

Prestimulus hemodynamic activity in dorsal attention network is negatively associated with decision confidence in visual perception

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Rahnev DA, Bahdo L, de Lange FP, Lau H. Prestimulus hemodynamic activity in dorsal attention network is negatively associated with decision confidence in visual perception. *J Neurophysiol* 108: 1529–1536, 2012. First published June 20, 2012; doi:10.1152/jn.00184.2012.—Attention is thought to improve most aspects of perception. However, we recently showed that, somewhat surprisingly, endogenous attention can also lead to low subjective perceptual ratings (Rahnev et al., 2011). Here we investigated the neural basis of this effect and tested whether spontaneous fluctuations of the attentional state can lead to low confidence in one's perceptual decision. We measured prestimulus functional magnetic resonance imaging activity in the dorsal attention network and used that activity as an index of the level of attention involved in a motion direction discrimination task. Extending our previous findings, we showed that low prestimulus activity in the dorsal attention network, which presumably reflected low level of attention, was associated with higher confidence ratings. These results were explained by a signal detection theoretic model in which lack of attention increases the trial-by-trial variability of the internal perceptual response. In line with the model, we also found that low prestimulus activity in the dorsal attention network was associated with higher trial-by-trial variability of poststimulus peak activity in the motion-sensitive region MT+. These findings support the notion that lack of attention may lead to liberal subjective perceptual biases, a phenomenon we call “inattentive inflation of subjective perception.”

attention; functional magnetic resonance imaging; spontaneous fluctuation; perceptual decision making

A LARGE NUMBER OF STUDIES have clearly demonstrated that endogenous attention improves perception (for review, see Carrasco, 2011). However, the exact relationship between the two can be fairly complex (Reynolds and Heeger, 2009). We recently showed that attention can lead to low subjective visibility ratings (Rahnev et al., 2011). This is in line with another study that demonstrated that attention can improve accuracy without influencing confidence (Wilimzig et al., 2008). Together, these studies suggest that accuracy can dissociate from confidence under attention. In Rahnev et al. (2011), we proposed a formal model that accounts for this effect. According to the model, lack of attention increases the variability of the internal perceptual response, and confidence ratings are given using the same unified criteria for both attended and unattended stimuli (Fig. 1). Thus, the “low attention” distributions are marked by high variability. This makes these distributions, compared with the “high attention” distributions, extend further into the high confidence regions, thus producing more high confidence trials.

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Here we used functional magnetic resonance imaging (fMRI) to investigate the neural bases of the above effects (Rahnev et al., 2011). In particular, we tested whether spontaneous fluctuations of attention would lead to differential effects on accuracy and confidence ratings, as well as whether such effects would be accompanied by a decrease in variability of the perceptual signal (as predicted by our model). We measured the prestimulus blood-oxygenated level dependent (BOLD) activity in the dorsal attention network (DAN) (Corbetta and Shulman, 2002), which is implicated in directed attention and working memory and is part of the task-positive system in the brain. The name “dorsal attention network” distinguishes it from the “ventral attention network,” which is specialized for the detection of behaviorally relevant stimuli, particularly when they are salient or unexpected (Corbetta and Shulman, 2002). The fluctuations of BOLD activity in the DAN have been investigated in a number of previous resting-state studies (Fox et al., 2005, 2006, 2007; Sadaghiani et al., 2009, 2010) and have been theorized to reflect the attentional level of the subject (Eichele et al., 2008; Sapir et al., 2005). As in previous studies (Hesselmann et al., 2008a,b; Sadaghiani et al., 2009), we focused on prestimulus activity in the DAN because it is not contaminated by stimulus-related activity and reflects ongoing neural fluctuations.

Based on our previous findings, we hypothesized that high prestimulus BOLD activity in the DAN would be associated with low confidence ratings and higher accuracy in the motion discrimination task. Furthermore, we predicted that these effects would be accompanied by an increase in the variability of the perceptual signal as measured by the variance in the evoked responses in the motion-sensitive region MT+.

METHODS

Participants. Fifteen volunteers (9 women; mean age = 22; range = 19–26 yr) participated in the experiment. All subjects were naive regarding the purposes of the experiments, had normal or corrected-to-normal vision, and signed an informed-consent statement approved by the local ethics committee (CMO region Arnhem-Nijmegen, The Netherlands).

Stimulus and procedure. In each trial (Fig. 2), subjects were required to indicate the overall direction of motion of white dots (density = 2.4 dots/degree²; speed = 6 degrees/s) presented inside a black annulus (outer circle radius = 10°; inner circle radius = 1°). The motion direction was either contracting or expanding. Incoherent dots moved randomly with the same speed as coherent dots. All dots had infinite lifetime: they were never removed from the screen during the motion presentation. A small fixation square was presented for the duration of the trial, and subjects were required to maintain fixation on it. The stimuli were presented on gray background and were generated using the Psychophysics Toolbox (Brainard, 1997) in MATLAB.

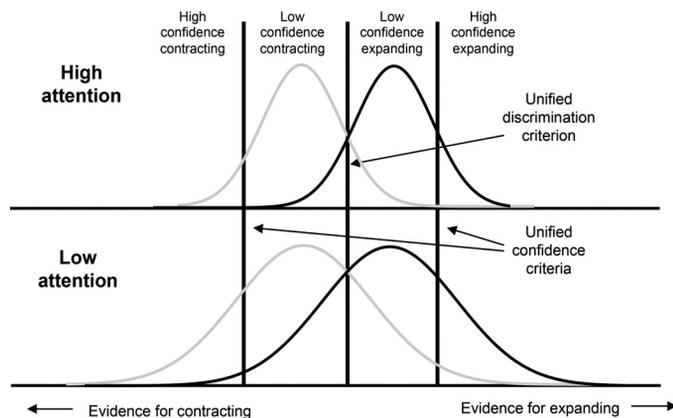


Fig. 1. Signal detection model based on Rahnev et al. (2011). According to signal detection theory (Green and Swets, 1966), stimuli with contracting (gray curve) or expanding (black curve) motion produce overlapping distributions on a single decision dimension. Based on previous research (Gorea and Sagi, 2000), decision criteria are assumed to be the same for the different attention conditions. The model postulates that lower attention leads to increased variability of the perceptual signal (hence the wider distributions in the lower panel). Due to the higher variability of the “low attention” distributions, they produce a higher percentage of high confidence trials, because the tails of the distributions extend further into the “high confidence” regions.

We employed a sparse event-related design (Hesselmann et al., 2008a,b; Sadaghiani et al., 2009) where each trial began with 20–40 s of no motion stimuli. This period allowed for the BOLD signal to return to baseline after each trial. We then presented 100 ms of coherent motion and followed it with a “mask” of 400 ms of random motion. The masking was employed to increase task difficulty and to avoid retrospection based on iconic memory (Sperling, 1960). We elected to use motion stimuli because of ease of control of the stimulus properties and localization of the relevant brain regions. These have also been used in previous studies of spontaneous fluctuations of BOLD activity (Hesselmann et al., 2008a; Sapir et al., 2005). Subjects were required to indicate the direction of motion (expanding/contracting) and give a confidence rating with separate button presses made with their right hand. Confidence was judged on a four-point scale, where one represented low and four represented high confidence. Subjects were instructed to use the scale as evenly as possible. Nevertheless, since some subjects had a bias toward using one side of the confidence scale, and to maximize power, we defined what constituted high and low confidence for each subject individually using a median split. Overall low confidence was defined as a rating of one or two for nine subjects and as a rating of one for the other six subjects. If both button presses were not completed within 6 s, the trial was marked as unanswered and excluded from further analyses. Subjects completed 104 trials separated in two scans of 52 trials. Each scan took about 26 min. After these two scans, we acquired a 307-volume “resting state” scan (Fox and Raichle, 2007) that took about 10 min.

Before the fMRI experiment, each subject took part in a 1-h training session on a separate day, in which the subject practiced 520 trials that were identical to the trials in the scanner but for a shorter intertrial interval of 1–3 s. During the first half of the training session,

subjects were given trial-by-trial feedback. The feedback was discontinued during the second part of the training to prepare subjects for the experiment in the scanner environment. Based on the data from the training session, motion coherence levels were chosen for each subject to produce ~65% correct responses (mean motion coherence = 30.6%, SD = 27.5%). Just before the fMRI experiment, subjects practiced for an additional 5 min (68 trials) to remind them of the task.

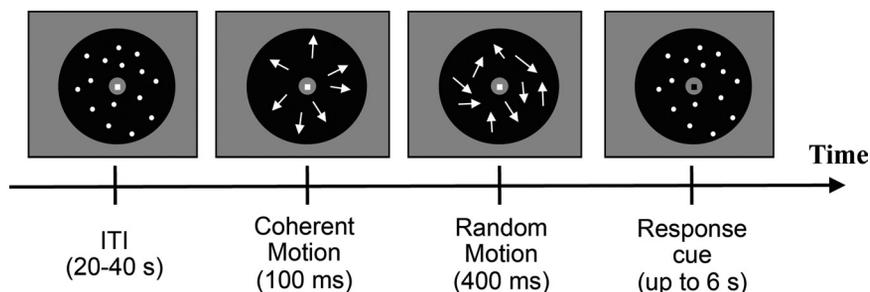
Behavioral analyses. We analyzed our data to check for the existence of trial-to-trial contingencies. For each subject, we investigated whether a correct or high confidence response on the current trial predicted correct or high confidence response on the subsequent trials. To do that, we estimated the proportion of correct and high confidence trials following correct, error, high confidence, and low confidence trials. We then compared these proportions for correct and error trials, as well as for high and low confidence trials. The comparison was done between subjects using a paired-sample *t*-test.

fMRI acquisition. Images were acquired on a 3-Tesla Trio MRI system (Siemens, Erlangen, Germany). Functional images were acquired using a 32-channel coil, with a single shot gradient echo-planar imaging sequence (repetition time: 1,950 ms; echo time: 30 ms; 31 ascending slices; voxel size: $3 \times 3 \times 3$ mm; flip angle = 80° ; field of view = 192 mm). A high-resolution anatomical image was acquired using a T1-weighted MP-RAGE sequence (repetition time: 2,300 ms; echo time: 3.03 ms; voxel size: $1 \times 1 \times 1$ mm).

fMRI preprocessing. Analysis was performed using SPM5 (Wellcome Department of Imaging Neuroscience, London, UK). The first 6 vol of each scan were discarded to allow for scanner equilibration. Preprocessing consisted of realignment through rigid-body registration to correct for head motion, slice timing correction to the onset of the first slice, coregistration of the functional and anatomical images, segmentation of the anatomical image, normalization to Montreal Neurological Institute space using the gray matter image obtained from the segmentation, interpolation of functional images to $2 \times 2 \times 2$ mm, and smoothing with a Gaussian kernel with a full width at half-maximum of 8 mm.

Definition of brain networks. We defined the attention, the default, and the alertness networks using a separate 10-min resting state scan and employing seed-based analyses as in previous studies (Fox et al., 2005, 2006; Sadaghiani et al., 2009, 2010). Briefly, using the MarsBaR toolbox for MATLAB, we extracted the time courses for the resting state scan for spheres with 10 mm radius. We used seeds in the right intraparietal sulcus (27, -58, 49) for the attention network (Fox et al., 2006; Sadaghiani et al., 2009), the posterior cingulate cortex (-5, -49, 40) for the default network (Fox et al., 2005; Sadaghiani et al., 2009), and dorsal anterior cingulate cortex (0, 15, 40) for the alertness network (Sadaghiani et al., 2010). Each time course was high-pass filtered (1/128 Hz), and the time courses for all gray matter voxels, all white matter voxels, and all cerebral spinal fluid voxels were regressed out in a multiple regression (Sadaghiani et al., 2009). This step was similar to the “global signal regression” that is typically performed in such experiments (Fox et al., 2005) whereby the average signal from the whole brain is regressed out. This preprocessing step is useful in that it removes BOLD activity from physiological (i.e., nonneuronal) origin (Fox et al., 2009), but it has been criticized for inducing artificial anticorrelations between networks (Anderson et al.,

Fig. 2. Task design. We employed a sparse design with intertrial intervals (ITI) of 20–40 s to allow for the blood-oxygenated level dependent (BOLD) signal to return to baseline. During that period, subjects viewed stationary dots. Trials consisted of 100 ms coherent dot motion that was followed by a “mask” of random motion (400 ms). Subjects were asked to judge the motion direction (expanding/contracting) and then provide a confidence rating on a 1–4 scale.



2011; Murphy et al., 2009). Nevertheless, the primary interest in this study was investigating the influence on behavior of the prestimulus activity in a specific network (the DAN) and thus we wanted to isolate its influence independent of physiological and other global influences. On the other hand, we were not concerned with potential anticorrelations that could result from this processing step.

The resulting time courses were used as regressors in separate general linear models (GLM) for each subject; the three networks were defined as the set of voxels correlated at $P < 0.001$ with the respective regressor. Each of the three networks was then combined at the second level. Each subject-specific network was a combination of that subject's network masked with the corresponding group network.

To test for the robustness of the findings, the DAN was alternatively identified using independent components analysis (ICA). We employed the GIFT toolbox (Calhoun et al., 2001) for MATLAB to extract the networks consistent across all subjects (Damoiseaux et al., 2006). We used the Infomax algorithm to find 16 components. The attention network was identified among these 16 components and was defined using a z -score threshold of 1. The region MT+ was removed from the attention networks defined using either seed-based methods or ICA.

Prestimulus activity analyses. After the networks were defined for each subject, we analyzed the data from the first two runs in which subjects engaged in the motion discrimination task. We extracted time courses for each network using the MarsBaR toolbox (<http://marsbar.sourceforge.net/>) and regressed out nuisance variables such as head motion and global signal fluctuations as above. Prestimulus activity was defined as the average of the two volumes preceding the onset of the motion stimulus. We used paired sample t -tests and repeated-measures ANOVAs to test whether prestimulus activity differed significantly between high and low confidence trials, as well as between correct and incorrect trials. Even though we tested for the effects in three different networks (see above), we did not correct for multiple comparisons because our main hypothesis was about the effects in the DAN, and the other networks were just included for completeness.

We also investigated whether prestimulus activity in the dorsal attention system influenced the variability in MT+. For each subject, we categorized trials as either having low or high prestimulus DAN activity if the prestimulus activity in the network was lower or higher than the average activity for that subject. We then computed the Fano factor of the MT+-evoked activity for these two types of trials. The evoked activity was defined as the maximum BOLD activity of the three scans that had highest activity on average (across all subjects and all trials). The Fano factor was defined as the variance divided by the mean for the evoked activity for each of the two types of trials for each subject (Carandini, 2004; Churchland et al., 2010; Gur et al., 1997).

MT+ localizer. We identified MT+ using a separate localizer scan after the main experiment and the resting state scan. Sixty blocks of moving dots (block duration of 16 s) were alternated with 10 blocks of stationary dots (block duration of 16 s), resulting in ~ 19 min scan duration. Motion-sensitive areas were obtained using the contrast moving dots > stationary dots. Local maxima near the ascending limb of the inferior temporal sulcus were defined bilaterally and combined to form area MT+ separately for each subject (Hesselmann et al., 2008a). MT+ defined in this was used as a region of interest in a separate GLM analysis (see below).

Standard GLM analysis. Regressors for the first-level analysis of evoked activity were obtained by convolving the unit impulse time series for each condition with the canonical hemodynamic response function. The motion stimulus was modeled with duration of 500 ms. Our model included four regressors, reflecting the combination of two levels of accuracy (correct/error) and two levels of confidence (high/low). We included 12 nuisance regressors related to head motion: three regressors related to translation and three regressors related to rotation of the head, as well as their derivatives (Lund et al., 2005).

Simulations. We performed simple computer simulations to investigate whether our model (Fig. 1) can provide an adequate explanation of the results, especially given that we did not observe a statistically significant effect of prestimulus BOLD signal in the DAN on motion discrimination accuracy (see RESULTS). The main idea of the model is that attention decreases the variability of the perceptual signal. We implemented this intuition in the equations below. We formalized that:

$$S(t) = E(t) + N_p[t, A(t)]$$

where S is the evidence available to the perceptual system, E is the evidence present in the stimulus, N_p is the amount of physiological noise inherent in the system, A is the level of attention in the current trial, and t indicates the trial. The prestimulus BOLD signal in the DAN was modeled as:

$$B(t) = e_A \times A(t) + N_B(t)$$

where B is the BOLD signal, N_B is the noise present in the BOLD signal, and e_A controls the effect of attention on the BOLD signal.

We modeled the level of attention present in each trial (A) using a uniform distribution in the interval (0, 1). The evidence present on each trial (E) was sampled from a normal distribution with a mean μ_E and standard deviation σ_E to reflect the fluctuations in the presentation of the random dot motion. N_p and N_B were modeled as Gaussian distributions with means μ_p and μ_B and standard deviations σ_p and σ_B , respectively. Since the absolute amount of evidence was not of interest, μ_E was set to one and μ_p was set to zero. For simplicity, we assumed a linear influence of attention on the decrease of variability in the perceptual signal and therefore modeled σ_p as $\sigma_p = m - d \times A$, where, m is the mean value of the noise in N_p while d controls the degree of attentional decrease of the variability in N_p . Finally, since the random variables E and N_p are both normally distributed, their sum will also be normally distributed and have a standard deviation that is the sum of the standard deviations of E and N_p . Therefore, rather than fitting σ_p and σ_E separately, we fit only their sum.

The perceptual decision was made by comparing $S(t)$ to zero: positive values indicated correct responses, while nonpositive values were coded as incorrect response. On the other hand, confidence was determined by comparing $S(t)$ to a set of criteria (c_1 , c_2). High confidence ratings were given if $S(t) < c_1$ or if $S(t) > c_2$. Because of lack of significant bias for expanding or contracting motion in our experiment, for simplicity, c_1 was set to $-c_2$. Thus, the set of confidence criteria we used was $(-c, c)$.

We fitted the above equations with the average data from all 15 participants using a simulated annealing procedure (Kirkpatrick et al., 1983). Each iteration of the fitting procedure generated 1,500,000 trials (roughly corresponding to 1,000 times the data from our experiment) based on the current values of the parameters. The fitting function attempted to minimize the error in overall percent of correct answers, overall confidence, and the mean prestimulus BOLD activity for all high confidence, low confidence, correct, and error trials. To test for the robustness of our findings, the fitting was done four different times using different starting values for the parameters. We varied the starting values of the parameters to avoid getting "stuck" in local minima. Each of the four fits provided a good fit to the data. Here we report the results from the first fit, which produced the best match to the observed values; the results of the other fits were consistent with the best one. Using the parameters from the best fit, we generated 10,000 experiments that consisted of 15 subjects each completing 100 trials (15,000,000 trials total) and checked the power to detect significant effects on confidence and accuracy.

RESULTS

We first checked for the existence of trial-to-trial contingencies in accuracy or confidence ratings. Paired-sample t -tests demonstrated that accuracy on the current trial predicted nei-

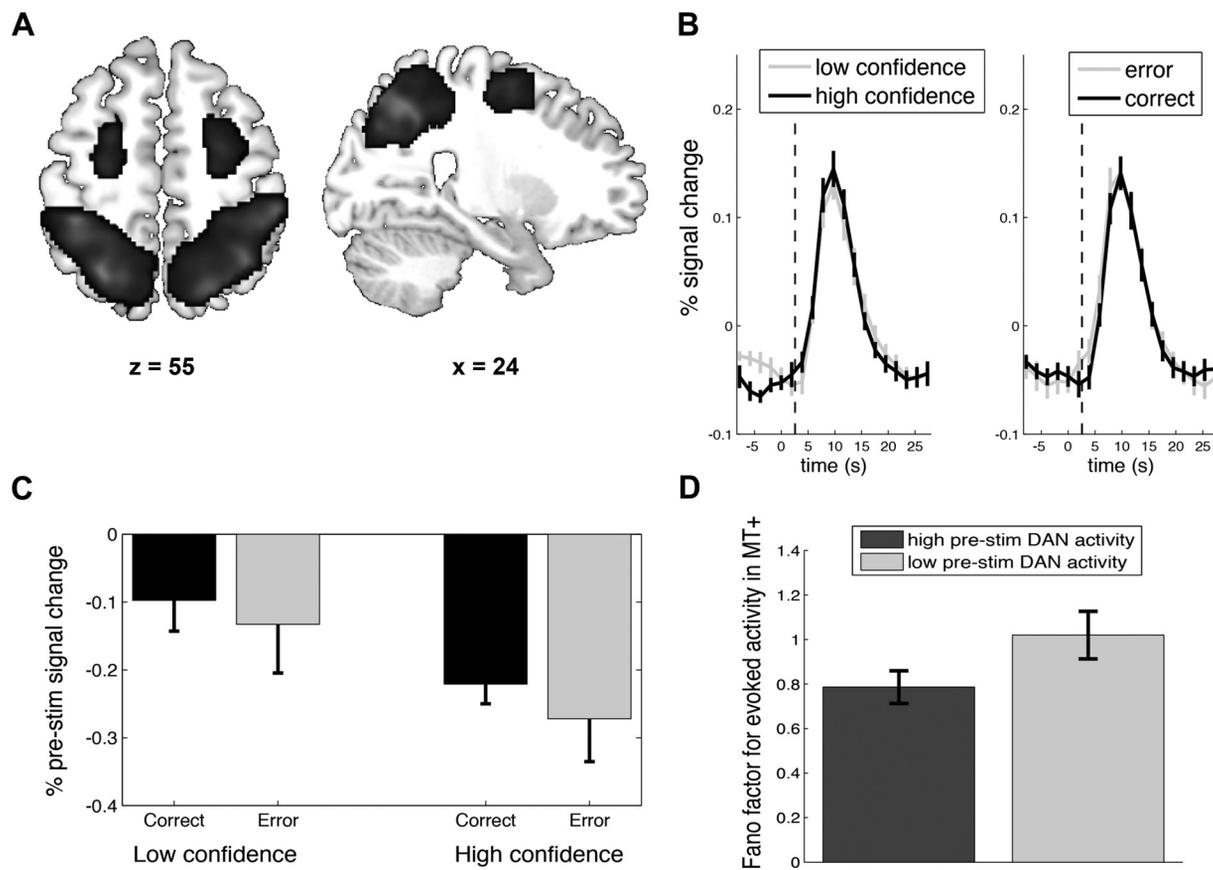


Fig. 3. Prestimulus dorsal attention network (DAN) activity was negatively associated with confidence. *A*: we identified the DAN using standard seed-based methods (see METHODS). The network included the frontal eye fields and intraparietal regions. *B*: counterintuitively, the prestimulus activity was higher for low confidence than for high confidence trials. There was no reliable difference in prestimulus activity for correct compared with error trials. The vertical dashed line shows the average time of the second button press (the confidence response). *C*: to facilitate our statistical analysis, we separated the trials by confidence and accuracy and plotted the prestimulus activity, which was defined as the average BOLD activity in the two scans prior to stimulus onset. *D*: to check if attention changed the variability of the internal perceptual response, we computed the Fano factor for the distributions of evoked responses of MT+ for the trials that had either low or high prestimulus DAN activity. Fano factor was lower in the latter distribution, suggesting that lack of attention increased the variability of the perceptual signal. The error bars represent the standard error of the mean.

ther accuracy [$t(14) = -0.83$, $P = 0.42$] nor confidence [$t(14) = -1.3$, $P = 0.21$] on the subsequent trial. Similarly, confidence on the current trial predicted neither accuracy [$t(14) = 0.2$, $P = 0.85$] nor confidence [$t(14) = -1.04$, $P = 0.32$] on the subsequent trial. Thus, it appeared that there were no reliable trial-to-trial contingencies indicating that our subjects were generating stochastic behavioral responses.

We identified the DAN using standard seed-based methods (Fig. 3A, see METHODS; other methods of identifying the network, such as ICA, gave similar results, see Table 1). Confirming our prediction, we found that high prestimulus BOLD activity in the DAN was associated with low confidence ratings [$F(1,13) = 6.68$, $P = 0.02$; Fig. 3, *B* and *C*]. On the other hand, prestimulus activity in this network was not reliably associated with accuracy [$F(1,13) = 0.45$, $P = 0.52$]. There was also no interaction between confidence and accuracy [$F(1,13) = 0.02$, $P = 0.89$]. The above analyses were performed using repeated-measures ANOVA. However, one subject needed to be excluded from that analysis because he did not have any high confidence error trials (i.e., one of the cells in the 2×2 design was empty). To include that subject, one could perform a simple t -test on the main effect of confidence and accuracy. This led to the same pattern of results for both confidence

[$t(14) = 2.69$, $P = 0.02$] and accuracy [$t(14) = 0.55$, $P = 0.59$].

Since the present experiment is based on detection of coherent motion, we also examined the BOLD signal in the motion-sensitive area MT+. Although this area is sometimes considered to be part of the DAN, in the above analysis, we delineated it as a distinct region so that we could look at its effects separately. Unlike the effect in the DAN, prestimulus activity in MT+ was not associated with the subjects' confidence ratings [$t(14) = 1.31$, $P = 0.21$]. This lack of significant effect on confidence suggests that the difference between high and low confidence trials in the DAN was not driven by fluctuations of activity in MT+. Similarly, prestimulus activity in MT+ for error trials (mean activity = -0.03) and correct trials (mean activity = -0.01) was not significantly different [$t(14) = 0.39$, $P = 0.7$]. Furthermore, standard GLM analyses showed that, for poststimulus evoked activity, high activity in MT+ was associated with a high level of confidence ratings [$t(14) = 2.98$, $P = 0.01$]. Thus, in this study, the activity in MT+ played a bigger role in reflecting stimulus processing rather than prestimulus fluctuation of attentional states.

We further tested the relationship between confidence and prestimulus activity in two other networks. We found that prestimulus activity in neither the default mode network (Dam-

Table 1. Prestimulus activity in other common brain networks

Network	Signal Change, %				Statistical Effects		
	High confidence, correct	High confidence, incorrect	Low confidence, correct	Low confidence, incorrect	Effect on confidence	Effect on accuracy	Confidence \times accuracy interaction
Dorsal attention network	-0.221	-0.272	-0.098	-0.133	$F(1,13) = 6.68$ $P = 0.02$	$F(1,13) = 0.45$ $P = 0.52$	$F(1,13) = 0.02$ $P = 0.89$
Default network	0.175	0.153	0.144	0.076	$F(1,13) = 0.58$ $P = 0.49$	$F(1,13) = 0.24$ $P = 0.64$	$F(1,13) = 0.14$ $P = 0.71$
Alertness network	-0.23	-0.275	-0.215	-0.17	$F(1,13) = 2.17$ $P = 0.16$	$F(1,13) = 0$ $P = 0.99$	$F(1,13) = 1.31$ $P = 0.27$
Dorsal attention network (ICA)	-0.157	-0.244	-0.052	-0.117	$F(1,13) = 5.61$ $P = 0.03$	$F(1,13) = 1.48$ $P = 0.25$	$F(1,13) = 0.07$ $P = 0.8$

We computed the average prestimulus activity for each trial type (see Fig. 3) in different brain networks. The dorsal attention network was also defined in two different ways using either seed-based methods or independent component analysis (ICA, see METHODS). One subject was excluded from this statistical analysis because he did not have any high confidence error trials.

oiseaux et al., 2006; Eichele et al., 2008; Fox et al., 2005; Sadaghiani et al., 2009) nor the alertness network (Sadaghiani et al., 2009, 2010) predicted confidence or accuracy on the task (all P values >0.1 ; Table 1).

The results on the DAN corroborate our computational model (Fig. 1). One of the crucial assumptions of the model is that lack of attention increases the trial-by-trial variability of the perceptual signal. We provided an indirect test of this assumption by investigating whether prestimulus activity in DAN affected the variability in the evoked activity in MT+, a region that likely codes the perceptual signal. We computed the Fano factor of the distributions of evoked MT+ activity, a measure that has been used extensively to characterize neural variability (for example, see Carandini, 2004; Churchland et al., 2010; Gur et al., 1997). Confirming our model's prediction, high prestimulus activity in DAN led to a lower Fano factor in MT+ [$t(14) = 2.56$, $P = 0.02$; Fig. 3D]. No such relationship was found for the default network [$t(14) = -0.71$, $P = 0.49$] or the alertness network [$t(14) = 0.4$, $P = 0.7$]. We considered the alternative interpretation that the result for DAN was due to a ceiling effect: if the prestimulus BOLD activity is already high in DAN then prestimulus activity may be relatively high in MT+, and thus evoked activity in MT+ could potentially show ceiling effects. To explore this possibility, we computed the skewness of the distributions of evoked activity in MT+. A ceiling effect would manifest itself as negative skewness. Nevertheless, we found that skewness was positive for trials with either low (skewness = 0.30) or high (skewness = 0.28) prestimulus DAN activity, and there was no significant difference in skewness between the two distributions ($P = 0.92$).

Finally, to test whether our model (Fig. 1) in which attention decreases the variability of the perceptual signal can explain the observed data, we carried out simple computational simulations in which attention modulated linearly the standard deviation of the signal detection distributions (see METHODS). These simulations were largely motivated by the fact that we did not observe a statistically significant effect of prestimulus BOLD signal in the DAN on motion discrimination accuracy, yet this was one of the predictions of our detection theoretic model (Fig. 1). We performed the computational simulations four different times and obtained good fits of the data all four times (Table 2 reports the fit of the first simulation that provided the best fit). Furthermore, the parameter that controlled the attentional decrease of the variability of the perceptual signal was consistently positive across all four fits (see METHODS), suggesting that attention indeed decreased perceptual noise (note that the parameter was not constrained and that it could have taken negative values). For the fitted values of the parameters, we generated 10,000 replications of our experiment (by generating 15 sets of 100 trials for each replication). We compared the simulated prestimulus BOLD responses and found that simulated BOLD activity was significantly higher for low (compared with high) confidence trials on 7,188 trials (i.e., 72% of all simulations), whereas it was significantly higher for correct (compared with error) trials on 1,306 trials (i.e., 13% of all simulations). Thus our simulations suggest that there is a large difference in our statistical power to detect effects on confidence vs. effects on accuracy, which may explain why in our dataset only the effect on confidence was significant. Therefore, the lack of a significant effect of prestimulus BOLD signal in the dorsal attentional network on

Table 2. *Fit from our computational simulations*

Measure	Prestim DAN in Low Confidence Trials	Prestim DAN in High Confidence Trials	Prestim DAN in Correct Trials	Prestim DAN in Error Trials	Correct Trials, %	High Confidence Trials, %
Observed value	-0.129	-0.246	-0.172	-0.206	0.626	0.528
Fitted value	-0.126	-0.242	-0.173	-0.212	0.624	0.528

We carried out simple computer simulations (see METHODS) to investigate if our model (Fig. 1) can fit the observed data from the experiment. The fitting procedure was performed four different times to ensure that the fitting procedure did not get “stuck” in local minima. This table reports the fitted values produced by the first fit which provided the best match to the observed values. The values were generated by simulating 15,000,000 trials. DAN, dorsal attention network.

accuracy may well be due to the lack of statistical power (as estimated from these simulations), and thus does not necessarily contradict our detection theoretic model (Fig. 1).

DISCUSSION

We found that low prestimulus DAN activity was associated with high confidence in a motion discrimination task, as well as higher trial-by-trial variability in poststimulus peak activity in MT+. Our signal detection theoretic model (Fig. 1) predicted this pattern of results though its last prediction (that low prestimulus DAN activity should lead to lower accuracy) was not confirmed. Overall, our data provide preliminary support of our noise-based account of the phenomenon of “inattentive inflation of subjective perception” (Lau and Rosenthal, 2011; Rahnev et al., 2011).

Our results are novel in a number of ways. First, they demonstrate that attention may lead to dissociations between accuracy and confidence ratings. This is especially surprising since many previous studies have reported that accuracy and confidence typically increase or decrease together (e.g., Busey et al., 2000). Second, our analysis on the influence of prestimulus activity in the DAN on the evoked activity in MT+ suggests that attention decreases the trial-by-trial variability of the perceptual signal. Our model implies that this noise reduction is a critical feature that explains the observed dissociation between accuracy and confidence. On the other hand, most previous models of attention focus primarily (or exclusively) on the attentional increase on gain and have placed less focus on attention’s influence on the trial-by-trial variability of the internal perceptual response (e.g., Desimone and Duncan, 1995).

One may worry that our finding of prestimulus BOLD in the DAN being negatively correlated with confidence could seem contradictory to previous single-neuron recording research. For example, Kiani and Shadlen (2009) investigated the response of LIP neurons when monkeys were given the opportunity of choosing a safe option (thus indicating low confidence in their decision). The researchers found that the monkeys chose the safe option when the activity in LIP neurons was at an intermediate level and therefore the activity in the recorded neurons did not provide strong evidence for either decision option. Thus Kiani and Shadlen’s results could be interpreted as predicting that the population response of LIP neurons would not distinguish between high and low confidence responses. Nevertheless, although Kiani and Shadlen found neurons that commonly code for both accuracy and confidence, this finding does not necessarily imply that we cannot find dissociation elsewhere in the brain, or even within the same region. Also, Kiani and Shadlen’s study was mainly concerned with poststimulus neuronal activity and did not investigate

prestimulus activity, which is the focus of the current study. Finally, the relationship between measures of individual neurons and a population measure like fMRI can be complex, and higher activity for low compared with high confidence has indeed been reported in previous fMRI studies for parietal and frontal areas (Fleming et al., 2012). Thus, we believe that Kiani and Shadlen’s work is not incompatible with our current results reporting higher prestimulus DAN activity for low confidence trials.

In another study on the spontaneous fluctuation of activity in the DAN, Sadaghiani et al. (2009) reported that low prestimulus DAN activity led to more hits in an auditory detection task. Sadaghiani et al.’s findings may suggest that low level of attention improves detection capacity, at least for auditory stimuli. However, the increase in detection rate can be attributed to either an enhancement of capacity or a change of detection criterion toward the liberal direction (responding “yes” more often). Compatible with this interpretation, we previously reported empirical and theoretical data that demonstrated that there is a close relationship between high subjective perceptual ratings and more liberal detection criteria (Rahnev et al., 2011). Thus our results that high prestimulus activity in DAN leads to low confidence ratings suggest that Sadaghiani et al.’s findings may be partially explained by a liberal detection bias caused by lack of attention.

Alternatively, Sadaghiani and colleagues (2009) suggest that the negative relationship between prestimulus DAN activity and detection performance may be due to the fact that sounds are not spatial (but see Tark and Curtis, 2009). In contrast with our results, in their study, DAN did not show considerable evoked activity. Given the differences in task (discrimination vs. detection) and stimuli used (motion patches vs. auditory tones) between our study and that of Sadaghiani et al. (2009), it is possible that the influence of DAN depends on the specific context of the experiment as well. We should note that our detection theoretic account of Sadaghiani et al.’s findings and their own interpretation are not necessarily mutually exclusive.

In a related study, Hesselmann et al. (2008) investigated the influence of prestimulus activity in MT+ on the perception of coherent motion. They found that high prestimulus activity in right MT+ biases subjects to perceive coherent motion. Here we used motion that was always coherent, and subjects simply needed to identify the direction of that motion. We did not find significant differences in prestimulus activity in MT+ for error and correct trials. It is likely that prestimulus activity in MT influences the perception of coherence but does not necessarily lead to more accurate identification of the direction of motion.

Although the finding that attention decreased the variability of the sensory responses (Fig. 3D) is compatible with previous research (Mitchell et al., 2007; Bressler and Silver, 2010;

Cohen and Maunsell, 2009), it needs to be interpreted with caution. The two categories of motion stimuli used in this study (contracting and expanding) are both expected to activate MT+. Thus, the average activity in MT+ does not directly reflect the evidence for one motion direction or the other. Also, BOLD activity is dominated by scanner and physiological noise (Fox and Raichle, 2007) that are not necessarily directly meaningful to the perceptual decision itself.

Another limitation of the study is that, if our model (Fig. 1) is correct, one may expect the increase in noise associated with lack of attention to be reflected by higher discrimination accuracy as well, something that we did not find in our dataset. We note that the relative sizes of the impact of an increase in noise on accuracy and confidence may not be the same and depend on factors such as how the confidence criteria are set. We also had limited statistical power since due to the sparse event-related design employed we only had a limited number of trials (~100) for each subject. Indeed our computational simulations suggest that, even if our model (Fig. 1) is correct, we may have nevertheless had limited statistical power to detect a significant positive association between prestimulus DAN activity and discrimination accuracy. The simulations were intended as a proof of concept and were not meant as a formal model of how attention influences prestimulus BOLD or the internal perceptual distributions. Nevertheless, our simulations demonstrate that the negative finding on the relationship between prestimulus BOLD activity on accuracy does not necessarily contradict our model (Fig. 1).

It is also important to note that our signal detection theoretic model is not intended as a general mechanism about how attention, accuracy, and confidence are related since this relationship is likely complex and could depend on the exact setting of the experiment (Kiani and Shadlen, 2009; Reynolds and Heeger, 2009; Wilimzig et al., 2008). Our model is also largely agnostic about the specific neural mechanisms that support the generation of confidence ratings. In particular, we do not believe that prestimulus DAN activity codes confidence ratings; instead, confidence is likely coded in structures related to metacognition (Fleming et al., 2010, 2012) or self-referential evaluative operations (Northoff and Bermpohl, 2004). Rather, the model depicted in Fig. 1 attempts to give a formal explanation of the surprising negative relationship between attention and confidence in certain circumstances such as when attended and unattended stimuli are considered together in the same context.

We also have to be cautious not to assume that prestimulus activity in the DAN can be absolutely equated with the subject's attentional level. There are many other factors that contribute to activity in any large brain network (Fox and Raichle, 2007). Nevertheless, our interpretation of the current data is compatible with previous studies that have shown that the brain modulates the attentional level by changing the state of cortical networks (Harris and Thiele, 2011) and that the DAN in particular reflects positively on one's attentional state (Eichele et al., 2008; Sapir et al., 2005).

Another limitation of the current study is the lack of behavioral effects between conditions, independent of the fMRI results. This is because, in this study, unlike in many other behavioral studies of attention, we did not try to experimentally manipulate the subjects' attention (Rahnev et al., 2011; Wilimzig et al., 2008). Instead, we relied on spontaneous fluctu-

ations of the neural activity in the dorsal-attention network to indicate different presumed attentional states. Future studies should explore novel ways to determine the attentional state of subjects without explicitly manipulating attention, as well as to directly manipulate attention while measuring neural activity, to further investigate the neural mechanism involved in the putative negative relationship between attention and confidence.

Finally, even though one interpretation of our results is that prestimulus activity in the DAN influences the perception of the stimulus, our data are also consistent with the interpretation that what is being influenced is a late, cognitive stage of the information processing. Nevertheless, we favor the former interpretation because in our previous study (Rahnev et al., 2011) we showed that attention not only led to lower visibility ratings, it also led to more conservative detection biases. In addition, these effects were resistant to feedback and payoff manipulations, as if they were automatic and part of the perceptual processes themselves.

To sum up, our results corroborate our previous psychophysical findings (Rahnev et al., 2011) in that lack of attention may lead to liberal subjective biases such as higher subjective ratings, a phenomenon that we call inattentive inflation of subjective perception. Such liberal subjective biases for unattended objects may partially explain why we find it surprising that we fail to perceive unattended objects (such as in inattentive and change blindness experiments) and can perhaps shed some light on why we think we see the whole visual scene in front of us, despite the fact that we seem to only be able to process a few objects effectively within our focus of attention (Kim and Blake, 2005).

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

Author contributions: D.A.R., F.P.D.L., and H.L. conception and design of research; D.A.R. and L.B. performed experiments; D.A.R., F.P.D.L., and H.L. analyzed data; D.A.R., F.P.D.L., and H.L. interpreted results of experiments; D.A.R. prepared figures; D.A.R., F.P.D.L., and H.L. drafted manuscript; D.A.R., F.P.D.L., and H.L. edited and revised manuscript; D.A.R., L.B., F.P.D.L., and H.L. approved final version of manuscript.

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