Relative blindsight in normal observers and the neural correlate of visual consciousness

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By using a paradigm based on metacontrast masking, we created experimental conditions in which the subjective report of consciousness differs but the objectively measured ability to discriminate visual targets does not. This approach allowed us to study the neural correlate of consciousness while having performance levels carefully matched in healthy human subjects. A comparison of the neural activity associated with these conditions as measured by functional MRI showed that conscious perception is associated with spatially specific activity in the mid-dorsolateral prefrontal cortex (area 46). Further analysis confirms that this activation is not only free from any performance confound, but is also not driven by differences in the timing of the physical stimuli. Our results suggest that the prefrontal cortex is important for the essentially subjective aspects of conscious perception.

masking

Blindsight refers to the phenomenon that, after a lesion to the primary visual cortex, a subject can exhibit above-chance performance in detecting or discriminating visual stimuli in a forced-choice setting, despite the lack of acknowledged consciousness of the stimuli (1, 2). In some instances, blindsight subjects can perform at an impressively high level of accuracy (>80%) in the forced-choice task, even when the subjects believe that they are guessing. This potentially high level of performance makes blindsight an interesting case study for visual consciousness, because it indicates that it is consciousness, but not the basic capacity to process information, that is completely abolished. This dissociation of visual consciousness and performance also allows for the opportunity to compare conditions in which visual consciousness is present in one but not the other while having performance levels matched (3). This approach is particularly promising in regard to the search of the neural correlate of consciousness (NCC) because the resulting difference between the conditions cannot be explained in terms of a mere difference in performance levels. Therefore, the result would be more likely to reflect some essential properties of consciousness *per se* rather than simply being due to a difference in the effectiveness of information processing in regard to the visual stimuli.

Here we try to apply this approach to normal human subjects, and use functional MRI (fMRI) to uncover the NCC. Attempts to unequivocally demonstrate blindsight in normal observers have proved to be controversial, resulting in findings that are sometimes hard to replicate (4–6). However, this difficulty dissolves when we consider the fact that, in brain-imaging studies, a statistical comparison between two conditions is valid so long as the factor in question differs in relative terms: we need not produce conditions in which visual consciousness is either completely present or absent. Instead of looking for a complete dissociation of performance and visual consciousness as in the case of blindsight, we set out to look for a relative difference in the level of visual consciousness in two conditions in which performance levels are matched. We call this phenomenon "relative blindsight" because, as in blindsight subjects, there is a dissociation between consciousness and performance, although here the dissociation is relative across conditions.

We demonstrate that these conditions can be created by using a psychophysical paradigm based on metacontrast masking. This approach relies on the fact that type II metacontrast masking (7) gives rise to a nonlinear, U-shaped, masking function. In metacontrast masking, a figure that overlaps with the contour of the target is presented after the target. Discrimination performance for a target stimulus decreases and then increases as the temporal distance between the target and a metacontrast mask increases gradually; this distance is referred to as stimulus onset asynchrony (SOA). Fig. 1 shows the schematic diagram for a visual discrimination task that involves metacontrast masking. Typically, when the mask is effective, there is a perceived decrease in the clarity and luminance of the target. The masking function characterizes the relationship between SOA and masking effectiveness. The U-shaped nature of the masking function (e.g., Fig. 2 *Upper*) implies that there are two SOA points at which the same performance level can be found. We conjectured that the subjective level of visual consciousness might not be exactly the same at these SOA points, which was confirmed by a psychophysical study. Based on this behavioral finding, we conducted an fMRI study to uncover the NCC.

Results

Behavioral Study. We studied both the performance and the subjective report for conscious perception in a metacontrast masking paradigm (Fig. 1) to behaviorally demonstrate the phenomenon of relative blindsight. Volunteers had to make forced-choice judgments as to whether the target was a square or a diamond. We assessed the level of consciousness immediately after the participants made the forced-choice discrimination by asking them to press keys to indicate whether they actually saw the identity of the target or simply guessed what it was. Fig. 2 *Upper* shows the data for the eight participants. For the SOA points at 33 and 100 ms, the performance levels (i.e., accuracy rates for the square vs. diamond discrimination) were very similar. However, the subjective judgment of consciousness differed ($P = 0.036$, two-tailed Wilcoxon signed-rank test) in that at the earlier SOA point volunteers were more likely to claim to have just guessed the answers. Therefore, we confirmed our hypothesis: The subjective level of consciousness can differ in the absence of a difference of performance levels.

fMRI Study. Fourteen volunteers participated in this experiment. The data for one participant were discarded because of unsatisfactory behavioral performance. The task in the fMRI study was the same as in the behavioral experiment (Fig. 1). Inspection of the data in that experiment suggested that the temporal

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Abbreviations: fMRI, functional MRI; mid-DLPFC, mid-dorsolateral prefrontal cortex; NCC, neural correlate of consciousness; SOA, stimulus onset asynchrony.

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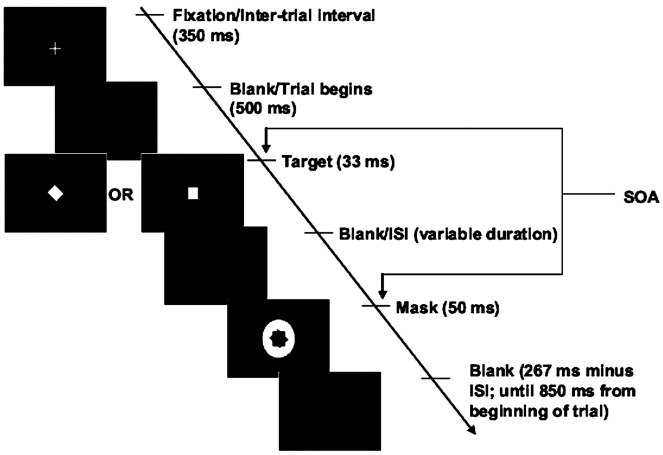

Fig. 1. Visual discrimination task with metacontrast masking. The stimuli were presented on a black background. The mask overlaps with part of the contour of the target without leaving gaps or overlapping with the target spatially. After the presentation of the target and the mask, the participants were first asked to decide whether a diamond or a square was presented. Then they had to indicate whether they actually saw the target or whether they simply guessed the answer. Shown in the brackets are the durations of each stimulus.

profile of the masking function differed across subjects. Therefore, to maximize power in the fMRI study, we recreated the conditions according to the individual temporal profile of each participant. Every participant was tested with both a short SOA condition for which the SOA was at 33 ms and a long SOA condition for which the SOA points were computed online to ensure that the performance level in this condition was similar to that of the short SOA condition. To achieve this matching, we used an adaptive procedure to search for a long SOA time point for each participant such that performance level in both the short and long SOA conditions would be as similar as possible. This approach bypassed the problem of the variability of the temporal profile of the masking function mentioned above. The group average for the resulting long SOA value was 104 ms (SD, 40 ms).

The behavioral results are shown in Fig. 2 *Lower*. The participants were on average 68.27% correct (SD, 4.54%) in the short SOA condition, and 70.22% (SD, 5.24%) correct in the long SOA condition. The two measures did not differ significantly ($P = 0.213$, two-tailed Wilcoxon signed-rank test). We also used the criterion-free measure, d', to assess performance and found that they did not differ significantly across the conditions either ($P = 0.26$, two-tailed paired t test): They were 0.99 and 1.12 for the short and long SOA conditions, respectively (SD, 0.25 and 0.31, respectively). In addition, the reaction times for visual discrimination in both conditions did not differ significantly ($P = 0.858$, two-tailed paired t test): They were 723 and 717 ms for the short and long SOA conditions respectively (SD, 180 and 192 ms, respectively). The reaction times for correct and incorrect trials were considered together so that the difference between all trials in the two task conditions were reflected, given that they were all analyzed in the fMRI analysis. These results suggest that not only was the performance of identification in the two conditions matched, but also that the task difficulty as measured by reaction times was very similar.

However, as predicted, the levels of subjective consciousness differed significantly ($P = 0.007$, two-tailed Wilcoxon signed-rank test). The "seen" rates were 49.17% and 60.13% for the

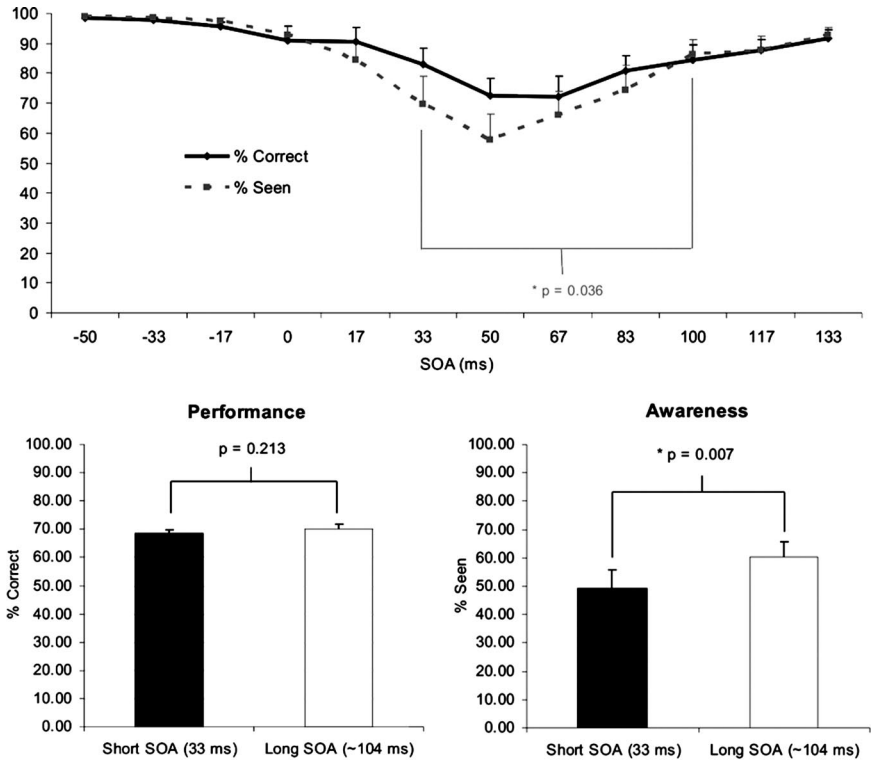

Fig. 2. Behavioral results. (*Upper*) Results from the behavioral study, which used the procedure described in Fig. 1, except that it also included trials during which the mask was presented before the target (paracontrast masking). The data were averaged over eight participants, and the error bars represent one SEM. Note that at the SOA values for which the performance levels (% correct) were the same (e.g., 33 ms and 100 ms), the awareness levels (% seen) differed significantly. (*Lower*) The behavioral results from the fMRI study. The data were averaged over 13 participants, and the error bar represents one SEM. We managed to create two conditions (short SOA and long SOA) that differed significantly in terms of subjective awareness but not in terms of discrimination accuracy.

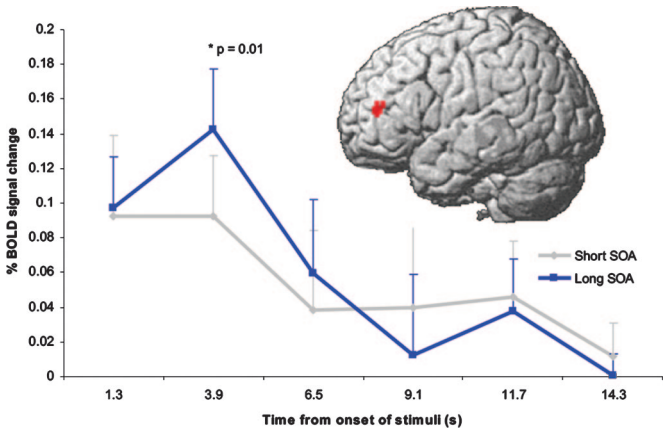

Fig. 3. Activity in the mid-DLPFC reflects visual consciousness (long SOA > short SOA). The activity in this area is higher in the long SOA condition than in the short SOA condition, despite the fact that the two conditions did not yield different discrimination accuracy. There were, however, more trials during which the stimuli were classified by the participants as consciously seen in the long SOA condition than in the short SOA condition. This area was the only one found to be activated in this comparison; parietal activity did not differ significantly even at liberal thresholds. The plot shows the time courses of the hemodynamic activity in the two conditions, as measured by the percentage of signal change from baseline. The data were averaged over 13 participants, and the error bar represents one SEM. Marked by an asterisk is the time point at which the signal differed significantly as reflected by a paired *t* test.

short and long SOA conditions, respectively (SD, 23.17% and 19.79%, respectively). All but one participant showed the effect in the same direction, and 7 of the 13 participants showed a significant effect when their data were analyzed individually ($P < 0.05$, χ^2 test).

In the long SOA condition there was a significantly higher level of subjective awareness as compared with the short SOA condition, which was associated with a significant increase in activity in the left mid-dorsolateral prefrontal cortex (mid-DLPFC) (coordinates = −46, 48, 14). This analysis included both the correct and incorrect trials. The significance level of this activation was assessed by directly estimating the probability that the area under curve for the hemodynamic time course is bigger in the long SOA than in the short SOA condition. This Bayesian approach has the advantage of bypassing the problem of multiple statistical comparisons. The probability of activation was 0.97. The location of this activation and the time courses of activity for the two conditions are shown in Fig. 3. This activation lies specifically in Brodmann's area 46, the macaque monkey homologue of which lies around the principal sulcus (8).

We also performed a conventional analysis with standard parameters by fitting the canonical hemodynamic response function to the data, and we assessed the significance by using classical frequentist statistics (the *t* test). This approach is less sensitive because the canonical hemodynamic response function peaks at 5–6 s, and the present data do not support this assumption (Fig. 3). Nonetheless, the activation in the left mid-DLPFC survived a threshold of $P < 0.001$ (uncorrected), which suggests that the activation was not due to any idiosyncratic features of the initial analysis.

Although the performance levels did not differ significantly between the two conditions, the averaged value was higher in the long SOA condition than in the short SOA condition by ≈2%. To ensure that the activation in the mid-DLPFC was not due to this difference in performance, we performed another analysis, excluding the three participants who showed the biggest magnitude of superior performance in the long SOA condition. This exclusion resulted in a reversal of the trend for performance: The averaged performances in the short SOA condition and in the long SOA condition in the remaining 10 participants were 69.58% correct and 69.33% correct, respectively (they did not differ significantly, $P = 0.890$). Similarly, the trend reversed for the averaged d' values for the short and long SOA conditions, which were now 1.07 and 1.06, respectively (they did not differ significantly, $P = 0.940$). However, the difference in subjective level of consciousness remained: The seen rates for the short and long SOA conditions were 55.04% and 62.79%, respectively (difference significant, $P = 0.034$). The activation in the left mid-DLPFC also remained significant (probability of >0.95).

We also tried to test whether parietal activity differed in the two SOA conditions, perhaps by a degree that was only marginally below threshold. We lowered the threshold to a probability of >0.9 for the comparison between the two SOA conditions and found no parietal activity. We also tested this hypothesis by using the canonical hemodynamic response function approach. At a liberal threshold of $P < 0.01$ uncorrected, we did not find any parietal activity.

We performed another analysis to test whether the activity in the left mid-DLPFC merely reflected the physical difference in the stimuli (the SOA) or whether it genuinely reflected a difference in the subjective level of consciousness. We took the activity in the mid-DLPFC at the peak of the activation for each subject for the short SOA condition, because the SOA in this condition was the same for every subject. The variability (standard deviations) in the peak location for the subjects were 6, 10, and 10 mm in the *x*, *y*, and *z* directions, respectively. We tested whether the level of activation correlated with the level of subjective consciousness across subjects. We found a correlation indicating that the higher the activity in the left mid-DLPFC, the higher the percentage of trials the subjects declared that they were conscious of the identity of the stimuli ($r = 0.512$). Because we predicted the direction of the correlation based on the results of the comparison between the short and long SOA conditions, a one-tail statistical test is justified. Under this test the correlation was significant ($P = 0.037$; Fig. 4).

To identify the brain areas where activity reflected discrimination performance in general, we also analyzed the fMRI results by comparing correct and incorrect trials, combining short SOA and long SOA trials. We found widespread activations in the ventral prefrontal, premotor, parietal, and temporal cortices. There also were activations in the basal ganglia and cerebellum that may relate to the fact that the reaction times for correct trials (683 ms) were quicker than for incorrect trials (815 ms) ($P = 0.0001$, two-tailed *t* test). The cortical activations were similar to those previously identified as parts of the NCC (9), as shown in Fig. 5. These activations include those in the right ventrolateral prefrontal cortex (coordinates = 36, 40, 2; probability of activation, 0.98), right intraparietal sulcus (coordinates = 42, −58, 38; probability of activation, 0.99), and middle temporal gyrus bilaterally (coordinates = 50, −36, −8 and −48, −36, −6; probability of activation, 1.00 and 0.99, respectively). However, at these coordinates, the probabilities that the activity reflected the difference in the subjective level of consciousness (i.e., long SOA > short SOA) were, in general, low: 0.45 (right ventrolateral prefrontal cortex), 0.59 (right intraparietal sulcus), 0.35 (left middle temporal gyrus), and 0.48 (right middle temporal gyrus).

Discussion

Inspired by the phenomenon of blindsight, we have demonstrated a phenomenon that we call "relative blindsight." Subjects can be performing equally well in two conditions in terms of their accuracy and reaction times in a forced-choice discrimination task and yet show a relative difference in the frequency of their acknowledged consciousness for identity of the stimulus. The

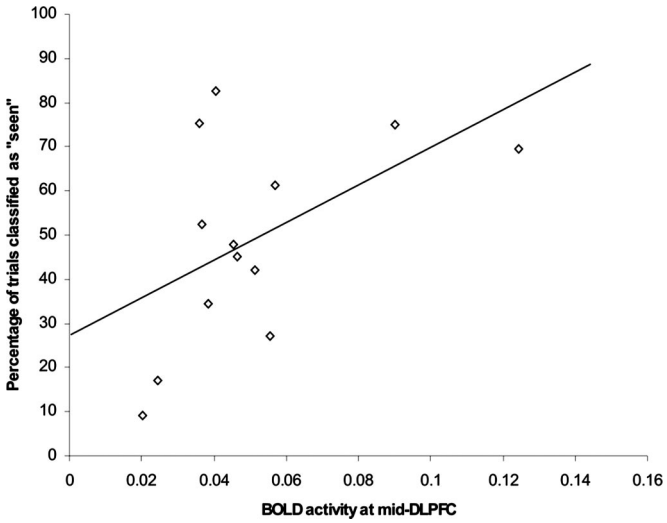

Fig. 4. Activity in the mid-DLPFC across subjects under the same SOA. This correlation was performed to test whether the activation shown in Fig. 3 merely reflects a stimulus confound (long vs. short SOA). Each point represents a single subject, and the data were taken from the short SOA condition, for which the SOA was the same for each subject at 33 ms. As shown in the plot, the higher the activity in the mid-DLPFC, the more likely the identity of the stimulus was declared as consciously seen. This correlation was weak (r = 0.512, P = 0.037, one-tailed), but it shows that the fact that activity in the mid-DLPFC reflects the subjective criterion for conscious perception cannot be explained simply in terms of SOA.

stimuli used in the two conditions are similar, with only a subtle difference in the temporal distance between the target and the metacontrast mask (the SOA). This matching allowed for a comparison of different levels of consciousness, even when performance level is controlled. This comparison revealed specific brain activation in the left mid-DLPFC, which corresponds to Brodmann's area 46 (8).

One possible criticism of blindsight is that, after the brain lesion, subjects adopt an extremely conservative criterion for declaring the stimuli to be consciously perceived. Here, however, the two conditions were intermixed within the same experiment and presented to the same subjects. In addition, the stimuli were similar and presented at the same spatial location. Even if the difference in the frequency of acknowledged consciousness could be formulated in terms of a difference in criterion setting, this difference is not trivial: One still needs to explain why the same individual would set the criteria differently in the different conditions. It seems that the most likely explanation seems to be that the subjects are actually more frequently conscious of the identity of the stimuli in the long SOA condition than in the short SOA condition.

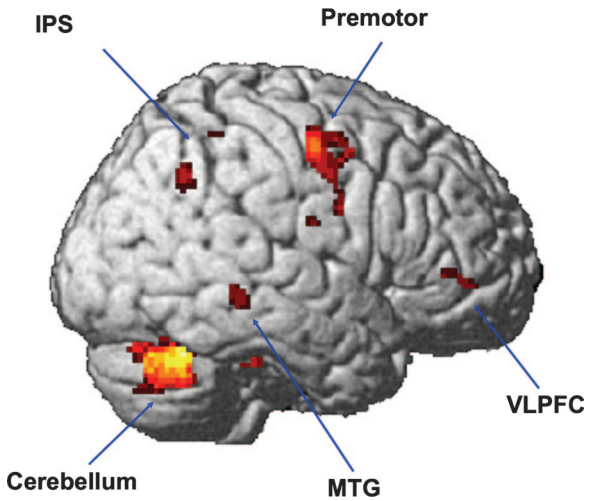

Fig. 5. Activations reflecting performance in general (correct trials > incorrect trials). Activations were found in these areas when correct trials were compared against incorrect trials, combining all trials of both SOA conditions. The pattern of these activations resembles that in a so-called frontal–parietal network, typically reported in previous studies of visual consciousness. VLPFC, ventrolateral prefrontal cortex; IPS, intraparietal sulcus; MTG, middle temporal gyrus.

It could be argued that the activity in the mid-DLPFC merely reflects the difference in the physical properties (i.e., the SOA) of the stimuli in the two conditions. This criticism, of course, also holds for many previous studies of the NCC. However, a previous fMRI study of metacontrast masking suggests that stimulus-timing-driven effects can only be found in the early visual areas but not in the prefrontal cortex (10). Therefore, we think it is unlikely that the activation in the left mid-DLPFC is simply driven by the SOA difference. To check this hypothesis, we performed an across-subjects correlation analysis to show that, given the same SOA, the level of activity in the left mid-DLPFC is correlated with the percentage of trials in which the subjects claim to be conscious of the identity of the stimuli. This means that the results we found in the prefrontal cortex cannot be explained by a stimulus confound.

Given that the activation is not likely caused by a stimulus confound, it is tempting to generalize that the results belong to other stimuli involving different masking methods. However, this possibility is not easy to unequivocally demonstrate because we achieved the matching of performance levels depending on whether the metacontrast masking gives rise to a U-shaped masking function. One reason to speculate that the present result is specific to metacontrast masking is that the mid-DLPFC has been formally characterized (11) as a final converging point for information from the dorsal and ventral visual streams (12, 13). It has been proposed that the mechanism of metacontrast masking depends critically on the interaction between the magnocellular and parvocellular pathways, which roughly maps to the dorsal and ventral streams, respectively (7). However, an imaging study of blindsight (14) suggests that the prefrontal cortex may be involved in consciousness in general.

Sahraie *et al.* (14) have reported results related to the present study from an experiment on a blindsight subject (known as GY). The subject has a lesion to the primary visual cortex that affects roughly half of his visual field, stimuli presented to which yield no phenomenal visual awareness. The authors presented to this "blind field," slowly moving (3° per second) stimuli of which the subject was unaware and found that the subject could nonetheless discriminate the direction of the horizontal movement at slightly >80% correct. This visual stimulation was associated with a lack of significant activation in Brodmann's area 46. However, when the speed of the movement of the stimuli was increased to 20° per second, the subject reported a sense of awareness even though the visual presentation was to the "blindfield" (a phenomenon known as type II blindsight, see refs. 1 and 2), and the performance of discrimination was above 90% correct. This visual stimulation was also associated with a significant activation of Brodmann's area 46. The performance levels for discrimination task in these conditions were different, but could be considered roughly matched, because they were both well above chance. This suggests that activity in area 46 may be important for the awareness of visual stimuli, even when performance level is not an important contributing factor. Incidentally, when visual stimuli were presented to the unimpaired field of the blindsight subject, there was also significant activation in area 46. Along with the currently reported findings,

these results are compatible with the dominant theoretical views that awareness depends critically on anterior regions of the brain (15–17) and possibly only a limited number of neurons located in a restricted region (18).

As in our result, a recent study on perceptual decision making (19) also found an activation that was specific to the left mid-DLPFC. Heekeren *et al*. (19) suggest that the activation was associated with the computational mechanism underlying a perceptual decision task in such a way that the intensity of the activation reflects the contrast of the strength of the signal of the competing stimuli. When the contrast was high, the stimulus was less ambiguous, and the participants were presumably more conscious of its identity. Also, they performed better when the contrast was high. It was found that in this situation there was more activity in the left mid-DLPFC. The similarity between that result and the present one is intriguing because it highlights the possibility that conscious report is essentially related to a computational mechanism that is general for perceptual decisions. However, the critical difference between the two studies is that performance was controlled in the present study, which means that even if conscious reports are related to perceptual decisions, they do not necessarily depend on same the mechanism that drives basic visual discrimination performance.

If the conscious reports studied in this experiment depend on a decision mechanism, one could argue that they do not reflect the phenomenal experiences *per se*, but only reflect higher cognitive aspects of consciousness. One might therefore seek to look for correlates of phenomenal experiences in lower or early cortical areas such as the visual cortex. However, the present study shows that performance could be an important confound in the study of consciousness, so one must be cautious in ensuring that the earlier correlates do not simply reflect performance. In many visual tasks, performance also is characterized by reports, although most are forced-choice reports of properties of the stimuli. Our conscious reports (the Seen vs. Guess judgements) are however reports of the experiences themselves. The phenomenal experiences themselves are not directly observable, but studying their immediate subjective reports is still closer than studying the reports of something else (i.e., the stimuli).

Although activity in the parietal cortex was found to be related to performance in general, it did not significantly differ between the conditions in which the subjective criteria for conscious perception differed. It could be argued that the lack of significant activity in the parietal cortex could be due to a lack of statistical power. However, we failed to find activity, even when we lowered the threshold to a very liberal level ($P < 0.01$, uncorrected). This seems to differ from the results of many previous NCC studies, which have found parietal activity to be as significant as the prefrontal activity, if not more so (9, 20–25). However, it is possible that some of those previously reported activations in the parietal cortex may reflect performance, given that a difference in consciousness level is typically associated with a difference in performance. Future work should aim at further clarifying this issue.

It has been argued that a lesion of the prefrontal cortex does not affect visual consciousness (26). However, in most typical experiments we assess objectively measured performance levels in a visual task, and we argue that it is the subjective reports of consciousness that is mediated by the mid-DLPFC. Latto and Cowey (27) have made bilateral lesions on the posterior lateral surface (i.e., frontal eye fields and Brodmann's area 8) of the prefrontal cortex in the macaque monkey brain, and they report a significant increase of luminance threshold. These findings suggest that the prefrontal cortex may indeed be essential to some aspects of visual consciousness. This issue could be further clarified by giving the task used in the present study to patients with lesions that include the mid-DPLFC. This study should help contribute further to our understanding of the role of the prefrontal cortex in subjective conscious perception.

Materials and Methods

Behavioral Study. Eight people participated in this study. At the beginning of the experiment, a fixation cross (0.5°) was presented at the center of a computer screen (20-inch liquid crystal display monitor, 60-Hz refresh rate), at which the participants were instructed to fixate their gaze whenever the cross was present. The disappearance of the cross marked the beginning of a trial and served as a ready signal. After 500 ms, in most trials (where SOA > 0; see the next paragraph), either a square (1°) or a diamond (i.e., a square of the same size rotated by 45°) was presented at the center of the screen for 33 ms. This presentation was followed by a blank period with a variable duration time and then a 50-ms metacontrast mask (2°) (Fig. 1) that overlapped with part of the contour of the target but not the target itself. Then, the screen went blank until 850 ms after the beginning of the trial. In the other trials (where SOA < 0), the order of presentation of the mask and the target (square or diamond) was reversed.

After the variable blank period, matched for all SOA conditions, a question appeared at 3° above the center of the screen (in Helvetica font with a size set at maximum height = 1°) that read either "Diamond or Square?" or "Square or Diamond?" (counterbalanced across participants). In the former case, the participant pressed the left key if a diamond was thought to be presented and the right key if a square was thought to be presented; the opposite was required in the case of "Square or Diamond?" After the response, a second question appeared at 3° degree below the center of the screen (same font and font size), which read "Seen or Guessed?" The participant pressed the left key if the target was actually consciously perceived and the right key if it was not and the previous response was based on intuition. After the response, the fixation cross reappeared. The trial ended at 3,650 ms after the beginning. If the participants failed to respond to both questions after this time, the question disappeared, the fixation cross reappeared, and the trial was discarded. There was an additional intertrial interval of 350 ms such that, including its following interval, each trial took exactly 4,000 ms in total. The participants were told that accuracy, but not speed, was important, so long as they were fast enough to avoid failing to respond within the 2,800-ms limit in a significant amount of trials.

The SOA values, or the differences between the onset of the target and the mask, were −50, −33, −17, 0, 17, 33, 50, 67, 83, 100, 117, and 133 ms. These time points were selected to accommodate for the refresh rate limitation of the projector used in the fMRI scanner for the main experiment. The projector operates at 60 Hz. There were 80 trials for each time point, and they were presented in a randomized order. The participants were given a chance to take a break for as long as they wished after every 40 trials.

fMRI Study. Fourteen right-handed people (nine females) participated in this study (mean age ± SD, 24.2 ± 2.4 years), one of whom was discarded from the analysis (see below). Each volunteer gave informed consent and was screened for MRI safety before participating in the experiment. The task was similar to the one used in the pilot study, but backward masks (SOA > 0) were used so that the mask always followed the target. The participants were given a short training session (≈3 min) outside of the scanner before the fMRI experiment began to make sure that they understood and were comfortable with the tasks.

In the scanner, the participants viewed the stimuli on a projector screen through inverting mirrors, and they responded by using an MRI-compatible button box. An adaptive staircasing procedure (28) was used to ensure that every participant gave

similar performance levels in the two experimental conditions. In the short SOA condition, the SOA was set at 33 ms. The SOA of the long SOA condition was 100 ms at the beginning of the experiment and was continually updated throughout the experiment according to a two-down–one-up rule: The SOA decreased by one step (16.6 ms) after two successive correct responses and increased by one step after an incorrect response. This procedure ensures that the target performance level would be at ≈71%, but it requires that there is a monotonic relationship between SOA and performance. This relationship was ensured by constraining the SOA in the long SOA condition so that it could not fall to <50 ms. To ensure that the short SOA condition matched the long SOA condition, a similar staircasing procedure was used that computed the size of the stimuli online throughout the experiment. Varying size instead of SOA for the short SOA condition has the advantage of fixing the value for the short SOA at 33 ms so that it would never be too close to that of the long SOA condition. In addition, by making sure that the performance would be at ≈71% at SOA = 33 ms, we ensured that the stimuli were sufficiently small so that the masking function would not be flat at the ceiling level for all SOA values. The size of the target started at 1° wide, as in the pilot study, but it decreased by one step (0.05°) after two successive correct responses and increased by one step after an incorrect response; the size of the mask was scaled accordingly. To ensure that the sizes of the stimuli for the two conditions were the same, a long SOA trial always used the same value obtained by the staircasing procedure from the previous short SOA trial. This procedure similarly ensures that the target performance level for the short SOA condition would be at ≈71%. The minimum target size was set at 0.25°, and the maximum was at 3°. One participant remained at the ceiling level for most of the experiment, and her overall performance was therefore far from 71% in the short SOA condition. The data for this participant were therefore discarded from the analysis.

To maximize the efficiency for detecting hemodynamic differences between the two conditions, the trials were organized such that six trials of the same condition would be presented in succession after the presentation of a series of six trials of the other condition. (The fMRI data analysis was, however, event-related.) In the train of six short SOA trials, the size of stimuli could vary, and in the train of six long SOA trials, the SOA could vary. These variations were based on the staircasing procedure described above and could last throughout the experiment to ensure that performance levels were constant across conditions and time. However, in practice, the parameters stabilized quickly in the first few minutes. Participants in total performed 240 trials for each condition (short SOA and long SOA). These were divided into four runs, between which the participant remained inside the scanner but could communicate with the experimenter. Within each run, there was also a compulsory break of 26 s given to the participant after every 40 trials, during which the participant was instructed to relax. The entire fMRI experiment lasted for ≈45 min for each participant, including the breaks between experimental runs.

Further details for the procedures of imaging data acquisition and analysis can be found in *Supporting Materials and Methods*, which is published as supporting information on the PNAS web site.

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