Disentangling perceptual awareness from nonconscious processing in rhesus monkeys (*Macaca mulatta*)

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Scholars have long debated whether animals, which display impressive intelligent behaviors, are consciously aware or not. Yet, because many complex human behaviors and high-level functions can be performed without conscious awareness, it was long considered impossible to untangle whether animals are aware or just conditionally or nonconsciously behaving. Here, we developed an empirical approach to address this question. We harnessed a well-established cross-over double dissociation between nonconscious and conscious processing, in which people perform in completely opposite ways when they are aware of stimuli versus when they are not. To date, no one has explored if similar performance dissociations exist in a nonhuman species. In a series of seven experiments, we first established these signatures in humans using both known and newly developed nonverbal double-dissociation tasks and then identified similar signatures in rhesus monkeys (*Macaca mulatta*). These results provide robust evidence for two distinct modes of processing in nonhuman primates. This empirical approach makes it feasible to disentangle conscious visual awareness from nonconscious processing in nonhuman species; hence, it can be used to strip away ambiguity when exploring the processes governing intelligent behavior across the animal kingdom. Taken together, these results strongly support the existence of both nonconscious processing as well as functional human-like visual awareness in nonhuman animals.

animal consciousness | conscious and nonconscious perception | nonhuman primates | double dissociation of awareness | visual awareness

Conscious awareness to the events and stimuli around us is a central part of our everyday experience. Yet are humans the only species that experiences conscious awareness? Since nonverbal species cannot report their internal states, philosophers and scientists have long debated whether the question of animal consciousness is empirically testable, and it still remains a topic of speculation (1, 2). In the large spectrum of views, some advocate that consciousness may require complex processes like language, which is unique to adult humans (3) or a human-like theory of mind (4), which may extend to only a few selected species such as great apes (5, 6). In contrast, based on neuroanatomical similarities, some argue that a number of species (including some birds and octopuses) are likely to be capable of generating conscious experience (7). Others consider animal intelligent behaviors which, in humans, seem to coincide with conscious awareness [behaviors such as planning (8) or metacognition (9, 10)], as supporting evidence for animal consciousness (for review, see refs. 11–13). Yet, since many complex human behaviors and high-level functions can be performed outside of conscious awareness (14–16), it is difficult to determine whether nonhuman animals that display intelligent behaviors are indeed conscious or not (17).

Additional attempts to study animal consciousness focused on various methodological approaches including: demonstrating analog forms of human neural deficits of awareness in animals [e.g., blindsight-like phenomena (18)]; documenting differences between more implicit forms of memory (e.g., memory for behavioral habits) and more explicit forms (e.g., memory for an image presented in a single trial) (19–24); testing correlates of attentional awareness in auditory local–global neurosignature violations (25); finding parallels with human visual illusions/binocular rivalry (26, 27) and anesthesia (28); and attempting to obtain an animal's reports on the subjective identification of the presence or absence of a subliminal stimulus (29, 30), including a very recent demonstration in a corvid bird (31). All these important single dissociations of awareness exploration convincingly show that animals display properties similar to those seen in conscious or nonconscious processes. These data are encouraging and provide strong support for our main hypothesis here: Humans are not alone in having two types of cognitive processes

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Significance

Many animals perform complex intelligent behaviors, but the question of whether animals are aware while doing so remains a long debated but unanswered question. Here, we develop a new approach to assess whether nonhuman animals have awareness by utilizing a well-known double dissociation of visual awareness—cases in which people behave in completely opposite ways when stimuli are processed consciously versus nonconsciously. Using this method, we found that a nonhuman species—the rhesus monkey—exhibits the very same behavioral signature of both nonconscious and conscious processing. This opposite double dissociation of awareness firstly allows stripping away the long inherent ambiguity when interpreting the processes governing animal behavior. Collectively, it provides robust support for two distinct awareness modes in nonhuman animals.

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that are meaningfully different—one nonconscious and the other accompanied by awareness. Yet given the ambiguity and difficulty in disentangling conscious from nonconscious processes in nonverbal species (17), many consider the question of animal consciousness as far from resolved (1, 2). For many, the "explanatory gap" in evidence that is needed to unambiguously infer animal consciousness is considered "as wide as ever" (32).

By departing from all previous attempts to study consciousness, we developed an empirical approach that can allow disentangling of the two modes of processing. Specifically, we harnessed well-established double dissociations between nonconscious and conscious visual awareness in humans. In special circumstances, humans show characteristically opposite performance signatures when processing consciously accessible stimuli versus stimuli that are just below the threshold of conscious detection. Using this paradigm, we tested whether rhesus monkeys (*Macaca mulatta*) also show these same opposite double-dissociation signatures of visual awareness. Because this approach predicts that completely opposite signatures of performance would emerge only if there were both conscious and nonconscious processing modes, this framework can be used to reliably disentangle the two levels of processing in a nonhuman animal. Crucially, our approach can provide evidence for the presence of nonconscious processing in nonhuman animals and the immediate corollary of conscious visual awareness (or a similarly characterized processing mode) in animals.

Much work in human cognitive science has shown that under certain circumstances, people display opposite behavioral signatures when they are consciously aware of stimuli (i.e., when they are exposed to clearly visible stimuli—supraliminal stimuli) versus when they are not aware (i.e., when they are exposed to stimuli that are flashed for a few milliseconds on the screen—subliminal stimuli). In one well-known double-dissociation task, human participants are asked to complete a word stem (e.g., "SPI__") without using a reference word that had been flashed on the screen just before it (e.g., "SPICE"). When the reference word is presented supraliminally—that is, when it is consciously seen—participants can easily refrain from using it (and fill the stem with a different word, e.g., "SPIKE"). In contrast, when the reference word is presented subliminally, participants tend to perform poorly, using the primed word more often than in a control condition in which no reference word is presented (33, 34). Researchers have argued that this phenomenon stems from the difficulty of disregarding a stimulus that is nonconsciously processed (33, 34). This dissociation between conscious and nonconscious processing is a central characteristic of the cognitive processes of the human species, with important implications for human behavior, broadly defined (35, 36). To date, we have no evidence for such a double dissociation with opposite predictions of awareness in other species. Crucially, establishing nonconscious influence in animals will not only provide a solid evidence for a nonconscious mode of processing but will also allow us to gain important insights into the possible existence and functions of conscious visual awareness in animals other than humans.

Establishing a Double Dissociation of Awareness Using a Nonverbal Spatial-Cueing Paradigm

To examine nonconscious influence in monkeys, we adopted a spatial-cueing paradigm (37–40). In this task, a target appears in one of two locations and participants are requested to identify the target location as quickly as possible. Critically, the target is preceded by a cue presented either supraliminally (for 250 ms) or subliminally (17/33 ms) in the opposite location, long before the target appearance (Fig. 1 *A*, *Left*). The cue predicts the location of the target but in an incongruent manner—the targets always appear in the opposite location. In the supraliminal condition, in which stimuli are consciously accessible, we predicted that participants will be able to use the cues to identify the targets faster, but only if they become aware of the predictive nature of the cues (i.e., recognizing that the target will appear in the opposite side of the cue). In contrast, in the subliminal condition, we hypothesized that the presentation of the incongruent cue would have the opposite effect: It would attract attention to the cue location, thereby working against identifying the actual target location without participants' awareness. As a control, we also presented two nonpredictive cues, both in the supraliminal and subliminal conditions. Thus, the participants in this control condition could not use the spatial cues to predict the target location (Fig. 1 *A*, *Right*). Participants were exposed to the supraliminal cues and subliminal cues in a counterbalanced block design* and participants' eye gaze was recorded and used as the mode of response. Participants needed to saccade and hold their fixation for 200 ms on the chosen target in order to select it. Importantly, if participants' gaze happened to be at the incorrect location at the moment of the target onset, they could still move their gaze to the correct target location before fixating to select their final response.

Note that in this task monkeys and humans need to inhibit the more dominant (congruent) response in order to successfully choose the opposite incongruent target. Hence, one may expect that subjects will likely experience more difficulty inhibiting the congruent response when seeing supraliminal stimuli of higher saliency. Yet, in contrast, we hypothesize that subliminal stimuli that are barely noticeable and low in saliency will be harder, if not impossible, to disengage in order to properly produce an incongruent nondominant response (while subjects are unaware). In other words, our predictions for implicating visual awareness and nonconscious processing are predicted in the reverse direction of what would typically be expected when inhibiting salient versus nonsalient incongruent stimuli. Thus, if results show the predicted opposite performance (slower responses compared to baseline with subliminal stimuli but faster than baseline with supraliminal stimuli), they will strongly support that awareness, or lack thereof, is the source for the observed discrepancy.

Results

Experiment 1† first tested the spatial-cueing paradigm in humans. As hypothesized, participants were considerably faster to identify the target location following supraliminal incongruent cues than subliminal incongruent cues of which they reported not being aware [$F(1,3585) = 315.66$, $P < 0.0001$, Fig. 1*B*]‡ and faster compared to the two nonpredictive supraliminal cues' baseline [$F(1,1492) = 554.67$, $P < 0.0001$, Fig. 1 *C*, *Right*]. In contrast, participants in the same supraliminal condition, who reported that they were not aware of the supraliminal cue's predictive value, were not facilitated (mean = 324 ms) relative to baseline (mean = 312 ms), [*SI Appendix*, Fig. S2*A*, $F(1,2032) = 1.46$, $P = 0.227$]. These results thus suggest that participants did indeed need a conscious strategy to harness the incongruency of the cues to improve performance. Importantly, all of the participants performing in the subliminal condition, regardless of block order, reported that they did not see any cues§ yet showed a significant slowdown in detecting the target location compared to the baseline with two nonpredictive subliminal cues [$F(1,2989) = 13.36$, $P < 0.0001$, Fig. 1 *C*, *Left*]. We tested participants' lack of

*Prior to the beginning of each condition, participants were also exposed to a short congruent training phase; see *Methods*.

†The results presented here are referring to the data collected with an eye-tracking modality in humans (the same paradigm and modality used in testing monkeys). For supporting data of participants in a key-press modality (suited to only detect facilitations) with and without masking, please see *SI Appendix*, Fig. S1 *A* and *B*, respectively.

‡All statistics were performed on log response time for correct responses using linear mixed models; see *Methods*. Error rates were low (1.2%) and did not differ significantly between the supraliminal and subliminal conditions.

§Two participants did report seeing the cues and were excluded from the experiment based on our preregistered awareness exclusion criteria; please see *Methods*. The results of these participants are presented in *SI Appendix*, Fig. S2*F*.

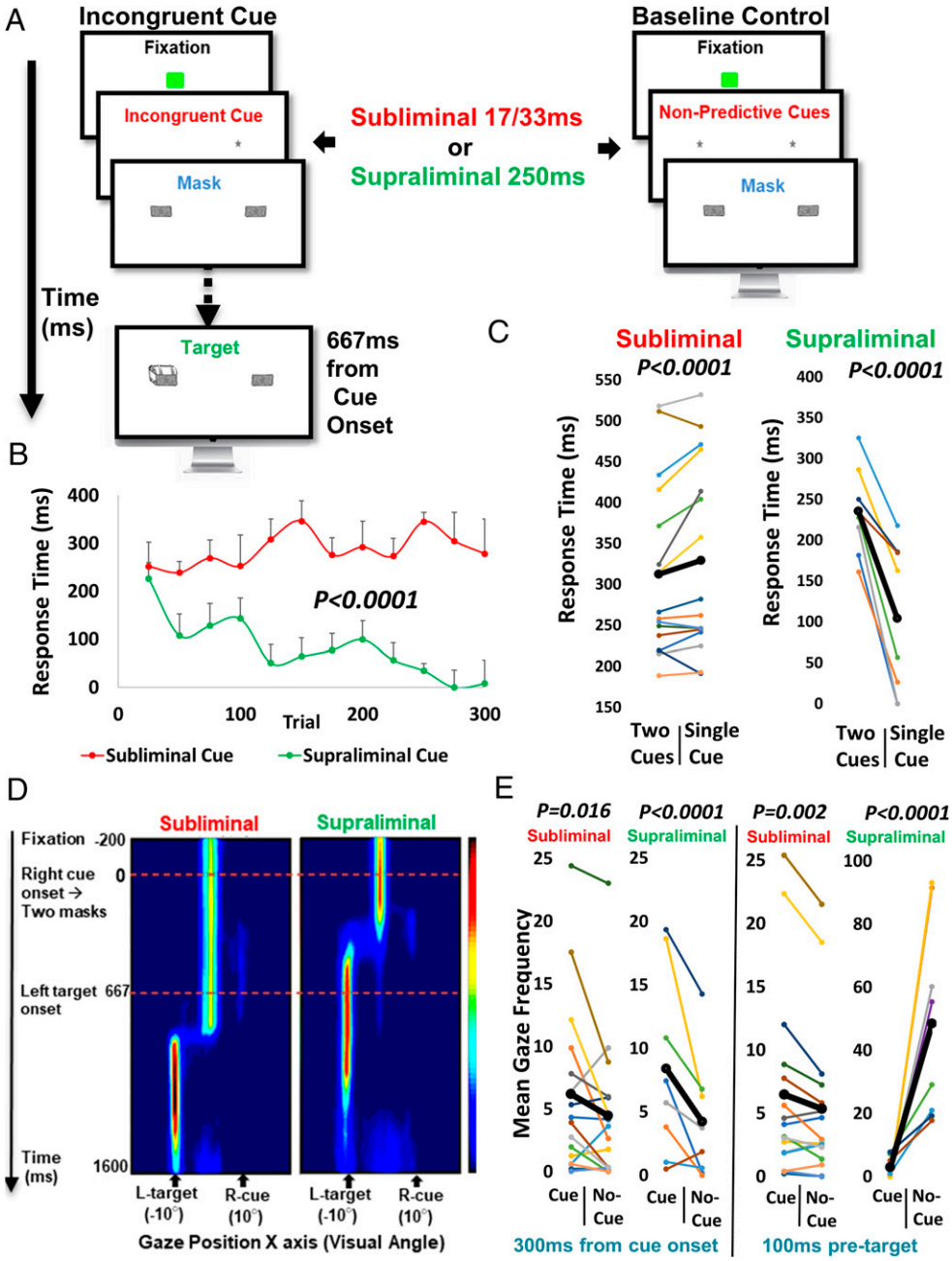

Fig. 1. Spatial-cueing paradigm in humans. (*A*) Illustration of the experimental conditions in the task. Following a fixation square, a star cue is presented in one side of the screen for either a brief subliminal duration of 17/33 ms and then masked or for a consciously accessible supraliminal duration of 250 ms and masked. Following 667 ms from cue onset, a contra lateral target (treasure chest) appears on the opposite side until a selection is made. In the baseline control condition two nonpredictive cues are presented. (*B*) Median of participants' response times to select the target of participants who reported being aware of the supraliminal cue's predictability, following a supraliminal incongruent cue versus a subliminal incongruent cue. Participants were faster with supraliminal cues than with subliminal cues [$F(1,3585) = 315.66$, $P < 0.0001$]. This facilitation improved with time as indicated by the interaction of cue type with experimental trials [$F(2,3585) = 167.06$, $P < 0.0001$; $r = -0.86$, $P < 0.001$]. Subliminal and supraliminal trials appeared in different counterbalanced blocks. Error bars denote SEM. (*C*) Individual participants' response time to respond to the target following a single incongruent cue versus two nonpredictive cues in the subliminal and supraliminal conditions. All participants in the subliminal condition were unaware of the presence of cues yet were slower to locate the target following incongruent cues relative to the two cues baseline [$F(1,2989) = 13.36$, $P < 0.0001$] (*Left*). In contrast, participants in the supraliminal condition who were aware of the cue's predictability were faster to locate the target following incongruent cues relative to baseline [$F(1,1492) = 554.67$, $P < 0.0001$] (*Right*). Thick black lines depict mean response time. (*D*) An example heatmap of gaze frequencies of one participant performing the task. All trials are plotted as right cue → left target trials (left cue → right target trials are reversed and presented as well). The *y*-axis corresponds to time in milliseconds and the *x*-axis to the participant's gaze position on the horizontal axis on the screen. Left target and right cue positions are presented in degrees of visual angle from the central fixation. Warm colors represent higher frequency of gaze in that location across trials. The upper dashed line represents the onset of the cue, and the bottom dashed line the onset of the target. (*E*) Mean frequency of gaze in the cue location versus the opposite no-cue location of all participants during the first 300 ms from cue onset (*Left*) in the subliminal or supraliminal conditions and in the last 100 ms prior to the target appearance (*Right*). Thick black lines depict mean gaze frequency. Gaze frequency is measured as the mean duration of gaze within the specified time slots across trials; larger numbers signify higher frequency of gaze in that location.

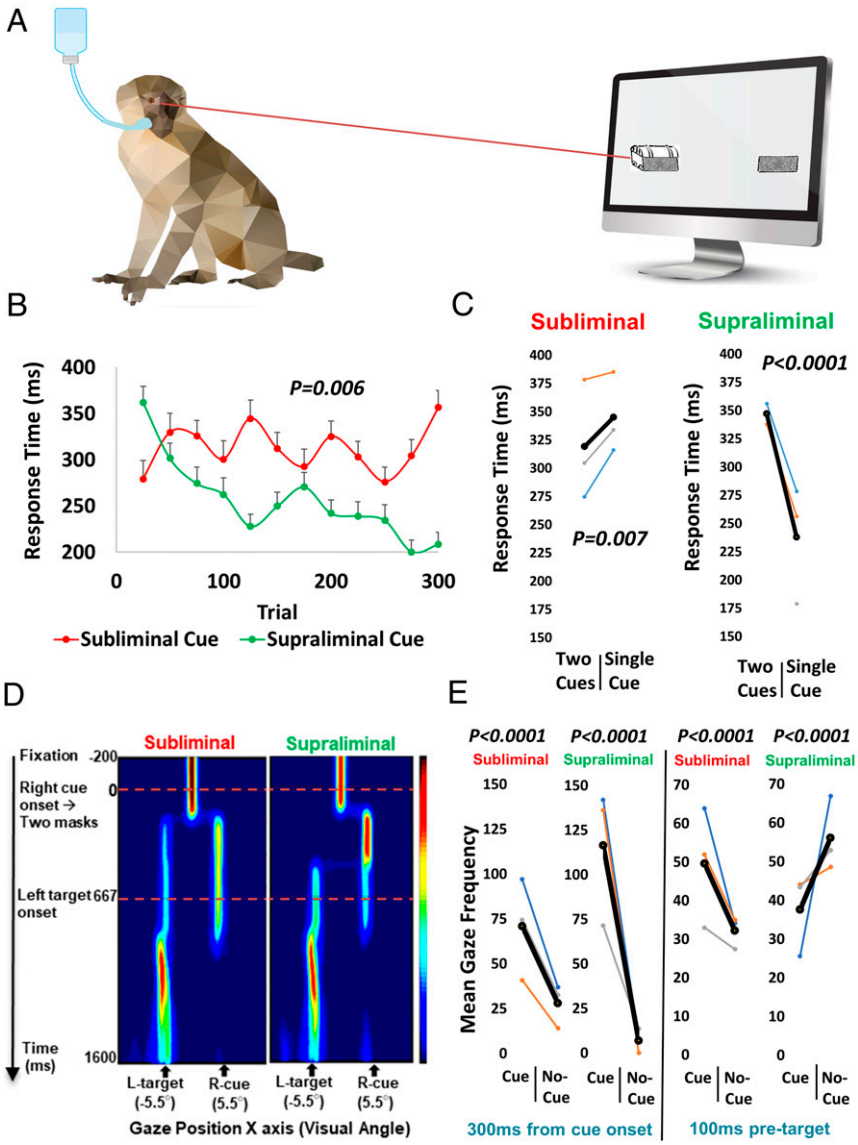

Fig. 2. Spatial-cueing paradigm in monkeys. (*A*) Illustration of the experimental apparatus. Animals faced a computer monitor on which cues and targets were shown and their eye movements recorded with an eye-tracking camera. When the animals correctly made a saccade to the target and held it for a specified duration of time, they received a juice reward. The experimental conditions are the same as the ones depicted in Fig. 1*A*. (*B*) Median of monkeys' response times to select the target. Monkeys were faster with supraliminal incongruent cues than with subliminal incongruent cues [$F(1,4066) = 7.66$, $P = 0.006$]. This facilitation improved with time as indicated by the interaction of cue type with experimental trial [$F(2,4066) = 25.09$, $P < 0.0001$; $r = -0.85$, $P < 0.001$]. Error bars denote SEM of monkey trials. (*C*) Individual monkeys' response time to respond to the target following a single incongruent cue versus two nonpredictive cues in the subliminal and supraliminal conditions. Thick black lines depict mean response time. (*D*) A corresponding gaze frequency heatmap example of a monkey task performance. Warm colors represent higher frequency of gaze in that location across trials. (*E*) Mean gaze frequency of all monkeys in the cue location versus the opposite no-cue location. Thick black lines depict mean gaze frequency. Gaze frequency is measured as the mean duration of gaze within the specified time slots across trials and is presented in arbitrary unites; larger numbers signify higher frequency of gaze in that location.

awareness to the presence of subliminal cues via self-reports after participation in that condition (*SI Appendix*, Fig. S2*C*) and via an objective awareness forced-choice test at the end of the experiment, which requested participants to identify on which side of the screen the subliminal cue appeared. Participants' performance did not differ from chance at the individual binomial level or at the group level (*SI Appendix*, Fig. S2*D*)[¶]. The observation that subliminal cues significantly hindered the detection of the targets relative to baseline, even though participants were unaware of the cues or their locations, demonstrates that these cues were processed nonconsciously.

In order to further verify that the observed effects are consistent with perceptually attending the subliminal cues nonconsciously, we analyzed the participants' eye-tracking data (Fig. 1*D*). Even though many human participants focused on the center until the target appeared, analyzing gaze frequencies (mean duration of gaze across trials) at the cue location versus the no-cue opposite location indicated that their gaze was still captured by the subliminal cue location more than the no-cue location immediately

[¶]Note that since the predicted effect of the cues in the subliminal condition is in the opposite direction to that of the supraliminal condition, the worries about selection (41) do not hold here. In fact, if we mistakenly categorize subjects as unaware, we are deflating the anticipated effect, not inflating it.

after the presentation of the cues [$F(1,7650) = 5.76$, $P = 0.016$, Fig. 1 *E*, *Left*] and during the final 100 ms prior to the target appearance [$F(1,20420) = 9.43$, $P = 0.002$, Fig. 1 *E*, *Right*], resulting in the observed slowdown without participants' awareness. Similarly, participants in the supraliminal condition first had their gaze captured by the cue location [$F(1,11042) = 35.39$, $P < 0.0001$, Fig. 1 *E*, *Left*], but they then quickly redirected their gaze to the no-cue location in the final 100 ms prior to the target appearance [$F(1,3832) = 3{,}080$, $P < 0.0001$, Fig. 1 *E*, *Right*], generating the observed facilitation in performance. However, participants in the supraliminal condition who reported they were not aware of the cue's predictive value showed gaze patterns similar to that of the subliminal condition; they tended to look more at the cue location in both time points [$F(1,11085) = 79.8$, $P < 0.0001$ and $F(1,3831) = 33.38$, $P < 0.0001$, respectively, *SI Appendix*, Fig. S2*B*], suggesting again that a conscious strategy was necessary in order for participants to redirect their gaze to the relevant location.

Monkeys Exhibit the Double Dissociation of Awareness in a Spatial-Cueing Paradigm

In Experiment 2, we implemented the spatial-cueing paradigm in rhesus monkeys. Monkeys, like human participants, were tested using an eye-tracking response apparatus, with similar training (see *) but with an added juice reward upon successful identification of the target location to motivate them to perform the task (Fig. 2*A*). Importantly, like the humans who were consciously aware of the cue's predictability, monkeys tested in the supraliminal condition used the incongruent supraliminal cues to identify the target faster than in the subliminal incongruent cue condition [$F(1,4066) = 7.66$, $P = 0.006$, Fig. 2*B*, *SI Appendix*, Fig. S3 *A–C*, and Movie S1][#] and relative to the two nonpredictive supraliminal cues' baseline [$F(1,3656) = 103.02$, $P < 0.0001$, Fig. 2 *C*, *Right*]. Critically, however, when the monkeys were tested in the subliminal condition, they were significantly slower to detect the target location compared to the control baseline condition with two nonpredictive subliminal cues [$F(1,1737) = 7.14$, $P = 0.007$, Fig. 2 *C*, *Left*], exactly like our human participants, who were completely not aware of the cues.

We further analyzed the monkeys' eye-tracking data in the same way we did for the human participants (Fig. 2*D* and *SI Appendix*, Fig. S4 *A* and *B*). We measured the monkeys' gaze frequencies (mean duration of gaze across trials) in the cue location and the opposite no-cue location. Indeed, although the monkeys' gaze in the subliminal condition was captured by the subliminal cue location more than the no-cue location immediately after the presentation of the cues [$F(1,2249) = 571.53$, $P < 0.0001$, Fig. 2 *E*, *Left*], subjects still failed to move their gaze to the target location ahead of time and maintained their gaze at the cue location during the final 100 ms prior to the target appearance [$F(1,6504) = 170.32$, $P < 0.0001$, Fig. 2 *E*, *Right*], thus resulting in a similar slowdown in performance as observed in humans. Importantly, monkeys also first looked at the cue location in the supraliminal condition [$F(1,2856) = 2{,}312.1$, $P < 0.0001$, Fig. 2 *E*, *Left*] but then quickly used the consciously accessible cue to move their gaze to the opposite location before the target appeared [$F(1,3067) = 96.4$, $P < 0.0001$, Fig. 2 *E*, *Right*, for the last 100 ms prior to the target appearance], yielding a similar improvement in performance seen only in humans who reported being consciously aware of the cue's predictability (Fig. 1*E*).

Developing a Double Dissociation of Awareness Using a Nonverbal Forced-Guessing Paradigm

Humans and monkeys showed strikingly comparable performance on the spatial-cueing paradigm, with both species demonstrating a double dissociation with opposite performance signatures in the two awareness conditions. Though these results provide compelling evidence for a double dissociation between visual awareness and nonconscious processing in monkeys, we decided to apply an even more stringent test by presenting monkeys and humans with a new double-dissociation task, one that makes the conscious identification of cues imperative to solving the task. Note that although participants who used the cues to predict the target location in Experiments 1 and 2 would respond faster, they could still be very accurate and obtain most rewards without using the cues. Indeed, monkeys and humans were more than 90% accurate and could have had insufficient motivation to use the cues just for the sake of speed. We thus modified the task to be a forced-guessing paradigm in which monkeys and humans had to choose which of two simultaneous targets contained a reward. As in the previous experiments, one of the targets was cued with a supraliminal or subliminal stimulus. Again, the reward was always hidden in the opposite target (Fig. 3*A*)[||]. In order to find the reward with more than 50% accuracy (chance level), participants have to use the incongruent cue. We hypothesized that monkeys and humans would successfully use the incongruent cue to find the reward when the cue was consciously accessible but would continue to perform significantly below chance in the subliminal condition. This pattern of below-chance performance would indicate that the subliminal stimuli were indeed processed nonconsciously and that they affected performance in a nonrandom fashion.

In Experiment 3, we tested humans on the forced-guessing paradigm using either eye-gaze or a key-press response modality. Participants successfully performed the task in the supraliminal condition, reliably choosing the target opposite to the cue (mean= 94.6% correct, SD = 3.7% in the eye-tracking modality and mean= 94.6%, SD = 3.5% in the key-press modality). In the subliminal condition, as hypothesized and preregistered (Dataset S2), we compared individuals' binomial test's *P* values of each participant against chance and examined if more participants than expected had obtained binomial *P* values in the most extreme lowest quartile as a group. Critically, there were significantly more participants in the lowest *P* value quartile (42%) than expected by chance (25%) regardless of response modality [$\chi(1) = 5.33$, $P = 0.021$], suggesting that more participants than expected were performing markedly below chance (see Fig. 3 *B* and *C* for examples of individual participant performance and *SI Appendix*, Fig. S5 *A* and *B* for the group). Participants also showed no signs of learning in the subliminal condition [flat learning slope, mean $r(383) = 0.005$, $P = 0.92$]. Critically, because participants' performance in the subliminal condition differed from random guessing, it suggests that the stimuli were processed nonconsciously. We also found that participants were unaware of the subliminal cues' influence, as evidenced by their self-reports, and were unable to detect the subliminal cues' location in an objective awareness test when instructed specifically to do so at the end of the experiment (both at the individual binomial level and group level, *SI Appendix*, Fig. S5*C*, see also ¶), suggesting that the cues were processed and affected participants' performance nonconsciously.

[#]Error rates were low and did not differ significantly between the subliminal condition (9.3%) and the supraliminal condition (7.9%).

[||]As in the previous experiments, all conditions began with a congruent training phase; see *Methods*.

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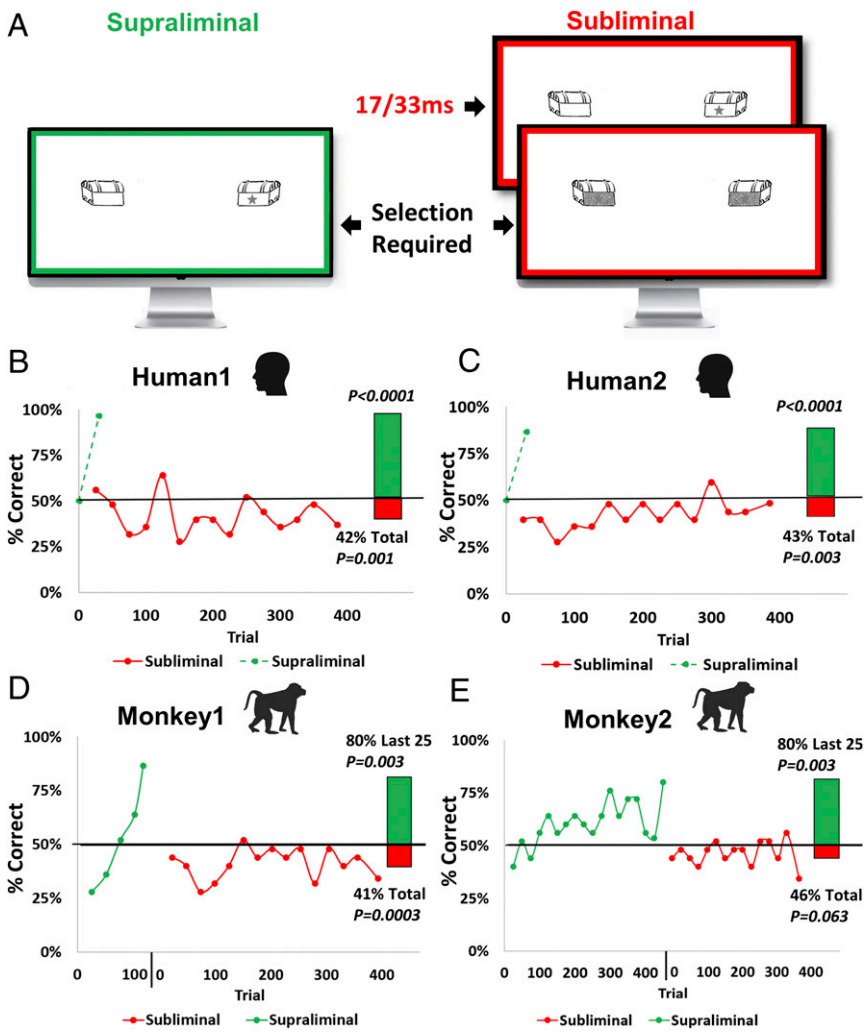

Fig. 3. Forced-guessing paradigm in humans and monkeys. (*A*) Illustration of the experimental array. In the supraliminal condition two treasure chests are presented with a star cue within one of them, whereas in the subliminal condition the star cue is immediately masked after 17/33 ms. A reward is always given in the location opposite of the cue. Participants are not informed of the rule and must guess where the reward is. (*B* and *C*) Example of the performance of two human participants in the supraliminal incongruent condition (green marker) and subliminal incongruent condition (red marker) performing with a keypress response modality (Human 1) or an eye tracking response modality (Human 2). Performance of humans in the supraliminal condition, which had only a single block of 30 trials, is plotted as a dashed line connected to the hypothetical chance level (50%). (*D* and *E*) Performance of two monkeys in the supraliminal incongruent condition (green marker) and subliminal incongruent condition (red marker). Monkeys in the supraliminal condition were run until reaching a stopping criterion of 80% accuracy in the last 25 trials ($P = 0.003$), which determined successful learning of the task. In the subliminal condition, monkeys were run for 385 trials, as humans were, or until reaching the success criterion.

Monkeys Exhibit the Double Dissociation of Awareness in a Forced Guessing Paradigm

In Experiment 4, we presented monkeys with the same forced-guessing paradigm as humans tested in Experiment 3, using the same eye-tracking response apparatus, with similar training phases (see [||]), and with an added juice reward upon correct selections. Like humans, monkeys performed very well in the supraliminal condition (Fig. 3 *D* and *E*, green marker) but critically performed significantly below-chance level in the subliminal condition (mean = 43.5% correct, with a combined binomial probability of $P = 0.00018$, Fig. 3 *D* and *E*, red marker; Movie S2). Just as we observed in human participants, monkeys failed to ignore the subliminal cues and showed no signs of learning [flat learning slope, mean r(383) =0.0005, $P = 0.99$] throughout multiple trials, even when they had successfully learned the incongruent rule in the supraliminal condition before being tested on the subliminal condition (Fig. 3*D*) or even when performing it directly after the supraliminal condition without precongruent training (see *SI Appendix*, Fig. S5*D* for this control condition).

The results of Experiments 3 and 4 replicate those of Experiments 1 and 2 in a different paradigm: Monkeys demonstrate the same signature double dissociation with opposite performance between perceptual awareness and nonconscious processing as humans do. This pattern suggests that monkeys may experience the stimuli in this task under similar awareness as humans and process them nonconsciously in a similar way as humans do. These experiments provide robust evidence that nonhuman animals exhibit a classic human-like double dissociation of visual awareness.

Opposite Performance Signatures Are Driven by Nonconscious Processing

In the following experiments, we attempted to examine the underlying mechanism for the identified opposite performance signatures and tested for alternative explanations. Experiment 5

addressed a possible claim that participants in the subliminal condition might be aware of only a subset of the trials, a number that is not enough for participants to learn the incongruent rule successfully but enough to show a significant cueing effect. If this is the case, below-chance performance in the subliminal condition can result from congruent responses made on few aware trials before subjects learned rather than genuinely nonconscious influence. To test if participants can learn the incongruent rule with a small subset of consciously accessible trials, we exposed a group of human adults to the forced-guessing paradigm (see Experiment 3) with a small percentage of supraliminally cued masked trials (20%) randomly intermixed within 80% unsolvable masked trials with no cues whatsoever. We found that even in this design the majority of participants (75%) became aware of the cues and used them efficiently to choose the opposite target, scoring significantly well above chance [χ (3) = 16.67, $P < 0.001$, Fig. 4*A*]. In addition, it took most aware participants less than 10 of these trials to learn (merely 2.6% out of the 385 trials), see *SI Appendix*, Fig. S6*A*. These data suggest that awareness of a very small proportion of trials is sufficient to learn the rule, and this alternative explanation is thus unlikely to explain our findings.

Another important alternative explanation to be considered is that the subliminal cues were simply less salient and thus harder to learn than supraliminal cues. Thus, the reason for the observed below-chance performance may be merely a result of the difficulty in learning the rule with low-saliency subliminal cues, rather than lack of awareness to the cues. In order to examine this possibility, Experiment 6 tested a subset of human participants with the forced-guessing paradigm after informing them, halfway through the subliminal condition, about the presence of quick-flashing cues. Consequently, many participants became aware of the cues (Fig. 4*B*), learned the rule, and performed almost as well as in a supraliminal condition (with 67% of the participants who attested seeing the cues after being informed, now reaching the 80% success criterion and scoring ≥95% at the peak consecutive 25 trials, both in the key-press and eye-tracking modalities; e.g., see Fig. 4*C*). Even though participants performed below chance prior to being informed [χ (1) = 4.85, P = 0.028, *SI Appendix*, Fig. S6*B*], none reported seeing any cues prior to that point. This suggests that cue awareness rather than cue saliency (which remained constantly difficult to see, here at 33 ms) is the critical factor in performance on our studies.

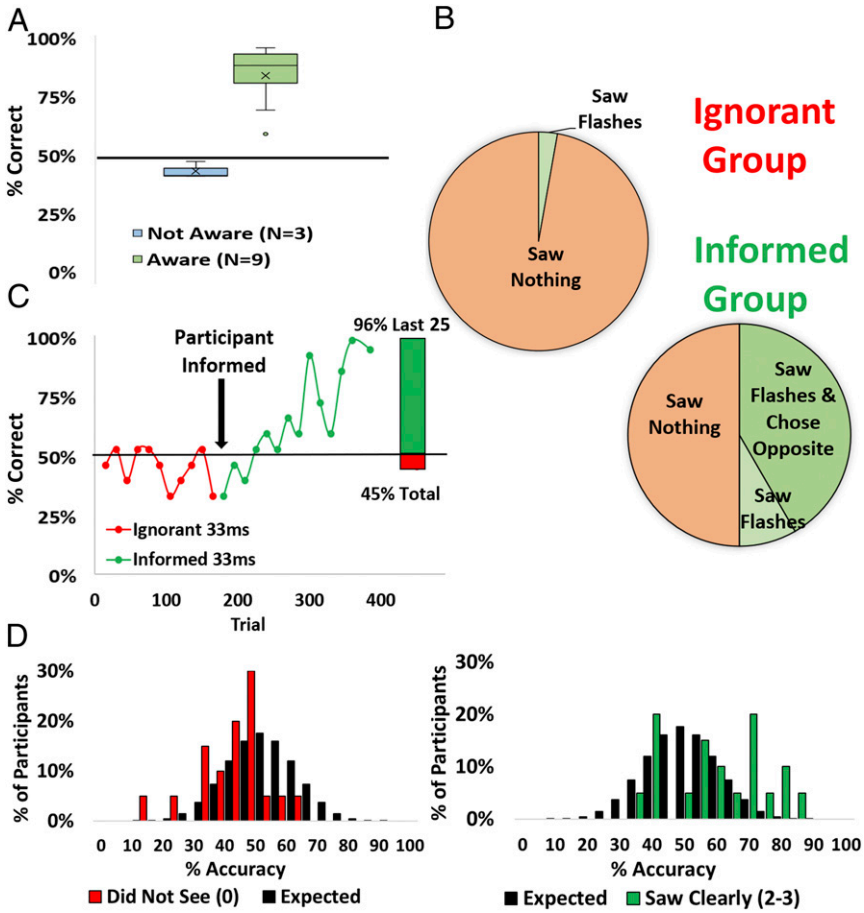

Fig. 4. Performance as a function of cue awareness. (*A*) Accuracies in percentages of cued trials during the forced-guessing paradigm with only 20% of supraliminal cued trials (Experiment 5) plotted for human participants who reported they noticed the cues and used them (n = 9) versus participants who did not (n = 3). (*B*) Distribution of naive participants responses in Experiment 3 and 6 to the question if the participants saw flashing cues on the screen in the subliminal condition and if they used them somehow. Only 1 participant of 36 ignorant participants (3%) reported to possibly have seen flashes but did not do anything with them and reported to have selected by using intuition. In contrast, in Experiment 6 after being informed, 50% of participants reported to have seen flashing cues, and 83% of those who saw also reported they chose opposite of the cues when they were spotted. (*C*) Accuracy of a participant in the informed group of Experiment 6, performing with a subliminal 33 ms interval throughout the task before being informed (red marker) and after being informed (green marker) about flashing cues. (*D*) Distribution of participants' accuracies performing in the 17 ms subliminal interval session in Experiment 7 for the trials they reported they did not see the location of the cue (0 ratings) (*Left*, red bars) compared to an expected random distribution of accuracies (black bars); and accuracy scores of the same participants on trials they reported being more confident in seeing the location of the subliminal cue (two to three ratings) (*Right*, green bars) versus an expected random distribution of accuracies (black bars).

Lastly, to better understand the mechanisms governing the task, Experiment 7 completely removed the learning aspect of the task, instructing participants from the very beginning to choose the opposite location of the cue if they see it (presented for only 17 ms). We further gauged participants' awareness after every subliminal trial (42, 43) from a scale of 0 (saw nothing at all) to 3 (saw it clearly), while urging participants to always choose the opposite location of the cue regardless of how sure they were. Remarkably, participants' performance was still significantly below chance when they reported no awareness of where the cue was presented (0 rating) (Fig. 4 *D*, *Left*), whereas it was significantly above chance when they were more confident that they saw the subliminal cue (2 to 3 rating), [Fig. 4 *D*, *Right* and *SI Appendix*, Fig. S6 *C* and *D*, χ (3) = 24.8, $P < 0.0001$]. These results strongly support the importance of cue awareness in driving the below-chance level performance.

Discussion

We successfully adopted one known empirical method and developed another paradigm to test for double dissociations between visual awareness and nonconscious processing in a nonhuman animal. We found that one nonhuman species—the rhesus monkey—exhibits a double-dissociation performance remarkably similar to that observed in humans. We observed that this dissociation in humans is centrally dependent on awareness. Indeed, exploring the underlying mechanism for the observed opposite performance in Experiments 5 to 7 indicated that the signature of nonconscious processing was present only when participants reported being unaware, whereas the signature of conscious processing was obtained only when participants indicated that they were aware of the stimuli predictability. While of course we could not linguistically probe awareness in monkeys, monkeys displayed similar incongruent responses that required awareness in humans and critically also showed similar opposite performance with subliminal cues. Since these opposite patterns of performance are predicted to emerge only if animals are aware in one condition (presenting functional facilitation) but unaware in the other (presenting persistent interference), they allow us to successfully disentangle the two types of processing in nonhuman species. These results thus provide clear evidence for the existence of two levels of processing in nonhuman primates, which at least in humans correspond to two modes of visual awareness. Establishing the existence of the two distinct processes through cross-over opposite predictions thus help strip away an inherent ambiguity that is typically present when assessing animal behavior.

In our tasks, awareness of the cues was identified as necessary to functionally overcome the dominant response and to adequately use incongruent cues. This pattern supports previous postulations that awareness might be important for "departure from routine behavior patterns to cope with novel and unpredictable challenges" (11). Yet from worms to humans, it remains elusive when along the evolutionary phylogenetic tree this capacity could have emerged (1, 44). The current paradigm can therefore be further adopted to test multiple additional species to try elucidating this puzzle. Future characterization of species that possess or lack perceptual awareness can ultimately help in understanding the necessary neural components required for awareness.

Note that our tasks employing gaze fixation as the response modality share similarities with the anti-saccade task, which similarly documents parallel performance across humans and monkeys (45). However, while anti-saccade tasks are commonly used in monkey studies, and sometimes in awareness contexts in humans (46), these tasks have not to date been used to illustrate the double dissociation of awareness. Thus, our task for the first time revealed opposite patterns of performance to subliminal and supraliminal incongruent cues. Whereas the nonconscious effect demonstrated here may possibly be generated by low-level nonconscious orienting of attention or from the subliminal cues' leftover visual traces, it should be noted that it critically influenced free behavioral choices without participants awareness in both humans and monkeys.

It is also noteworthy that while previous single-dissociation studies are very powerful in terms of testing the neural correlates of conscious reports of animals (30), they typically rely on the assumption that the animals' reporting behavior is accompanied by conscious awareness. The double-dissociation approach allows the testing of these assumptions and to empirically disentangle aware and unaware processes in behaving animals. Our results in rhesus monkeys provide clear empirical evidence supporting nonhuman visual awareness and nonconscious visual processing. While we have not specifically collected the monkeys' subjective reports, we employed the exact same subliminal thresholds as in humans. These masked thresholds (i.e., 17 and 33 ms) were previously shown to be more often subjectively reported by monkeys as "stimulus not there" (29). Here, we showed that employing similar subliminal thresholds in double dissociation of awareness tasks with incongruent stimuli can reliably generate nonconscious interference in behavioral choices and response times. Yet, importantly, these nonconscious interference effects operate against subjects' motivation to succeed and in the opposite direction of the results obtained with supraliminal cues. Therefore, these counter motivational effects cannot be confounded by individual differences in decision criterions as in subjective reports studies (47).

Conclusions

In sum, while scholars long debated whether nonhuman species are aware, disentangling perceptual awareness from nonconscious processing in animals is considered necessary in order to inform this question (17). Our approach offers an empirical way to reliably disentangle the two modes of visual awareness in nonverbal animals. We obtained robust evidence that one nonhuman species exhibits two modes of processing. We observed that nonhuman primates' visual awareness, and susceptibility to nonconscious influence, appears highly comparable to our own. These results show that our species is not unique in terms of awareness to the environment or visual stimuli around us. Critically, by importing one of the strictest indicators of genuine nonconscious processing in human studies (37, 48) —the cross-over opposite predictions of the double dissociation of awareness—we were able to separate the two processes and strip away the inherent ambiguity when interpreting animal intelligent behavior. Doing so, we thus provide strict empirical support for both nonconscious processing and functional visual awareness in nonhuman animals.

Methods

Data for our experiments were collected from 4 adult rhesus monkeys (*Macaca mulatta*) and 145 human subjects. All procedures were conducted in accordance with the NIH guidelines and the Public Health Service's Guide for the Care and Use of Laboratory Animals and with approval from the Yale University Institutional Animal Care and Use Committee. All human experiments were approved by the Yale Human Subjects Committee (#2000022495) and the Hebrew University Human Subjects Committee. We obtained informed consent from all human participants. Full details of our tasks' design, materials, and data analysis are provided in *SI Appendix*.

Data Availability. Data from individual participants are included within the figures and/or supporting information. Additional source data have been deposited in the GIN repository with DOI: 10.12751/g-node.s8xoy1.

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