

OPEN

# Between-subject variability in the influence of mental imagery on conscious perception

N. Dijkstra<sup>1\*</sup>, M. Hinne<sup>2</sup>, S. E. Bosch<sup>1</sup> & M. A. J. van Gerven<sup>1</sup>

Mental imagery and visual perception rely on similar neural mechanisms, but the function of this overlap remains unclear. One idea is that imagery can influence perception. Previous research has shown that imagining a stimulus prior to binocular presentation of rivaling stimuli increases the chance of perceiving the imagined stimulus. In this study we investigated how this effect interacts with bottom-up sensory input by comparing psychometric response curves for congruent and incongruent imagery in humans. A Bayesian hierarchical model was used, allowing us to simultaneously study group-level effects as well as effects for individual participants. We found strong effects of both imagery as well as its interaction with sensory evidence within individual participants. However, the direction of these effects were highly variable between individuals, leading to weak effects at the group level. This highlights the heterogeneity of conscious perception and emphasizes the need for individualized investigation of such complex cognitive processes.

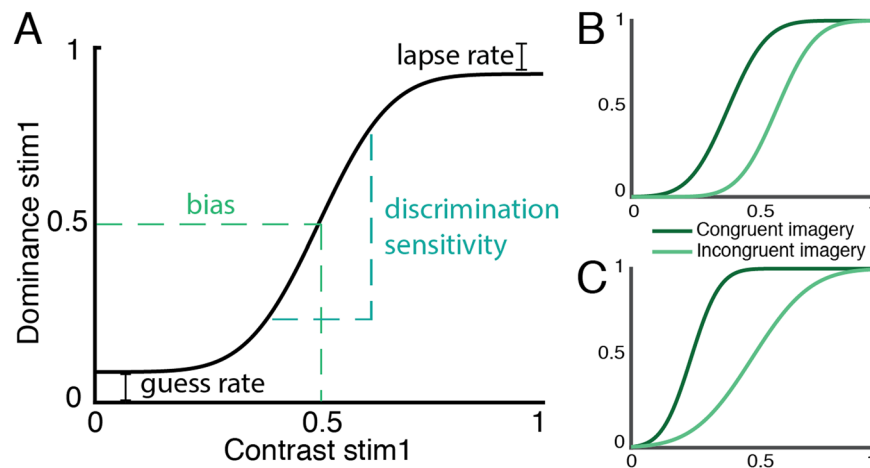
In daily life, we are bombarded with visual stimuli. When walking down the street, we see different colours, shapes and textures. At the same time, we are often caught up in thinking about future or past events, which is accompanied by mental imagery<sup>1</sup>. Mental imagery and visual perception rely on similar neural mechanisms<sup>2</sup>. Throughout the visual system, imagining objects and perceiving them elicits similar activation patterns<sup>3–5</sup> and similar top-down connectivity<sup>6</sup>. Given that we often engage in mental imagery while receiving visual input, the question arises to what extent imagery influences perception.

Few studies have directly explored the interaction between imagery and perception. One line of work has focused on the behavioural effects of imagery on conscious perception during binocular rivalry. Binocular rivalry is a phenomenon in which a different image is presented to each eye of an observer. In general, the observer will only perceive one of the images consciously, while the other image is suppressed<sup>7</sup>. Previous research showed that imagining one of two stimuli prior to binocular rivalry leads to a priming effect: it biases perception towards the imagined stimulus<sup>8</sup>. In contrast, *perceiving* one of the two stimuli prior to binocular rivalry leads to adaptation: decreasing the chance of subsequently perceiving that stimulus<sup>9</sup>. The priming effect of imagery has been dissociated from effects of attention<sup>8</sup> and is specific to the orientation and location of the stimulus<sup>10</sup>. This means that imagery can influence conscious perception.

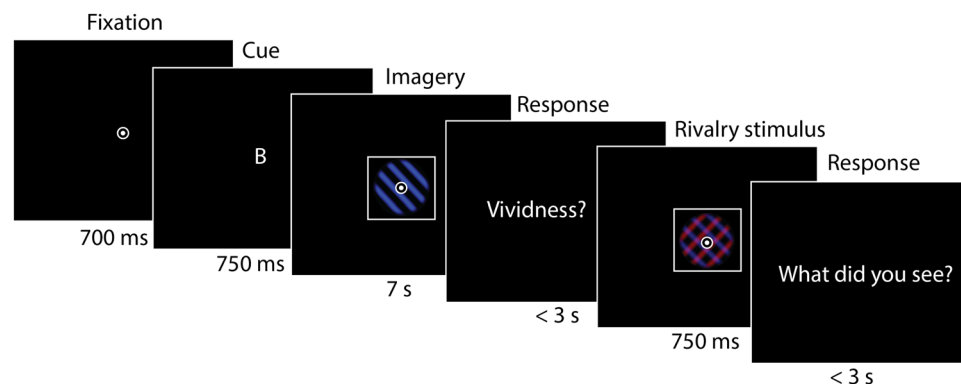
However, the exact nature of this influence remains unclear. According to predictive coding theories of perception, top-down signals should interact with bottom-up sensory evidence<sup>11–13</sup>. In the case of binocular rivalry, sensory evidence can be defined as the relative contrast of the two stimuli: increasing the contrast of one stimulus while keeping the other constant increases the proportion of trials where that stimulus is consciously perceived<sup>7,14,15</sup>. This can be illustrated clearly with a psychometric curve (see Fig. 1A). In this study, we investigated how top-down imagery and bottom-up sensory input interact by characterizing the effect of imagery on the parameters of this psychometric curve.

One possibility is that there is no interaction, but that imagery and sensory evidence influence perception independently. This would lead to a constant shift in the psychometric curve, such that for all dominance levels, a lower contrast is needed to achieve that dominance level when imagining the congruent stimulus compared to the incongruent stimulus (Fig. 1B). This would be reflected in a lower *bias* or offset for congruent versus incongruent imagery<sup>16</sup>. Alternatively, top-down imagery may interact in a systematic way with bottom-up sensory input. This would mean that the difference between congruent and incongruent imagery varies at different dominance levels. In terms of the psychometric curve, this would result in an effect of imagery on the steepness of the curve, which

<sup>1</sup>Donders Institute for Brain, Cognition and Behaviour, Radboud University, Nijmegen, The Netherlands. <sup>2</sup>University of Amsterdam, Amsterdam, The Netherlands. \*email: [n.dijkstra@donders.ru.nl](mailto:n.dijkstra@donders.ru.nl)



**Figure 1.** Illustration of psychometric curves. The contrast of the manipulated stimulus is plotted on the x-axis. The contrast of the other stimulus is fixed at 0.4. The y-axis indicates the proportion of trials on which the manipulated stimulus is reported dominant. **(A)** Standard psychometric curve based on the algorithm by Wichmann & Hill (2001). Four parameters determine the shape of the curve. The *bias* is the required contrast value to reach a dominance of 0.5. The *discrimination sensitivity* or slope is the difference in contrast value between 0.25 and 0.75 dominance. The *guess rate* is the dominance associated with a contrast of 0 and the *lapse rate* is 1 - the dominance associated with a contrast of 1. **(B)** Main effect of imagery is reflected in a shift in the bias during congruent versus incongruent imagery. **(C)** Interaction with sensory evidence is reflected in a change in discrimination sensitivity during congruent versus incongruent imagery.



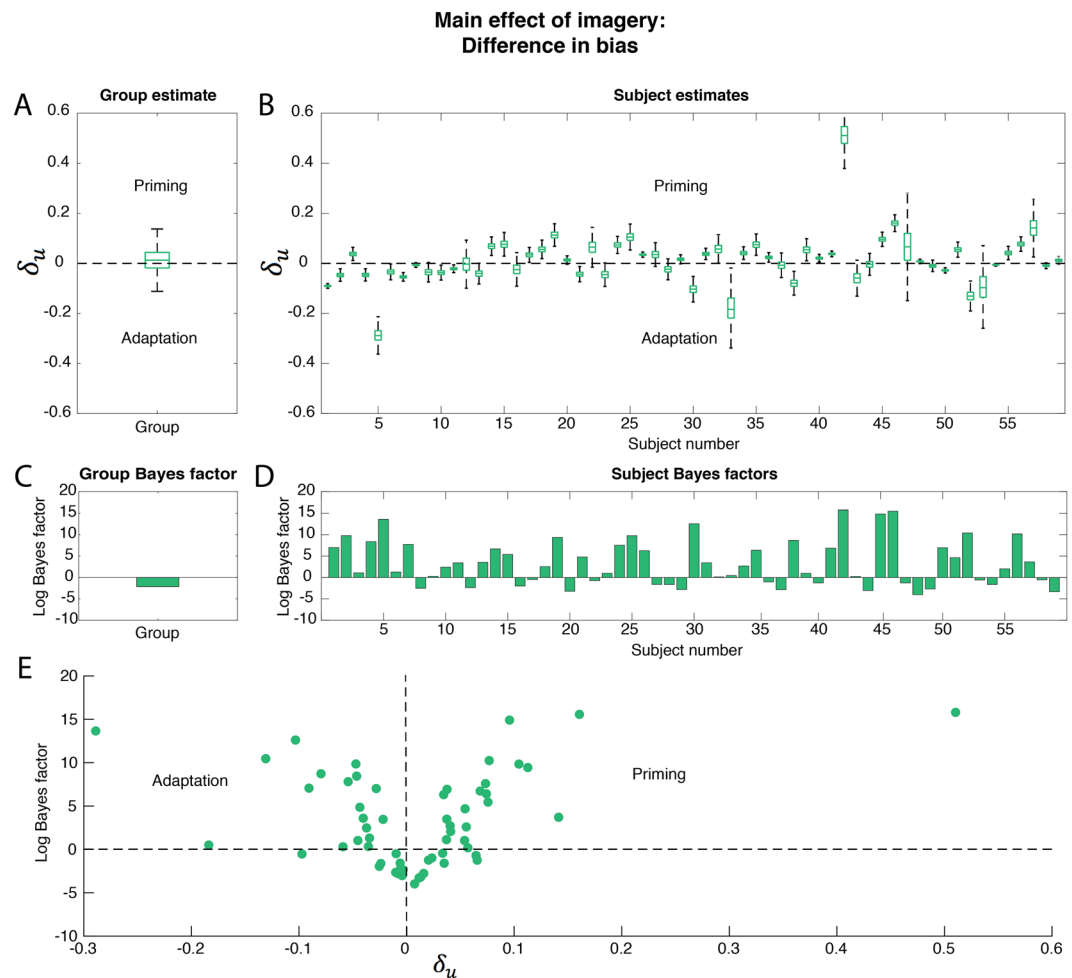
**Figure 2.** Experimental design. After fixation, a cue was presented for 750 ms indicating whether participants had to imagine the blue grating ('B') or the red grating ('R'). The cued grating was then imagined as vividly as possible for 7 s, after which participants indicated their experienced imagery vividness on a continuous scale using a sliding bar. Next, the rivalry stimulus was presented for 750 ms. Participants indicated whether they saw the blue grating, the red grating or a perfect mixture of the two.

is a measure of the *discrimination sensitivity* (Fig. 1C). Imagining a stimulus then makes people more or less sensitive to changes in congruent bottom-up sensory input.

We used an adapted version of a previously developed binocular rivalry imagery task<sup>8</sup>. The sensory evidence of the binocular rivalry display was manipulated by changing the relative contrast of the stimuli. A hierarchical Bayesian model was used to fit psychometric curves per participant on the dominance levels during congruent and incongruent imagery. We then compared the derived parameters between the conditions. This approach allowed us to characterize the presence as well as the absence of effects on the group level and on the individual participant level.

## Results

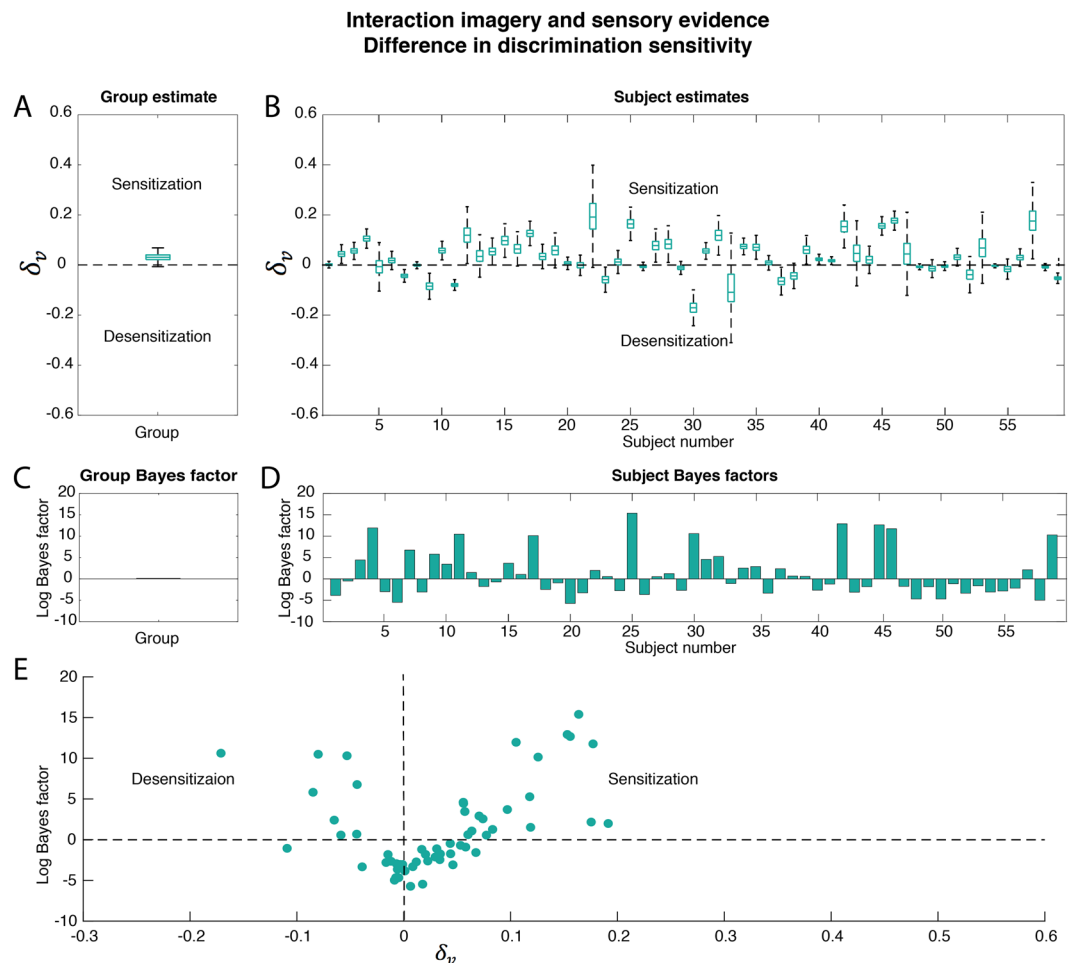
During each trial, a cue indicated which stimulus the participant had to imagine ('B' for blue grating, 'R' for red grating; Fig. 2). They then imagined the cued stimulus for 7 seconds and rated their experienced vividness. Then, they were briefly presented (750 ms) with a rivalry stimulus and indicated which stimulus was dominant; the red grating, blue grating or a mixture. By varying the contrast of one stimulus while keeping the other one fixed, we were able to estimate full psychometric response curve for the manipulated contrast. Congruent imagery in this context refers to imagery of the manipulated stimulus (for which the psychometric curve is estimated) and



**Figure 3.** Main effect of imagery: difference in bias. The difference in bias  $\delta_u$  between incongruent and congruent imagery was tested. A positive difference reflects a higher bias for incongruent imagery which indicates a priming effect while a negative difference indicates an adaptation effect. Boxplots reflect the distribution of the posterior samples. Outliers are not shown. The bottom of the box represents the first quartile, the middle line represents the median and the top, the third quartile. The distance between the bottom and the top of the box reflects the variance of the samples and is a measure of the uncertainty of the estimate. **(A)** Posterior group estimate of the difference. **(B)** Posterior subject estimates of the difference; each boxplot represents one participant. The logs of the BFs for the comparison between  $H_+$  (difference) and  $H_0$  (no difference) are shown. A positive log(BF) indicates evidence in favour of  $H_+$  and a negative log(BF) indicates evidence in favour of  $H_0$ . **(C)** Group log(BF) and **(D)** subject log(BF); each bar represents one subject. The order of the participants is the same in **(B,D)**. **(E)** Relation between Bayes factor and direction of the effect. On the x-axis, the median of the posterior samples for the difference between the two conditions is plotted. On the y-axis, the log(BF) of the effect is plotted. Negative log(BFs) indicate evidence in favour of  $H_0$  and positive log(BFs) indicate evidence in favour of  $H_+$ . Dots represent individual participants.

incongruent imagery refers to imagery of the fixed stimulus. The order of the cues and contrast values was randomized within participants, but for both conditions, the same contrast values were presented over the course of the experiment. This allowed us to estimate the psychometric curves separately for each participant for congruent and incongruent imagery. The parameters of these curves were estimated using a Bayesian hierarchical model.

**Replication imagery priming group-effect.** First, we aimed to replicate the main imagery priming effect reported in earlier studies. In these studies, the imagery effect was determined by first removing all mixed trials and then assessing whether participants perceived the imagined stimulus more often than chance<sup>8,17-19</sup>. A two-sided one-sample t-test revealed that the proportion of trials in which participants perceived the imagined stimulus was indeed significantly larger than 0.5 ( $M = 0.53$ ,  $SD = 0.05$ ,  $t(58) = 3.78$ ,  $p = 0.0004$ ,  $d = 0.6$ ). Note that for the analyses reported below, we did not remove the mixed trials, but instead used them as providing information about the relationship between sensory evidence and dominance (see *Materials and Methods: Deriving dominance per contrast*).



**Figure 4.** Interaction between imagery and sensory evidence: difference in discrimination sensitivity. The difference in discrimination sensitivity  $\delta_v$  between incongruent and congruent imagery was tested. A positive difference reflects an increase in sensitivity for congruent imagery whereas a negative difference indicates a decrease in sensitivity. Boxplots reflect the distribution of the posterior samples as in Fig. 3. **(A)** Posterior group estimate of the difference. **(B)** Posterior subject estimates of the difference, each boxplot represents one participant. The logs of the BFs for the comparison between  $H_{+\_difference}/H_{0\_no\_difference}$  are shown. **(C)** Group log(BF) and **(D)** subject log(BFs), each bar represents one subject. The order of the participants is the same in **(B,D)** and the same as in Fig. 3. **(E)** Relation between Bayes factor and direction of the effect. On the x-axis, the median of the posterior samples for the difference between the two conditions is plotted. On the y-axis, the log(BF) of the effect is plotted. Negative log(BFs) indicate evidence in favour of  $H_0$  and positive log(BFs) indicate evidence in favour of  $H_+$ . Dots represent individual participants.

**Response bias.** To assess whether there was a response bias, we looked at the responses to mock rivalry trials. During these trials, a mock rivalry stimulus was presented containing parts of both stimuli, which should elicit the response of a mixed percept. The response bias was assessed by determining whether participants were more likely to indicate that they had perceived the imagined stimulus during mock trials. Even though there was an indication of mock priming in some participants ( $M = 0.51$ ,  $SD = 0.04$ ,  $t(58) = 1.88$ ,  $p = 0.06$ ), there was no correlation between mock priming and binocular priming ( $r = 0.03$ ,  $p = 0.81$ ;  $BF = 0.17$ ). This means that people who had a strong response bias did not show a strong imagery effect on the binocular rivalry trials. Therefore, the imagery effects could not be explained by response bias.

**Main effect of imagery.** For the main analyses, we used a hierarchical Bayesian model to fit psychometric curves on the dominance responses during congruent and incongruent imagery. The main effect of imagery is reflected in the difference in *bias* (Fig. 1) between the two conditions. A positive difference indicates that the bias during congruent imagery was smaller than during incongruent imagery, so that less contrast was needed to reach the same dominance level. Thus, a positive difference indicates a *priming* effect of imagery. A negative difference shows that during congruent imagery more contrast was needed compared to incongruent imagery to achieve the same contrast levels, indicating an *adaptation* effect of imagery. The posterior estimates of the differences, together with their corresponding log Bayes factors are shown in Fig. 3.

BF	log(BF)	Strength of evidence
>100	4.6	Extreme evidence for $H_+$
30–100	3.4–4.6	Very strong evidence for $H_+$
10–30	2.3–3.4	Strong evidence for $H_+$
3–10	1.1–2.3	Moderate evidence for $H_+$
1–3	0–1.1	Anecdotal evidence for $H_+$
1	0	No evidence for $H_0$ or $H_+$
1/3–1	–1.1–0	Anecdotal evidence for $H_0$
1/3–1/10	–2.3––1.1	Moderate evidence for $H_0$
1/10–1/30	–3.4––2.3	Strong evidence for $H_0$
1/30–1/100	–4.6––3.4	Very strong evidence for $H_0$
<1/100	<–4.6	Extreme evidence for $H_0$

**Table 1.** Interpretation of Bayes factors (BF). Interpretation of Bayes factors according to Jeffreys (1961) and Lee and Wagenmakers (2014). First column shows the BF which shows how much more likely the alternative hypothesis ( $H_+$ ) is compared to the null hypothesis ( $H_0$ ). The second column shows the log of the BF, which is used for visualization in Figs 3 and 4. The third column shows the interpretation of the BFs.

The group log(BF) is  $-2.14$  (Fig. 3C), which is interpreted as moderate evidence for the absence of an effect (see *Materials and Methods*; Table 1). Note that this is in contrast to the results of the t-test reported above which showed a significant group priming effect. However, individual subject level Bayes factors were very high with a median log(BF) of 2.44 (Fig. 3D) which corresponds to a Bayes factor of 12, meaning that the probability of an effect was 12 times more likely than the probability of no-effect; i.e. strong evidence for the alternative hypothesis (Table 1). The reason for the discrepancy between the group-level effect and the participant-level effects is the inconsistency of the effect across participants. That is, the direction of the effect varied strongly between participants (Fig. 3B), leading to a null effect on the group level (Fig. 3A). A large proportion of participants showed a strong priming effect associated with a high Bayes factor (Fig. 3E; upper right quadrant). However, almost as many participants showed a reliable adaptation effect (Fig. 3E; upper left quadrant). Furthermore, there was also a proportion of participants who reliably did not show an effect, i.e. for which there was evidence in favour of  $H_0$  (Fig. 3E; log(BFs) below 0). See Fig. 5 for examples of psychometric curve fits for a few different participants.

**Interaction with sensory evidence.** The interaction between imagery and sensory evidence is reflected in a difference in slope or *discrimination sensitivity* (see Fig. 1) between congruent and incongruent imagery. The discrimination sensitivity reflects how much increase in contrast is needed to achieve an increase in dominance. A low slope means that small changes in contrast are enough to influence perception whereas a high slope means that larger changes are necessary. Thus, a positive difference in discrimination sensitivity means that the slope is higher for incongruent imagery, indicating that congruent imagery *increases* sensitivity to bottom-up sensory input. In contrast, a negative difference indicates that imagery *decreases* sensitivity. The results are shown in Fig. 4.

The group BF is 0.02, which reflects no clear evidence for either  $H_+$  or  $H_0$  (Fig. 4A,C). The individual participant's BFs for the difference in *discrimination sensitivity* (Fig. 4D) are less high than those for the difference in *bias* (Fig. 3D). Most participants do not show a clear interaction with sensory evidence (Fig. 4E; log(BFs) below 0). However, there are still a number of participants who do show a reliable increase in discrimination sensitivity for congruent imagery (Fig. 4E; upper right quadrant, e.g. Fig. 5A), and participants who show a reliable decrease (Fig. 4E; upper left quadrant).

To test the robustness of our results, we checked whether the Bayesian model gave similar results if we used a wider or narrower prior (see Supplementary Materials). Changing the prior did not significantly change the results, indicating that the findings were not influenced strongly by the choice of prior parameters.

**Relation between vividness and imagery effects.** We also investigated the relation between subjective vividness ratings and imagery's influence on conscious perception. We first aimed to replicate the findings from earlier studies. To this end, we binned the trials into four levels based on the vividness ratings and for each bin we calculated the priming effect, operationalized as the proportion of non-mixed trials that the imagined stimulus was perceived, as in<sup>18</sup>. In line with earlier findings<sup>20</sup>, there was a main effect of vividness on imagery priming ( $F(2.45, 134.72) = 3.77, p = 0.018$ , Huyn-Feldt-corrected for violation of sphericity). This effect was linear ( $F(1, 55) = 6.29, p = 0.015$ ), indicating that the effect of imagery on binocular rivalry was stronger for more vivid imagery. In contrast to earlier findings, we did not find a correlation between VVIQ and imagery priming ( $r = 0.09, p = 0.47, BF = 0.17$ ), showing that off-line VVIQ scores did not predict participant's imagery priming.

Finally, we tested whether the difference in psychometric curve parameters derived by using all data (including mixed trials) showed a relationship with imagery vividness. Since it was impossible to obtain binned psychometric curve values, we only focused on group-level correlations with VVIQ and averaged vividness ratings. There was no correlation between the difference in bias and VVIQ ( $r = -0.03, p = 0.80, BF = 0.17$ ) or averaged vividness rating ( $r = -0.06, p = 0.66, BF = 0.18$ ). There was also no correlation between the difference in discrimination sensitivity and VVIQ ( $r = -0.02, p = 0.87, BF = 0.17$ ) or averaged vividness rating ( $r = -0.04, p = 0.76, BF = 0.17$ ). This indicates that the individual differences in the interaction between imagery and perception reported above are not easily linked to self-report measurements of imagery vividness.

## Discussion

In this study, we set out to characterize how imagery influences conscious perception. We tested whether the influence of imagery was influenced by bottom-up sensory input by estimating psychometric response curves during congruent and incongruent imagery. We first replicated the priming group-effect of imagery on binocular rivalry. Using standard analyses, the results indicated that participants are more likely to perceive a stimulus that they had just imagined. However, using a hierarchical Bayesian model to estimate full psychometric response curves per participant revealed a variety of effects. First, whereas a large proportion of participants did indeed show an imagery priming effect, almost as large a group showed an imagery adaptation effect and another large proportion reliably showed no effect. Furthermore, while most participants did not show a clear interaction between imagery and sensory evidence, some participants still showed a reliable increase in sensitivity for congruent imagery and some participants even showed a clear decrease in sensitivity. These results indicate that the influence of imagery on conscious perception is more complicated than previously reported and that there are large variations in the nature of this process.

The existence of both priming and adaptation effects of imagery is in line with the fact that both of these effects are found for prior perception<sup>8,9</sup>. Presenting a stimulus prior to a binocular rivalry display can bias dominance towards or away from the presented stimulus depending on the contrast. Brief, low-contrast stimuli tend to result in a priming effect whereas long, high-contrast stimuli result in an adaptation effect. The idea is that prior perception pre-activates low-level neural populations involved in later stimulus processing during binocular rivalry. This prior activation builds up depending on the duration and contrast of the stimulus, leading to a stronger priming effect until it reaches some threshold after which it leads to adaptation<sup>9</sup>. Given the large neural overlap between imagery and perception, it is not surprising that imagery can also elicit both priming and adaptation effects. If the same mechanism is at work, we would expect that imagery adaptation is caused by stronger and/or longer low-level activation than imagery priming. We did not find a relationship between self-report measurements of imagery vividness and the direction of this effect. This might be due to the fact that vividness does not fully capture the strength and the duration of imagery. Future research should investigate whether there is a direct link between neural activation and imagery's influence on conscious perception.

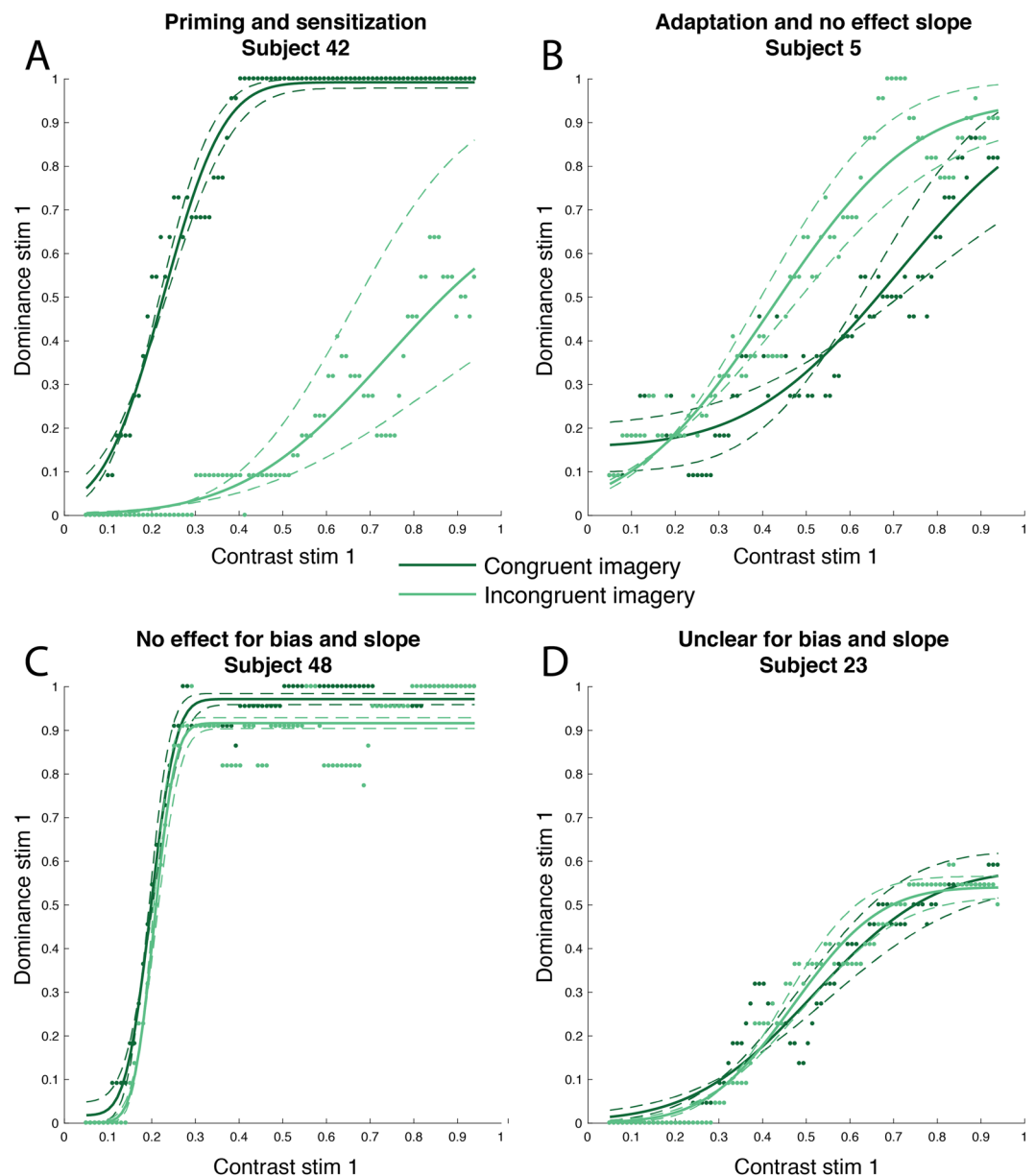
Furthermore, most participants did not show an effect of imagery on discrimination sensitivity. However, for some participants there was a clear effect, indicating that the strength of the influence of imagery can depend on the bottom-up sensory evidence. This means that the influence of imagery on perception might not always be linear. An increase in discrimination sensitivity indicates that imagery enhances differences in sensory input and can thereby facilitate detecting sensory input congruent to our internal goals. In contrast, a decrease in discrimination sensitivity means that the visual system becomes less sensitive to sensory input congruent to imagery. Participants showing desensitization usually showed a main adaptation effect, suggesting that desensitization might also be caused by some form of neural fatigue caused by strong activations.

Because we only roughly estimated eye-dominance using the Miles test, it is still possible that differences in eye-dominance between participants have influenced our results<sup>21</sup>. Eye-dominance would be reflected in a shift in the offset of the psychometric curve: to the left if the dominant eye corresponded to the manipulated stimulus and to the right for an eye-dominance of the other stimulus. This shift would be the same for the congruent and incongruent condition. However, for extreme cases this shift might make it hard to fully characterize the difference between the two conditions (e.g. Fig. 5C,D). This has likely caused us to underestimate the effect in some participants. Note that eye-dominance could not have increased or changed the direction of the effect. Therefore, our results provide a lower bound on the imagery effects (for more details, see Supplementary Materials). Differences in eye-dominance might contribute to why we did not find a relationship with vividness and why our general priming effect was lower than in other studies. In order to circumvent this issue, future research could use different techniques to assess eye dominance<sup>22</sup> and determine the stimulus strength needed to estimate the full psychometric curve in a separate session. Furthermore, the use of anaglyph glasses to elicit binocular rivalry is known to cause more bleed-through of the stimuli compared to other methods such as using a mirror stereoscope. This might have made our data noisier, increasing the uncertainty of the estimates and therefore decreasing the Bayes factors.

An important question is whether the differences between participants reported here are stable over time. Previous studies have linked between-subject differences in the effect of imagery on binocular rivalry to other cognitive processes such as working memory and metacognition<sup>20,23</sup>, indicating that they reflect meaningful differences in cognition. However, whether these individual differences are stable over time and not influenced by the specific experimental context is an independent question. For example, it is possible that both imagery priming and working memory are influenced by the amount of sleep the participant had the night before the experiment, which would mean that observed between-subject differences do not necessarily indicate interesting individual differences. One previous study has investigated whether the imagery effect could be trained and found no effect of training after a 2–3-week test-retest period<sup>24</sup>, suggesting that these effects are indeed stable. Furthermore, the imagery priming effects has been shown to correlate with visual cortex anatomy<sup>25</sup>, something that can clearly not be influenced by the experimental context. However, future research should investigate the stability of these effects more systematically before we can conclude that these differences reflect true individual differences in cognition.

If the observed variation does reflect true differences between individuals, an interesting next step is to investigate the prevalence of these different effects in the population. One straightforward way to do this is to extend the Bayesian model put forward here to include a term that assigns participants to a group depending on their effects (primer, adapter, sensitizer, etc.) and test this model on new data. An important question that can then be answered is to what extent these individual differences relate to psychopathology. For example, people with very strong priming effects were more likely to perceive sensory input congruent with their imagery even when incongruent signals were stronger. Perceiving internally generated content despite counteracting sensory evidence has

## Individual psychometric curves



**Figure 5.** Psychometric curves for four participants. The dominance for the manipulated stimulus is shown on the y-axis and its contrast on the x-axis. Dots represent individual trials, solid lines the posterior estimate of the fitted curve and dashed lines its uncertainty. Dark green shows dominance during congruent imagery and light green during incongruent imagery. (A) A participant showing a reliable imagery priming effect as well as an increase in sensitivity during congruent imagery. (B) A participant showing a reliable imagery adaptation effect and no difference in discrimination sensitivity between conditions. (C) A participant reliably showing no main imagery effect and no interaction with sensory evidence. (D) A participant whose data did not allow dissociation between  $H_+$  and  $H_0$ .

been put forward as an explanation for hallucinations<sup>26</sup>. In contrast, underweighting internal signals with respect to external signals has been put forward as an explanation for perceptual differences in autism spectrum disorder<sup>27</sup>. Investigating to what extent these effects correlate with other perceptual and cognitive variations could have important clinical implications.

In conclusion, our results show that there is a large variation in the way in which imagery influences conscious perception. Imagery can bias perception towards and away from the imagined stimulus and can increase and decrease sensitivity to congruent sensory input. These interactions are probably supported by a neural mechanism involving imagery's recruitment of low-level visual processes. Future research should investigate whether this variation is stable within individuals and if so, whether individual differences can be linked to clinical

populations. This study furthermore highlights the importance of investigating within-participant effects and proposes a way to do so.

## Materials and Methods

**Participants.** Sixty-one participants gave written informed consent and participated in the study. One participant was excluded due to a very high response bias (above two standard deviations from the mean) and one was excluded because no responses were logged due to technical issues. Fifty-nine participants were included in the reported analyses (mean age  $\pm$  SD = 23.10  $\pm$  2.59). The study was approved by the local ethics committee and conducted according to the corresponding ethical guidelines (Commissie Mensgebonden Onderzoek region Arnhem-Nijmegen). To determine the number of participants required, we performed a power calculation (see Supplementary Material 1.1).

**Apparatus.** The experiment took place in a darkened room with dark walls. Participants sat with their head on a chin rest, and wore red-blue anaglyph glasses. The stimuli were generated using MATLAB and the Psychophysics Toolbox (RRID: rid\_000041) and presented on a luminance-calibrated Iiyama Vision Master CRT screen (resolution: 1280  $\times$  1024 pixels, refresh rate: 86 Hz). The distance to the screen was 42.5 cm. Stimuli comprised coloured sinusoidal annular gratings of 5.56 degrees of visual angle (red stimulus oriented at 45°, blue stimulus oriented at 135°) that were presented around a central fixation bulls-eye (radius, 0.5°). The luminance-value of the red stimulus at full contrast was set to half the luminance-value of the blue stimulus.

**Experimental paradigm.** We adapted the imagery binocular rivalry task from<sup>25</sup>. Prior to the experimental task, participants filled in the Vividness of Visual Imagery Questionnaire 2 (VVIQ2)<sup>28,29</sup>. Then, eye-dominance was determined (see *Manipulating sensory evidence*) and participants' binocular stereovision was tested. After that, the rivalry stimulus was shown continuously for a brief time to familiarise participants with the binocular stimulus. Participants briefly practised the main task, and were given the opportunity to ask questions.

The task started with a fixation bulls-eye, after which a cue indicated whether to imagine the red ('R') or blue ('B') grating (Fig. 2). Participants imagined the cued grating for 7 s and then indicated their experienced imagery vividness using a sliding bar on a continuous scale which, due to the resolution of our screen, ranged from -150 to 150 where values below 0 indicated low vividness and values above 0 indicated high vividness. If no response was given within 3 s, the trial continued. Subsequently, the rivalry stimulus was presented for 750 ms, after which participants indicated whether they saw the red stimulus, a perfect mixture or the blue stimulus. Participants were instructed to only indicate 'mixed' if both stimuli were equally dominant. Again, if no response was given within three seconds, the experiment continued. Responses were recorded with a keyboard. Vividness ratings were given with the left hand and rivalry responses were given with the right hand. Participants executed ten blocks of 22 trials each, leading to 220 trials in total. The number of R and B imagery trials was counterbalanced within blocks. The total experimental time was around 60 minutes, excluding practice and instruction.

To control for response bias, 10 percent of the trials were catch trials. These trials contained mock-rivalry stimuli which were a spatial mix of half a red and half a blue stimulus. These displays had blurred edges and the exact split varied on each trial to resemble actual piecemeal rivalry<sup>18,30</sup>. On these trials, participants should respond 'mixed' and there should be no effect of imagery on the response for these trials. If there was an effect of imagery, this indicated that the participant had a response bias.

**Manipulating sensory evidence.** We varied the contrast of one grating between 0 and 1 and kept the contrast of the other grating fixed at 0.4. To be able to test our hypotheses, we wanted to estimate the full psychometric curve. Low dominance levels are easily obtained when the contrast of the manipulated grating is set to zero. However, high dominance levels are more difficult to obtain, because even when the manipulated grating has a contrast value of 1, the fixed grating with a contrast of 0.4 could still dominate in a large percentage of the trials if the participant has a strong bias towards the eye corresponding to the fixed grating. Therefore, we decided to manipulate the grating corresponding to the dominant eye of the participant. This increased the chance of reaching high dominance levels for the manipulated grating. We determined which eye was dominant using a variation of the Miles test<sup>31,32</sup>. During this test, participants view an object through a triangle created by holding their hands together, thumbs extended and arms outstretched. They focus on the object with both of their eyes open and then close one eye. If the object shifts outside of the triangle, that eye is the dominant eye.

**Deriving dominance per contrast.** For each participant, and for each condition, we measured 100 contrast levels between 0 and 1. The order of presentation of the different contrasts was randomized within each participant to prevent order-effects. To infer the dominance levels at different contrast values, we calculated the percentage the manipulated grating was dominant using a sliding window over 11 subsequent contrast values. Mixed responses were counted as a dominance of 0.5. For instance, for the 11 trials with a contrast between 0.2 and 0.31, the participant saw the manipulated grating two times and had a mixed percept one time. This means that the midpoint of those contrasts (0.255) was assigned a dominance level of 2.5/11 = 0.23. Then, for the trials between 0.21 and 0.32, the participant saw the manipulated grating three times, giving the middle contrast (0.265) a dominance level of 3/11 = 0.28.

**Bayesian hierarchical model.** To analyse the effect of manipulated sensory evidence on dominance, we constructed a Bayesian hierarchical model (a discussion of the advantages of Bayesian inference is beyond the scope of this paper, but we refer the interested reader to<sup>33,34</sup>). Details of the model specification, its inference and Bayesian model comparison are described in the Supplementary Material. With this model we simultaneously estimated the participant-level psychometric response curve parameters, as well as their noise levels and group-level response curve parameters, for both the congruent and the incongruent imagery condition. This



allowed us to (1) test whether there was in general an effect of imagery and an interaction with sensory evidence; (2) establish whether those effects were present for each individual participant, and finally; (3) estimate the size and variability of an effect, both at the group-level as well as per participant.

The result of the inference procedure was the posterior distribution of both group-level and participant-level parameters, for each condition. In addition, it provided the distribution over the *differences* in these parameters between conditions. Using Bayesian model comparison, we tested whether these differences differed from zero. For example, consider the parameter  $u$  that represents the bias in the psychometric curve (i.e. its horizontal offset; see Fig. 1). Let  $\delta_u = u^{\text{congruent}} - u^{\text{incongruent}}$  be the difference in this parameter between the two conditions. We write  $\delta_u$  to indicate the group-level difference and  $\delta_u^{(i)}$  to indicate the difference for parameter  $\mu$  for participant  $i$ . Using the Savage-Dickey method<sup>35</sup>, we computed the Bayes factor that quantifies how much more likely the observations are under the alternative model  $H_+$  in which there is a difference between the conditions, versus under the null model  $H_0$  of no difference. That is, we obtain:

$$BF_{+0}^{\delta_u} = \frac{p(D|H_+ : \delta_u \neq 0)}{p(D|H_0 : \delta_u = 0)},$$

for the test of a difference in  $u$  at the group-level. Note that all these tests were performed on the one posterior distribution of the full hierarchical model. This caused participant-level parameters to be pulled towards the group-mean (a phenomenon known as *shrinkage*), which is the Bayesian hierarchical way of mitigating false alarm rates<sup>36</sup>. To interpret the (logarithm of the) Bayes factors, we used the interpretation table provided by<sup>37,38</sup>, as presented in Table 1.

### Data availability

All data can be downloaded from <https://data.donders.ru.nl>.

### Code availability

All experimental and analysis code is available at: <https://github.com/NadineDijkstra/BRIMA>.

Received: 3 May 2019; Accepted: 8 October 2019;

Published online: 30 October 2019

### References

- Delamillieure, P. *et al.* The resting state questionnaire: An introspective questionnaire for evaluation of inner experience during the conscious resting state. *Brain Res. Bull.* **81**, 565–573 (2010).
- Dijkstra, N., Bosch, S. E. & van Gerven, M. A. J. Shared neural mechanisms of visual perception and imagery. *Trends Cogn. Sci.* **23**, 18–29 (2019).
- Reddy, L., Tsuchiya, N. & Serre, T. Reading the mind's eye: decoding category information during mental imagery. *Neuroimage* **50**, 818–825 (2010).
- Lee, S.-H., Kravitz, D. J. & Baker, C. I. Disentangling visual imagery and perception of real-world objects. *Neuroimage* **59**, 4064–73 (2012).
- Dijkstra, N., Bosch, S. E. & van Gerven, M. A. J. Vividness of visual imagery depends on the neural overlap with perception in visual areas. *J. Neurosci.* **37**, 1367–1373 (2017).
- Dijkstra, N., Zeidman, P., Ondobaka, S., Van Gerven, M. A. J. & Friston, K. Distinct top-down and bottom-up brain connectivity during visual perception and imagery. *Sci. Rep.* **7** (2017).
- Levitt, W. J. M. The alternation process in binocular rivalry. *Br. J. Psychol.* **57**, 225–238 (1966).
- Pearson, J., Clifford, C. W. G. & Tong, F. The functional impact of mental imagery on conscious perception. *Curr. Biol.* **18**, 982–6 (2008).
- Knapen, T. H. J., Brascamp, J. W., van Ee, R., Kanai, R. & van den Berg, A. V. Flash suppression and flash facilitation in binocular rivalry. *J. Vis.* **7**, 12 (2007).
- Chang, S., Lewis, D. E. & Pearson, J. The functional effects of color perception and color imagery. *J. Vis.* **13**(10), 1–10 (2013).
- Bastos, A. M. *et al.* Canonical microcircuits for predictive coding. *Neuron* **76**, 695–711 (2012).
- den Ouden, H. E. M., Kok, P. & de Lange, F. P. How prediction errors shape perception, attention, and motivation. *Front. Psychol.* **3** (2012).
- Friston, K. A theory of cortical responses. *Philos. Trans. R. Soc. London B Biol. Sci.* **360** (2005).
- Chen, X. & He, S. Local factors determine the stabilization of monocular ambiguous and binocular rivalry stimuli. *Curr. Biol.* **14**, 1013–1017 (2004).
- Carter, O. & Cavanagh, P. Onset rivalry: Brief presentation isolates an early independent phase of perceptual competition. *PLoS One* **2** (2007).
- Wichmann, F. A. & Hill, N. J. The psychometric function: I. Fitting, sampling, and goodness of fit. *Percept. Psychophys.* **63**, 1293–1313 (2001).
- Bergmann, J., Genç, E., Kohler, A., Singer, W. & Pearson, J. Smaller primary visual cortex is associated with stronger, but less precise mental imagery. *Cereb. Cortex* **26**, 3838–3850 (2016).
- Pearson, J., Rademaker, R. L. & Tong, F. Evaluating the mind's eye: The metacognition of visual imagery. *Psychol. Sci.* **22**, 1535–1542 (2011).
- Keogh, R. & Pearson, J. Mental imagery and visual working memory. *PLoS One* **6**, e29221 (2011).
- Pearson, J., Rademaker, R. L. & Tong, F. Evaluating the Mind's Eye. *Psychol. Sci.* **22**, 1535–1542 (2011).
- Mapp, A. P., Ono, H. & Barbeito, R. What does the dominant eye dominate? A brief and somewhat contentious review. *Percept. Psychophys.* **65**, 310–317 (2003).
- Gayet, S., Naber, M., Ding, Y., Van der Stigchel, S. & Paffen, C. L. E. Assessing the generalizability of eye dominance across binocular rivalry, onset rivalry, and continuous flash suppression. *J. Vis.* **18**, 6 (2018).
- Shine, J. M. *et al.* Imagine that: elevated sensory strength of mental imagery in individuals with Parkinson's disease and visual hallucinations. *Proc. R. Soc. B Biol. Sci.* **282**, 20142047–20142047 (2014).
- Rademaker, R. L. & Pearson, J. Training visual imagery: Improvements of metacognition, but not imagery strength. *Front. Psychol.* **3**, 224 (2012).

25. Bergmann, J., Genç, E., Kohler, A., Singer, W. & Pearson, J. Smaller primary visual cortex is associated with stronger, but less precise mental imagery. *Cereb. Cortex*, <https://doi.org/10.1093/cercor/bhv186> (2015).
26. Powers Iii, A. R., Kelley, M. & Corlett, P. R. Hallucinations as top-down effects on perception. <https://doi.org/10.1016/j.bpsc.2016.04.003> (2016).
27. Skewes, J. C., Jegindø, E. M. & Gebauer, L. Perceptual inference and autistic traits. *Autism* **19**, 301–307 (2015).
28. Marks, D. F. Visual imagery differences in the recall of pictures. *Br. J. Psychol.* **64**, 17–24 (1973).
29. Marks, D. F. New directions for mental imagery research. *J. Ment. Imag.* **19**, 153–167 (1995).
30. Keogh, R. & Pearson, J. The perceptual and phenomenal capacity of mental imagery. *Cognition* **162**, 124–132 (2017).
31. Roth, H. L., Lora, A. N. & Heilman, K. M. Effects of monocular viewing and eye dominance on spatial attention. *Brain* **125**, 2023–2035 (2002).
32. Miles, W. R. Ocular Dominance in Human Adults. *J. Gen. Psychol.* **3**, 412–430 (1930).
33. Berger, J. O. & Berry, D. A Statistical analysis and the illusion of objectivity (Letters to editor p. 430–433). *Am. Sci.* **76**, 159–165 (1988).
34. Wagenmakers, E. J. A practical solution to the pervasive problems of p values. *Psychonomic Bulletin and Review* **14**, 779–804 (2007).
35. Wagenmakers, E.-J., Lodewyckx, T., Kuriyal, H. & Grasman, R. Bayesian hypothesis testing for psychologists: A tutorial on the Savage–Dickey method. *Cogn. Psychol.* **60**, 158–189 (2010).
36. Kruschke, J. K. & Liddell, T. M. The Bayesian New Statistics: Hypothesis testing, estimation, meta-analysis, and power analysis from a Bayesian perspective. *Psychon. Bull. Rev.* **25**, 178–206 (2018).
37. Lee, M. D. & Wagenmakers, E. J. *Bayesian cognitive modeling: A practical course*. (Cambridge university press., 2014).
38. Jeffreys, H. *The Theory of Probability*. (OUP Oxford, 1961).

## Acknowledgements

S.E.B. and M.G. were supported by VIDI grant number 639.072.513 of The Netherlands Organization for Scientific Research (NWO). N.D. was supported by institutional funding. MH was supported by the European Research Council Consolidator grant number 647209 and the European Research Council Advanced grant number 743086. The authors would like to thank Surya Gayet for his extremely useful comments on the design of the experiment, Rebecca Keogh for important input regarding the binocular rivalry imagery task and Lynn Le for her invaluable role in data collection.

## Author contributions

N.D. wrote the main manuscript. N.D., S.E.B. and M.v.G. were involved in the design of the experiment. N.D. did the main data acquisition. N.D. and M.H. were involved in data analysis. M.H. created the Bayesian model to analyze the data. N.D., M.H. and M.v.G. were involved in the interpretation of the data.

## Competing interests

The authors declare no competing interests.

## Additional information

**Supplementary information** is available for this paper at <https://doi.org/10.1038/s41598-019-52072-1>.

**Correspondence** and requests for materials should be addressed to N.D.

**Reprints and permissions information** is available at [www.nature.com/reprints](http://www.nature.com/reprints).

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2019