that assays each of these components independently [4]. In our task, individuals must share information, and actively collaborate, to gain a performance benefit in a visual perceptual decision task. The task was performed by pairs of participants (dyads) who initially made a perceptual decision alone, enabling us to measure the sensitivity of each individual's non-social decision-making by estimating the slope (S_{indiv}) of their psychometric function (figure 1). Then, in trials where the dyad's initial responses diverged, one participant announced a collective decision (agreed on via direct verbal negotiation between dyad members), providing a psychometric function for the dyad ($S_{collective}$) that reflected collaborative sensitivity. To successfully collaborate, individuals must appropriately weight their own opinion and that of the others prior to a joint decision [5]. We were agnostic about testosterone's potential effects on individual decisions, but predicted that testosterone would causally disrupt collective decision-making.

2. METHODS

(a) *Participants*

Seventeen pairs of participants (dyads) comprised our study sample (mean age 21.7 years, range 18–30; one further dyad was excluded for below-chance behavioural performance). We confined our sample to women, in whom prior evidence links behaviour to both endogenous [12,13,21] and exogenous testosterone [17,26]. All 34 participants were healthy, had normal or corrected to normal visual acuity, took no medication other than long-standing contraceptives (seven took combined oestrogen and progestogen contraception; one took progestogen only contraception), reported regular menstrual cycles (29.1 ± s.d. 2.2 days, range 29–35 days) and were tested between days 1 and 14 of their cycle. All gave informed consent and were paid for attendance.

(b) *Experimental procedure*

In a randomized, placebo-controlled, double-blind, cross-over design, 80 mg testosterone undecanoate was administered orally (Restandol testocaps; figure 1*a*). Oral testosterone undecanoate is widely used clinically and has well-known pharmacokinetics [27–29], such that all participants consumed breakfast to aid drug absorption; and the gap between drug administration and the start of behavioural testing was 6–7 h. On two separate days (mean 5.9 days apart, range 3–7 days), the dyad attended at 08.45 when both members received either testosterone or placebo and returned at 15.00 for behavioural testing (figure 1*b*).

Blood samples were taken on each attendance at the laboratory. Total serum testosterone was measured with a standard, commercially available Roche Modular testosterone assay using electrochemiluminescence immunoassay methods in the University College London Hospitals biochemistry laboratory. Biochemical data were available from 14 of the 17 dyads, with hormonal data from the remaining three dyads incomplete owing to administrative errors in the biochemistry laboratory.

(c) *Behavioural methods*

In our task, both dyad members sat in a room and performed a 2-alternative forced choice task on identical stimuli presented on separate monitors (figure 1*c* and see the electronic supplementary material for full details). On each trial, there were two intervals and participants initially decided alone in which interval a target (a higher contrast grating) appeared. Target contrast varied between trials, enabling us to measure the sensitivity of each individual's non-social decision-making by estimating the slope (S_{indiv}) of their psychometric function (figure 1*d*), which was determined using standard methods ([30] and see the electronic supplementary material for details) by plotting the proportion of trials in which the target was reported in the second interval against the contrast difference at the target location (the contrast in the second interval minus the contrast in the first). A large slope indicated highly sensitive performance. After these initial individual decisions, participants then saw their partner's choice. In trials where the dyad's initial responses diverged, one participant was randomly selected to announce a collaborative decision reached after free discussion. As was the case for individuals, we derived a psychometric function for the dyad, where collaborative success was reflected in the slope ($S_{\text{collective}}$). Feedback either followed the individual decision if they initially agreed, or alternatively followed their joint decision.

(d) *Data analysis*

Statistical tests were carried out using paired or independent sample *t*-tests or mixed analyses of variance (ANOVA) in SPSS v. 17.0; reported *p*-values are two-tailed.

3. RESULTS

As expected, our hormonal manipulation engendered a large increase in total serum testosterone when comparing the time of behavioural testing (mean $9.3 \pm$ s.d. 9.0 nmol l^{-1}) with either morning baseline ($1.2 \pm$ s.d. 0.5; paired *t*-test $t_{27} = 4.7$, $p < 0.0001$) or placebo ($1.1 \pm$ s.d. 0.6; paired *t*-test $t_{19} = 4.2$, $p < 0.001$). Crucially, testosterone administration had no effect on individual decision-making. Individual sensitivity (S_{indiv}) under testosterone was no different from placebo when all 34 participants were considered (S_{indiv}; placebo $3.11 \pm$ s.d. 1.68; testosterone: $2.99 \pm$ s.d. 1.76; paired *t*-test $t_{33} = 0.5$, $p > 0.6$). This was also the case when considering either the better (S_{max} placebo $3.80 \pm$ s.d. 1.70; S_{max} testosterone $3.69 \pm$ s.d. 1.88; paired *t*-test $t_{16} = 0.2$, $p > 0.8$) or worse performing member of each dyad (S_{min} placebo $2.41 \pm$ s.d. 1.38; S_{min} testosterone $2.28 \pm$ s.d. 1.33; paired *t*-test $t_{16} = 0.5$, $p > 0.6$). The proportion of trials where the dyad's initial decisions diverged also remained unaffected by testosterone (placebo $0.37 \pm$ s.d. 0.10; testosterone $0.39 \pm$ s.d. 0.08; paired *t*-test $t_{16} = 0.9$, $p > 0.4$).

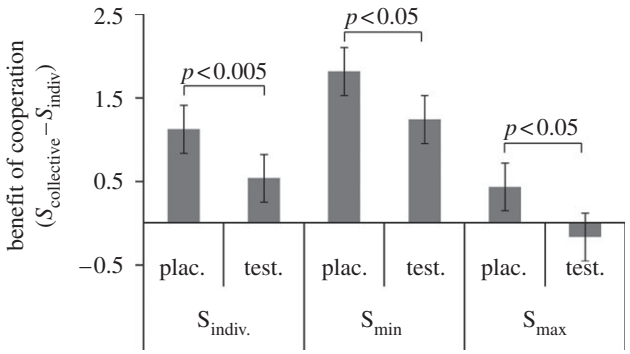

Figure 2. Individuals derive a performance benefit from collaboration. The dyad's collaborative decisions were more sensitive ($S_{\text{collective}}$) than the individuals' decisions alone (S_{indiv}). Our metric for this performance benefit on the vertical axis is the difference between an individual's sensitivity and the cooperative sensitivity achieved by their dyad (*Benefit of collaboration* $= S_{\text{collective}} - S_{\text{indiv}}$). This benefit is attenuated by testosterone when collapsed across all 34 participants (S_{indiv}) and also when only the better (S_{max}) or worse (S_{min}) members of each dyad are included. All *t*-tests shown are paired. Error bars indicate s.e.m.

Having shown that testosterone did not compromise individual decisions, we could then ask if it had a selective impact on the ability to successfully share information. The logic of effective collaboration is that, if achievable, it benefits the individuals more than acting alone [1–3]. We tested this by asking if testosterone affected the performance benefit each individual accrued from working together, measured by $S_{\text{collective}} - S_{\text{indiv}}$ (figure 2). We found that testosterone caused a marked decrease in the individual performance benefit arising from collaboration ($S_{\text{collective}} - S_{\text{indiv}}$ placebo $1.13 \pm$ s.d. 1.33, testosterone $0.54 \pm$ s.d. 1.02; paired *t*-test $t_{33} = 3.3$, $p < 0.005$). Furthermore, testosterone disrupted the benefit of collaboration for the better participant ($S_{\text{collective}} - S_{\text{max}}$ placebo $0.44 \pm$ s.d. 1.14, testosterone $-0.17 \pm$ s.d. 0.59; paired *t*-test $t_{16} = 2.2$, $p < 0.05$) as well as for the worse participant in each dyad ($S_{\text{collective}} - S_{\text{min}}$ placebo $1.82 \pm$ s.d. 1.15, testosterone $1.24 \pm$ s.d. 0.86; paired *t*-test $t_{16} = 2.4$, $p < 0.05$). Thus, even from a purely self-interested point of view both dyad members were handicapped when testosterone disrupted the performance benefits from collaboration.

In an evolutionary framework [2,7], our data implicate testosterone as a proximate, mechanistic modulator of collaboration, and specifically one that reduces the ability to collaborate. On this basis, we would expect testosterone to disrupt collaboration via a consistent bias in collaborative decision-making. To test this

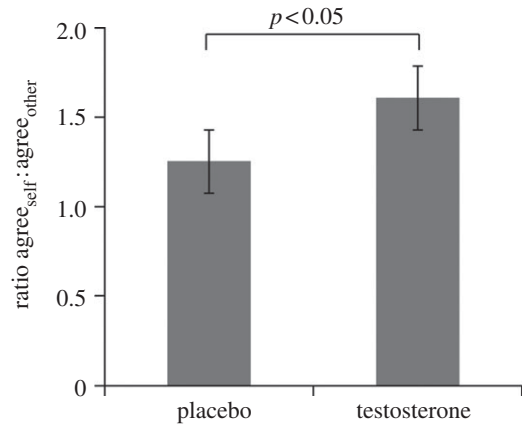

Figure 3. Testosterone disrupts collaboration by increasing the egocentricity of decision-making. Each member of the dyad announced the dyad's joint decision in half the trials where such a collaborative decision was required. The sensitivity of collaborative decision-making hinges on the distribution in weighting attributed to one's own and the other's opinions. For each participant, we measured this weighting by the ratio of times they agreed with themselves (egocentric decisions) to agreement with the other's opinion (allocentric decisions). An egocentric–allocentric ratio of 1 means that participants weight their own and the other's original judgement equally. On placebo, there is trend towards egocentricity bias (one-sample, $t_{33} = 1.8$, $p < 0.1$)—an egocentricity bias that becomes marked on testosterone (one-sample, $t_{33} = 3.0$, $p = 0.005$). We show a paired *t*-test for testosterone versus placebo ($t_{33} = 2.4$, $p < 0.05$). Error bars indicate s.e.m.

prediction, we focused on participants' responses as they announced collaborative decisions, where they must appropriately weight each dyad member's opinion. Two considerations might explain how testosterone interferes with this weighting. First, testosterone could lead to a consistent overweighting of the other's opinion, engendering allocentric (other-centred) decision-making, in line with its effect of increasing offers when given in a bargaining game [26]. Second, it could cause consistent overweighting of participants' own opinions, where such egocentricity parallels its effects on trade-offs in animals, for example to eschew parental responsibilities and increase courtship [31,32].

To arbitrate between these competing hypotheses, we computed an egocentric–allocentric (E–A) ratio of the number of trials where the announcer agreed with themselves to the number they agreed with the other. Each hypothesis makes a clear prediction: an allocentricity bias decreases the E–A ratio; and an egocentricity bias increases the E–A ratio. Our data fitted predictions from the second hypothesis, namely that testosterone consistently causes an egocentricity bias (figure 3). The E–A ratio increased under testosterone ($1.61 \pm$ s.d. 1.17) relative to placebo ($1.26 \pm$ s.d. 0.83; paired *t*-test $t_{33} = 2.4$, $p < 0.05$). This increased E–A ratio was consistent across both the best and worst-performing dyad members, as shown in a 2 decision-maker (S_{min}, S_{max}) by 2 drug (placebo, testosterone) mixed ANOVA in which there was a main effect of drug ($F_{1,16} = 5.8$, $p < 0.05$) but not decision maker ($F_{1,16} = 0.1$, $p > 0.7$) and no interaction ($F_{1,16} = 0.6$, $p > 0.4$). We also note that this egocentricity bias was not accompanied by altered deliberation time for collective decisions (placebo 7.56 s $\pm$ s.d. 3.25; testosterone $7.44 \pm$ s.d. 2.89; paired *t*-test $t_{33} = 0.5$, $p > 0.6$); which in the light of the broader choice literature suggests that the effect was not related to decision uncertainty that is usually accompanied by reaction time changes [33]. Neither E–A ratio nor sensitivity measures were related to total serum testosterone levels (details in the electronic supplementary material). Finally, given a recent study suggesting participants' beliefs about which drug had been administered might affect choice [26]; we tested for this and found no difference in E–A ratio when participants believed they had received placebo (mean $= 1.58 \pm$ s.d. 1.18, $n = 44$) compared with when they believed they had received testosterone ($1.21 \pm$ s.d. 0.62, $n = 20$; independent samples *t*-test $t_{62} = 1.3$, $p > 0.1$; details in electronic supplementary material).

4. DISCUSSION

In our paradigm, testosterone causally and selectively disrupted individuals' ability to successfully collaborate and aggregate their information in order to achieve a performance benefit. Further, this effect was selective because while disrupting collective decision-making, testosterone left individual decisions unaffected, which is important in the light of testosterone's widespread associations with aspects of non-social choice such as attention [20], working memory [22], spatial memory [23] and reward processing [24]. Finally, we demonstrated that, across both the better and worst-performing members of the dyads, testosterone disrupted collaboration by increasing the egocentricity in individuals' choices, operationalized as an enhanced weighting of one's own relative to another's evidence.

Our finding that testosterone increased egocentric choices accords with a broader literature concerning testosterone's role in social choice, and in particular with an interpretation of that literature which proposes that testosterone's role is to increase dominance or status-related behaviours [18,19]. High social status is associated with elevated testosterone in humans [13,19], chimpanzees [34] and other mammals [35]. A greater drive for social status leading to greater assertiveness during social interactions might reasonably be expected to impair an individuals' ability to appropriately weight the opinion of another, consistent with our findings. Indeed, the increased egocentricity in an individual's choices that we observe could be interpreted as a form of signalling, whereby the individual is signalling their dominance in the context of a collective decision.

Increased dominance can be detrimental to collaborative decision-making, as shown previously during reasoning tasks where high variance in the verbal contributions of group members (i.e. groups with highly dominant individuals) led to a significantly attenuated performance benefit from collaboration [6]. Other possible effects of testosterone previously related to its role in status-related behaviour [18] may also contribute to less effective information aggregation in our dyads, for example in reducing trustworthiness ratings of faces [17] and decreasing the ability to infer emotional states through photographs of eyes [16]. In addition to potential status-related effects of testosterone, our finding of

increased egocentricity has interesting parallels with testosterone's role in sexual and reproductive behaviours, where testosterone relates to more self-orientated behaviour as evident in reduced parenting and increased courtship in birds [31,32], rodents [36] and rural Senegalese men [37]. Importantly, our task involves no conflict over resources as accurate integration of information is in the best interest of the dyad members, which suggests that the effects of testosterone we observed are not caused by it rendering individuals more selfish.

While the idea that testosterone increases status-related or self-orientated behaviours accords well with the wider literature, future work could usefully examine potential causes of this increased egocentricity in choice that are not addressed in our current study. The observation that testosterone did not affect individual choices militates against explanations for more egocentric choices in terms of general motivational [38] or attentional [20] effects. Because we did not use monetary rewards, this militates against potential explanations in terms of testosterone's known effects on reward processing, which can explain results in more traditional economic paradigms [26]. However, another potential cause of increased egocentricity in individuals' choices is increased confidence in an individual's own original choices, an idea now testable within a framework that assays meta-cognition [39]. A second possibility is that testosterone disrupts collaboration by reducing an individual's ability to signal their confidence, and future work could extend our design such that only one dyad member received testosterone on each day to ask whether one or both dyad members exhibit a bias. A third possibility is that testosterone might render individuals less susceptible to social influence more generally, a potential cause of more egocentric choices that could be explored in variants of classic experiments such as those described by Asch [40].

Social animals reap benefits from collaboration across a wide variety of tasks, ranging from those involving information aggregation (as seen here), reasoning [6] or the division of resources such as food or money [1–3]. Indeed, the potential benefits from information aggregation, for example, are used to support the use of juries (i.e. groups of observers) in the criminal justice system [5]. However, collaborating too freely is not always beneficial, and therefore the biological mechanisms controlling the balance between more collaborative and self-oriented behaviours must dynamically tune behaviour to the social environment. While a previous focus has been on factors promoting collaboration [9–11], here we highlight an opposing biological influence that increases self-orientated or status-related behaviours at the expense of collaboration. Our data show that the humoral agent testosterone modulates the delicate trade-off between collaboration and a more egocentric disposition.

The experiment was approved by the local ethics committee.

C.D.F. is supported by the Danish National Research Foundation, and B.B. by a post-doctoral fellowship from the British Academy, the Danish National Research Foundation, the Danish Research Council for Culture and Communication and the European Union MindBridge project. This work was supported by Wellcome Trust Programme Grant 078865/Z/05/Z to R.J.D. The Wellcome Trust Centre for Neuroimaging is supported by core funding from the Wellcome Trust 091593/Z/10/Z. We thank Sanjay Manohar and Ben Pearson for helpful discussions on data analysis.

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Supplementary materials:

Testosterone disrupts human collaboration by increasing egocentric choices

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Supplementary methods

Participants

34 female participants completed the study (mean age 21.7 years, range 18-30). All participants were part of a dyad and had the same partner throughout. Dyad members did not know each other beforehand. In addition to these 17 dyads, two further dyads were excluded (one participant performed below chance and a second failed to attend both sessions). All were healthy females with normal or corrected to normal visual acuity, and took no medication other than long-standing contraceptives (7 participants took combined oestrogen and progestogen contraception; one took progestogen only contraception). All reported regular menstrual cycles (29.1 ± s.d. 2.2 days, range 29 to 35 days) and were tested between days 1-14 of their cycle. All gave informed consent and the experiment was approved by the local ethics committee.

Experimental procedure

In a randomised, placebo-controlled, double blind, cross-over design 80mg testosterone undecanoate was administered orally (Restandol® testocaps™). The unit of randomisation was the dyad, i.e. both participants received testosterone on one occasion and both participants received placebo on the other occasion. Oral

testosterone undecanoate has long been in widespread clinical use and its pharmacokinetics are well known [1–3]. Therefore, to provide a sufficient washout period each dyad attended the laboratory on two separate days 3 to 7 days apart (mean=5.9 days± s.d.=1.1); all had consumed or were given breakfast to aid drug absorption; and the gap between drug administration and the start of behavioural testing was 6-7 hours.

Given that testosterone has a circadian rhythm (highest in the morning), all participants attended the laboratory at the same times on each of the two testing days: 08:45 and 15:00. On each testing day, at 08:45 the pair of participants had a blood sample taken and then received testosterone or placebo. Participants then left the laboratory and returned at 15:00 to undergo venepuncture and then perform our behavioural task.

Hormonal measurement

Total serum testosterone was measured with a standard, commercially available Roche Modular testosterone assay using electrochemiluminescence immunoassay methods in the University College London Hospitals biochemistry laboratory. Biochemical data was available from 14 of the 17 dyads, with hormonal data from the remaining 3 dyads incomplete due to administrative errors in the biochemistry laboratory.

Behavioural methods

Display parameters and Response Mode

During the behavioural testing [4] dyad members sat in the same testing room and each viewed her own visual display. Display screens were placed on separate tables at right angle to each other. Participants could see each other by turning around. The two displays were connected to the same graphic card via a video amplifier splitter and controlled by the Cogent toolbox (www.vislab.ucl.ac.uk/Cogent/) for MATLAB

(Mathworks Inc). Each participant viewed an LCD display at a distance of approximately 60cm (resolution = 800×600 – Dell Ultra Sharp, 22") for which a look-up table linearized the output luminance. Background luminance was 62.5 Cd/m2 in both displays. The displays were connected to a personal computer through an output splitter that sent identical outputs to both of them. Within each session of the experiment, one participant responded with the keyboard and the other with the mouse. Both participants used their right hand.

Task, Stimuli and Procedure

A 2-Alternative temporal Forced Choice (2AFC) design was employed with two successive observation intervals. A target stimulus always occurred either in the first or the second interval and participants were instructed to choose the interval most likely to have contained the target. In each interval stimuli comprised 6 vertically oriented Gabor patches (standard deviation of the Gaussian envelope: 0.45 degrees; spatial frequency: 1.5 cycles/degree; contrast: 10%) placed equidistant from each other around an imaginary circle (radius: 8 degrees). The target stimulus was generated by increasing the contrast of one of the six patches. The target location and interval were randomized across the experimental session. The stimulus duration in each interval was 85 ms. Target contrast was determined by adding one of 4 possible values 1.5%, 3.5%, 7.0% or 15% to the 10% contrast of the non-target items.

Each trial was initiated by the participant responding with the keyboard after coordinating with their partner (see Fig. 1, main text). A black central fixation cross (width: 0.75 degrees visual angle) appeared on the screen for a variable period, drawn uniformly from the range 500-1000 ms. The two observation intervals were separated by a blank display lasting 1000 ms. The fixation cross turned into a question mark after the second interval to prompt the participants to respond. The question mark stayed on the screen until both participants had responded. Each

participant initially responded without consulting the other. The participant who used the keyboard responded by pressing “N” and “M” for the first and second interval, respectively; the participant who used the mouse responded with a left and right click for first and second interval, respectively. Individual decisions were then displayed on the monitor (Fig. 1, main text), so both participants were informed about their own and their partner’s choice of the target interval. Colour codes were used to denote keyboard (blue) and mouse (yellow) responses. Vertical locations of the blue and yellow text were randomised to avoid spatial biasing. If the partners disagreed, a joint decision was requested, with the request made in blue if the keyboard participant was to announce the decision and in yellow if the mouse participant was to announce the decision. The keyboard participant announced the joint decision in odd trials; the mouse participant on even trials. Participants were free to verbally discuss their choice for as long as they wanted and to choose any strategy they wished.

The participants received feedback either immediately after they made their decision, in cases where they initially agreed, or after the joint decision was announced, in cases where they initially disagreed. The feedback word was either “CORRECT” or “WRONG”, one for each participant (keyboard: blue; mouse: yellow) and one for the dyad (white), and it remained on the screen until the next trial was initiated by the keyboard (Figure 1, main text). Vertical order of the blue and yellow was randomized and the dyad feedback always appeared in the centre.

On Day 1 participants completed one practice block of 16 trials and then on both days completed 192 trials as 12 blocks of 16 trials (the first three dyads completed fewer trials, with a minimum of 128 trials per day). The experiment was self-paced.

Data Analysis

Psychometric functions were constructed for each participant and for each dyad by plotting the proportion of trials in which the target was seen in the second interval against the contrast difference at the target location (the contrast in the second

interval minus the contrast in the first). The psychometric curves were fit to a cumulative Gaussian function, whose parameters were bias, *b*, and variance, σ^2. We used standard psychophysical methods as previously employed in similar experimental designs (e.g. [4–7]). The assumptions of the cumulative normal distribution function have previously been tested empirically in humans [8] and accord with the nature and distribution of noise in visual cortex [9]. To further check the robustness of our findings, we re-analysed our data using a logistic function (which is simpler and does not carry the same assumptions of normality) and compared these results to those obtained with the standard analysis. In our standard psychometric analysis, to estimate the parameters (bias, b, and variance, σ^2) a probit regression model was employed using the *glmfit* function in Matlab (Mathworks Inc). A participant with bias *b* and variance σ^2 would have a psychometric curve, denoted $P(\Delta c)$ where Δc is the contrast difference between the second and first presentations, given by

$$P(\Delta c) = H\left(\frac{\Delta c + b}{\sigma}\right), \qquad \text{(S1)}$$

where $H(z)$ is the cumulative Normal function,

$$H(z) \equiv \int_{-\infty}^{z} \frac{dt}{(2\pi)^{1/2}} \exp\left[-t^2/2\right]. \qquad \text{(S2)}$$

As usual, the psychometric curve, $P(\Delta c)$, corresponds to the probability of saying that the second interval had the higher contrast. Thus, a positive bias indicates an increased probability of reporting that the second interval had higher contrast (and thus corresponds to a negative mean for the underlying Gaussian distribution).

Given the above definitions for $P(\Delta c)$, we see that variance is related to the maximum slope of the psychometric curve, denote *s*, via

$$s = \frac{1}{\left(2\pi\sigma^2\right)^{1/2}}. \qquad \text{(S3)}$$

A large slope indicates small variance and thus highly sensitive performance. We derive functions for each individual and for the dyad, providing a measure of sensitivity for each as S_{indiv} and $S_{collective}$ respectively. The sensitivity of collaborative decision-making hinges on participants appropriately weighting their own and the other's opinions. For each participant we measure this weighting by the ratio of times they agreed with themselves (egocentric decisions) to agreement with the other's opinion (allocentric decisions).

Statistical analysis

Statistical tests were carried out using paired or independent-samples t-tests, or mixed analyses of variance (ANOVA) in SPSS 17.0; reported p-values are two-tailed.

Supplementary results

The use of the cumulative Gaussian function carries empirical and theoretical support ([8] and see supplementary methods). To further check the robustness of our findings, we re-analysed our data using a logistic function (which is simpler and does not carry the same assumptions of normality) and compared these results to those obtained with the standard analysis. Using the standard cumulative normal distribution function we found that individual sensitivity was not affected by testosterone (S_{indiv}; paired two-tailed ttest of testosterone versus placebo $t(33)=0.5$, $P>0.6$) but that testosterone decreased the benefit of collaboration ($S_{collective}$ - S_{indiv}; t-test of testosterone versus placebo $t(33)=3.3$, $P<0.005$). Re-analysis using the logistic function gives virtually identical results: as before, individual sensitivity was not affected by testosterone (S_{indiv}; ttest of testosterone versus placebo $t(33)=0.5$, $P=0.6$) but testosterone decreased the benefit of collaboration ($S_{collective}$ - S_{indiv}; t-test of testosterone versus placebo $t(33)=3.0$, $P=0.005$). We also conducted a model comparison between the cumulative Gaussian and the logistic functions using a Chi-

Square cumulative test, which revealed that for all individual subjects and all dyads there was no significant difference in the fits between the models.

Given a recent study suggesting participants' beliefs about which drug had been administered might affect choice [10], we tested for this possibility. On each day, after completing the behavioural testing participants completed a questionnaire asking if they believed they had received testosterone or placebo. 2 of 34 subjects did not respond. *Accuracy of belief:* When receiving testosterone 9 of 32 subjects believed they received testosterone, and when receiving placebo 11 of 32 subjects believed they received testosterone. *Effect of belief on Egocentric-Allocentric (E-A) ratio:* There was no difference in E-A ratio when subjects believed they had received placebo (mean=1.58 ± s.d. 1.18, n=44) and when they believed they had received testosterone (1.21 ± s.d. 0.62, n=20; independent samples ttest t(62)=1.3, P>0.1).

We also assessed the effect of treatment order. The effect of testosterone on the benefit of collaboration (i.e. $S_{collective}$-S_{indiv}) was not altered by treatment order, as shown in a 2 order (placebo first, testosterone first) by 2 drug (placebo, testosterone) mixed ANOVA in which there was a main effect of drug ($F(1,32)=9.0$, $P=0.005$) but no interaction ($F(1,32)=0.2$, $P=0.7$). This was also the case for the effect of testosterone on E-A ratio, as shown in 2 order (placebo first, testosterone first) by 2 drug (placebo, testosterone) mixed ANOVA in which there was a main effect of drug ($F(1,32)=5.5$, $P<0.03$) but no interaction ($F(1,32)=1.2$, $P=0.3$).

Biochemical data is available from 14 of the 17 dyads, with hormonal data from the remaining 3 dyads incomplete due to administrative errors in the University College London Hospitals biochemistry laboratory in which they were processed. There were no significant correlations between total serum testosterone levels (individual or mean dyadic, at baseline or time of testing) and either sensitivity (S_{indiv} or $S_{collective}$) or Egocentric-Allocentric ratio.

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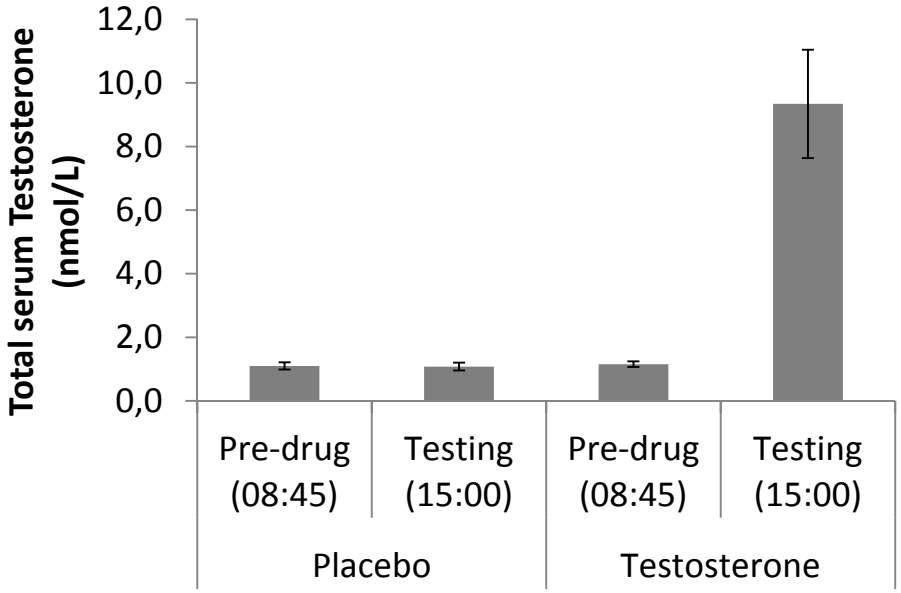
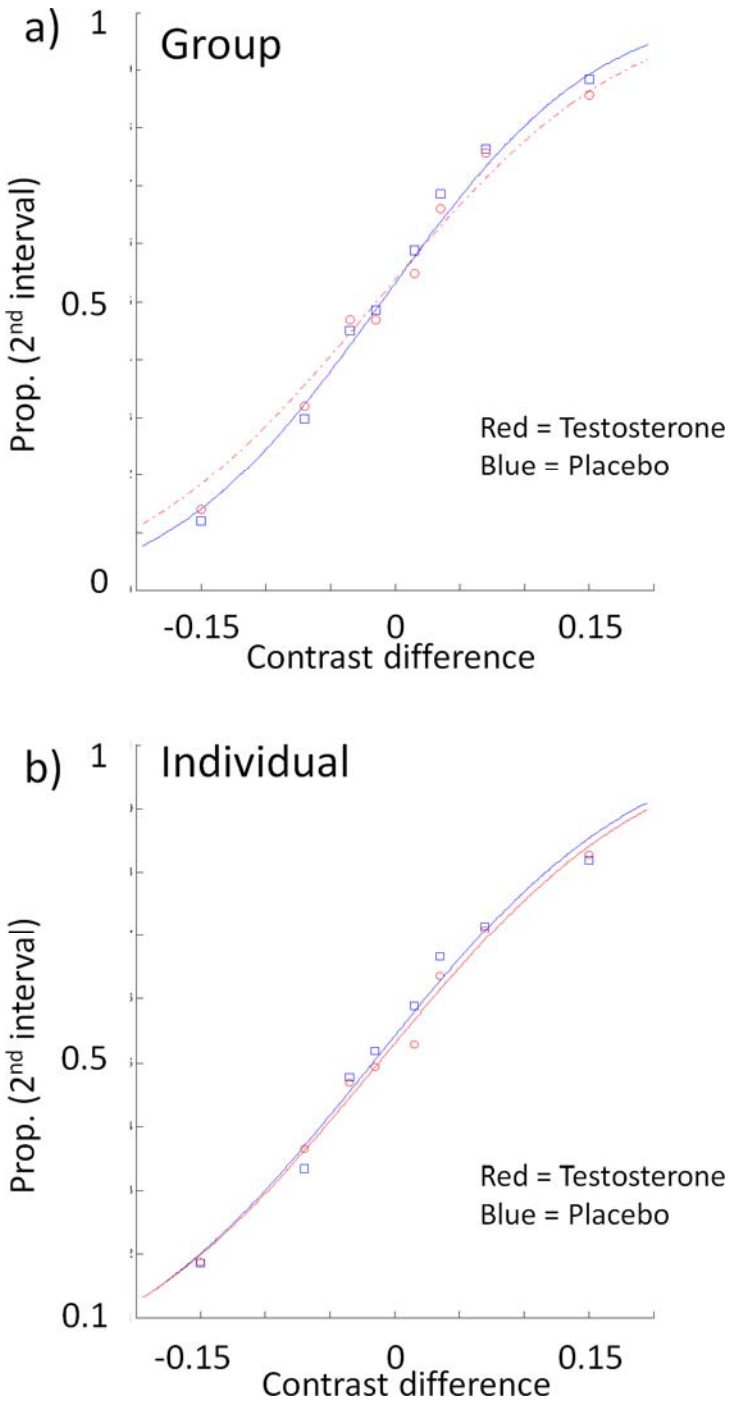
Supplementary Figures



Supplementary Figure 1 Effect of treatment on total testosterone levels This data is taken from the data shown in Supplementary Table 2, and includes data from all subjects who had testosterone measured in the morning and afternoon on testosterone. Biochemical data was available from 14 of the 17 dyads, with hormonal data from the remaining 3 dyads incomplete due to administrative errors in the biochemistry laboratory. Total testosterone was measured with a standard, commercially available Roche Modular testosterone assay using electrochemiluminescence immunoassay methods in the University College London Hospitals biochemistry laboratory. Error bars indicate s.e.m..



Supplementary Figure 2 Psychometric functions and raw data. **Panel a** shows the raw and estimated data for the dyads' decisions (and also comparing testosterone and placebo), plotting the proportion of trials in which the target was reported in the second interval against the contrast difference at the target location (the contrast in the second interval minus the contrast in the first). **Panel b** shows the data for individual decisions (again also comparing both testosterone and placebo). Across dyads the psychometric curve for the dyad is steeper under placebo than testosterone (and the raw data points are consistent with

this). This is not the case for the individual psychometric data. Note that reduced sensitivity for the raw accuracy measure relative to the psychometric analyses is to be expected, as the psychophysical analyses take advantage of the known shape of the psychophysical data (i.e. with a high contrast (easy) target in the first interval the probability of choosing second interval is low; with a low contrast (difficult) target the probability of choosing the second interval is intermediate; and with a high contrast target in the second interval the probability of choosing the second interval is high).

Supplementary Tables

		Placebo			Testosterone		
Dyad number	**Subject number**	**Pre-drug (08:45)**	**Testing (15:00)**	**Time2 - Time1**	**Pre-drug (08:45)**	**Testing (15:00)**	**Time2 - Time1**
2	4				1.4	2.1	0.7
	5				1.4	5.6	4.2
4	8				0.6	2.2	1.6
	9				1.8	2.7	0.9
5	10	1.1	1.1	0	0.9	4.4	3.5
	11	1	1	0	1	2	1
7	14	1.1	0.8	-0.3	1.1	4.7	3.6
	15	0.5	0.4	-0.1	0.7	6.4	5.7
8	16				1.9	5.4	3.5
	17				1	10.9	9.9
9	18	0.8	0.7	-0.1	1.1	11.9	10.8
	19	1.9	1.8	-0.1	1.5	4.3	2.8
11	22				1.4	3.9	2.5
	23				0.6	16.3	15.7
12	24	1	1.4	0.4	1.1	3.4	2.3
	25	1.6	1.7	0.1	2.2	2.5	0.3
13	26	0.5	0.7	0.2	0.6	1	0.4
	27	0.7	0.6	-0.1	0.8	8.5	7.7
14	28	0.9	0.7	-0.2	1.3	5.9	4.6
	29	1.1	0.9	-0.2	1.2	14.2	13
16	32	1	1	0	0.9	32.3	31.4
	33	2.2	2.1	-0.1	1.9	4.5	2.6
17	34	1.8	2.4	0.6	1.6	6.6	5
	35	1.3	1.4	0.1	1.5	12.9	11.4
18	36	1.3	1	-0.3	1	11.4	10.4
	37	1.4	1	-0.4	1	21.6	20.6
19	38	0.4	0.5	0.1	0.4	38.3	37.9
	39	0.4	0.4	0	0.4	15.6	15.2
	Mean	**1.1**	**1.1**	**0.0**	**1.2**	**9.3**	**8.2**
	St. Dev.	**0.5**	**0.6**	**0.2**	**0.5**	**9.0**	**9.2**

Supplementary Table 1 Effect of treatment on total testosterone levels Data is from all subjects who had testosterone measured in the morning and afternoon on testosterone. Biochemical data was available from 14 of the 17 dyads, with hormonal data from the remaining 3 dyads incomplete due to administrative errors in the biochemistry laboratory. Total testosterone was measured with a standard,

commercially available Roche Modular testosterone assay using electrochemiluminescence immunoassay methods in the University College London Hospitals biochemistry laboratory.

Testosterone administration

Dyad number	Subject number	Placebo			Testosterone		
		Pre-drug (08:45)	Testing (15:00)	Time2 - Time1	Pre-drug (08:45)	Testing (15:00)	Time2 - Time1
2	4				1,4	2,1	0,7
	5				1,4	5,6	4,2
4	8				0,6	2,2	1,6
	9				1,8	2,7	0,9
5	10	1,1	1,1	0	0,9	4,4	3,5
	11	1	1	0	1	2	1
7	14	1,1	0,8	-0,3	1,1	4,7	3,6
	15	0,5	0,4	-0,1	0,7	6,4	5,7
8	16				1,9	5,4	3,5
	17				1	10,9	9,9
9	18	0,8	0,7	-0,1	1,1	11,9	10,8
	19	1,9	1,8	-0,1	1,5	4,3	2,8
11	22				1,4	3,9	2,5
	23				0,6	16,3	15,7
12	24	1	1,4	0,4	1,1	3,4	2,3
	25	1,6	1,7	0,1	2,2	2,5	0,3
13	26	0,5	0,7	0,2	0,6	1	0,4
	27	0,7	0,6	-0,1	0,8	8,5	7,7
14	28	0,9	0,7	-0,2	1,3	5,9	4,6
	29	1,1	0,9	-0,2	1,2	14,2	13
16	32	1	1	0	0,9	32,3	31,4
	33	2,2	2,1	-0,1	1,9	4,5	2,6
17	34	1,8	2,4	0,6	1,6	6,6	5
	35	1,3	1,4	0,1	1,5	12,9	11,4
18	36	1,3	1	-0,3	1	11,4	10,4
	37	1,4	1	-0,4	1	21,6	20,6
19	38	0,4	0,5	0,1	0,4	38,3	37,9
	39	0,4	0,4	0	0,4	15,6	15,2
	Mean	**1,1**	**1,1**	**0,0**	**1,2**	**9,3**	**8,2**
	St. Dev.	**0,5**	**0,6**	**0,2**	**0,5**	**9,0**	**9,2**

Sensitivity (measured by the slope of the psychometric function)

Dyad number	Placebo			Testosterone		
	S_{min}	S_{max}	S_{collab}	S_{min}	S_{max}	S_{collab}
1	4,4186	4,549	7,0945	4,5732	8,7481	7,5493
2	3,8195	5,93	7,21	3,5003	4,0453	4,8619
3	0,1697	3,0623	2,2008	0,7323	2,4467	1,8089
4	0,6775	4,3637	2,6136	0,6561	3,2532	2,2913
5	3,1712	3,4694	4,273	3,066	3,3316	3,8229
6	1,7834	2,7381	2,9227	1,6924	3,0266	3,3084
7	4,3892	5,3465	6,8533	2,5884	4,7335	4,4519
8	2,3783	2,7979	3,2024	2,7422	3,2967	3,0181
9	3,5837	6,9635	8,1741	1,6048	3,7356	3,2973
11	1,7609	1,8125	2,22	3,7253	3,8848	4,7965
12	4,1364	6,9059	6,5944	2,5725	6,2374	5,6018
13	2,3647	3,8776	4,3255	1,4333	1,6603	1,7292
14	3,3566	3,4644	6,0013	4,8352	5,9056	6,2225
16	1,4302	2,1046	2,1074	1,0317	2,4964	1,9827
17	1,7048	3,76	3,1863	2,2522	2,9511	2,7158
18	1,2778	1,7697	1,8783	0,6218	1,4722	1,4089
19	0,6297	1,6319	1,092	1,1615	1,5542	1,0616

	Placebo		Testosterone	
	S_{collab}-S_{min}	S_{collab}-S_{max}	S_{collab}-S_{min}	S_{collab}-S_{max}
	2,6759	2,5455	2,9761	-1,1988
	3,3905	1,28	1,3616	0,8166
	2,0311	-0,8615	1,0766	-0,6378
	1,9361	-1,7501	1,6352	-0,9619
	1,1018	0,8036	0,7569	0,4913
	1,1393	0,1846	1,616	0,2818
	2,4641	1,5068	1,8635	-0,2816
	0,8241	0,4045	0,2759	-0,2786
	4,5904	1,2106	1,6925	-0,4383
	0,4591	0,4075	1,0712	0,9117
	2,458	-0,3115	3,0293	-0,6356
	1,9608	0,4479	0,2959	0,0689
	2,6447	2,5369	1,3873	0,3169
	0,6772	0,0028	0,951	-0,5137
	1,4815	-0,5737	0,4636	-0,2353
	0,6005	0,1086	0,7871	-0,0633
	0,4623	-0,5399	-0,0999	-0,4926
mean	1,817494	0,435447	1,243518	-0,167665

Egocentric-Allocentric Ratio

Dyad number	Placebo		Testosterone	
	Sub1	Sub2	Sub1	Sub2
1	1,33333	0,92857	0,3	0,63636
2	1,57143	0,75	3	1
3	1	1	1,41667	0,57143
4	1,22222	1,5	1,36842	5
5	0,36667	4,66667	0,66667	5,71429
6	1,3	0,57692	0,95	0,48485
7	1,0625	1	0,79167	1,3125
8	0,81481	1,15	1,26316	1,52941
9	1,10526	1,69231	1,13636	1,23077
11	2	0,55172	1,6	1,92857
12	0,4	0,84615	1,29412	1,64706
13	0,90476	0,85	1,91667	1,42105
14	1,29412	1	2,875	1,5
16	0,91304	1,58333	0,59375	2,55556
17	0,95	1,8	1,53333	1,4375
18	1,66667	0,5	0,75	0,91667
19	0,93333	3,42857	1,38462	3