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Expectations accelerate entry of visual stimuli into awareness

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How do expectations influence transitions between unconscious and conscious perceptual processing? According to the influential predictive processing framework, perceptual content is determined by predictive models of the causes of sensory signals. On one interpretation, conscious contents arise when predictive models are verified by matching sensory input (minimizing prediction error). On another, conscious contents arise when surprising events falsify current perceptual predictions. Finally, the cognitive impenetrability account posits that conscious perception is not affected by such higher level factors. To discriminate these positions, we combined predictive cueing with continuous flash suppression (CFS) in which the relative contrast of a target image gradually increases over time. In four experiments we established that expected stimuli enter consciousness faster than neutral or unexpected stimuli. These effects are difficult to account for in terms of response priming, pre-existing stimulus associations, or the attentional mechanisms that cause asynchronous temporal order judgments (of simultaneously presented stimuli). Our results further

suggest that top-down expectations play a larger role when bottom-up input is ambiguous, in line with predictive processing accounts of perception. Taken together, our findings support the hypothesis that conscious access depends on verification of perceptual predictions.

Introduction

How do prior beliefs and expectations affect the timing of conscious access for visually presented stimuli? Three competing hypotheses provide different answers to this question. First, the cognitive impenetrability hypothesis (Fodor, 1983; Pylyshyn, 1999) claims that perceptual content depends on low-level stimulus properties reflecting a modular separation of perception and cognition. This hypothesis is compatible with a large group of theories that see conscious access as resulting from a sensory stimulus winning a

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competition for access to a global workspace, when they do not incorporate explicit roles for expectations or priors in this process (Baars, 2005; Baars & Newman, 1994; Dehaene & Naccache, 2001). On this set of views expectations should not affect the timing of conscious access.

Two further hypotheses derive from the perspective of predictive processing (Barlow, 1961; Clark, 2013; Friston, 2010; Friston & Kiebel, 2009; Neisser, 1967; Rao & Ballard, 1999). According to this perspective the brain is continuously attempting to minimize the discrepancy between its inputs and its emerging models of the causes of these inputs, via neural computations approximating Bayesian inference. While evidence is accumulating for the role of prediction in perception (e.g., Kok, Jehee, & de Lange, 2012; Summerfield & de Lange, 2014), it is not yet known how the different components of this process influence the timing of conscious access.

According to the verification hypothesis, conscious contents emerge when predictive models are verified against sensory inputs so that prediction errors are minimized (Chang, Kanai, & Seth, 2015; Clark, 2013; Hohwy, Roepstorff, & Friston, 2008). This is compatible with theoretical accounts stressing the importance of reentrant or top-down connections in awareness (Di Lollo, Enns, & Rensink, 2000; Lamme & Roelfsema, 2000), as well as with recent evidence deriving from perceptual hysteresis (Denison, Piazza, & Silver, 2011; Lupyan & Ward, 2013; Melloni, Schwiedrzik, Müller, Rodriguez, & Singer, 2011; Panichello, Cheung, & Bar, 2012). The verification hypothesis also nicely explains why masking (Dehaene, et al., 2001; Greenwald, Klinger, & Liu, 1989) is effective in disrupting conscious access (since verification is disrupted by the appearance of the mask; see Bar et al., 2006). On this hypothesis, expected stimuli should have accelerated access to consciousness (compared to neutral and unexpected stimuli), because stronger priors need weaker evidence for confirmation (in a Bayesian scheme).

Alternatively, conscious access could depend on the violation of current predictions, since novel stimuli may have increased behavioral relevance (Blakemore, Frith, & Wolpert, 1999; Mudrik, Breska, Lamy, & Deouell, 2011; Pally, 2005). On this hypothesis, unexpected visual input should accelerate conscious access.

In a previous study, Melloni et al. (2011) had participants indicate the visibility of a visual stimulus embedded in random noise. The signal-to-noise ratio of stimuli followed a sequence such that the visibility of the target stimulus increased across trials, until a midpoint trial after which visibility progressively decreased. By this arrangement, targets were presented both with prior expectations (during gradual reduction in visibility) and without prior expectations (during

gradual increase in visibility). The data revealed that prior expectations led to an increase in reported visibility (for a given signal/noise contrast), and a reduced latency of an event-related-potential (ERP) signature of conscious perception. Similarly, Lupyan and Ward (2013) required participants to judge the visibility of objects in noisy displays, by presenting one eye with continuous flashes and the other eye with the image of an object. To investigate whether language could affect perception, a subset of trials was preceded by a verbal auditory cue, which indicated the likely identity or shape of the object. Afterwards participants indicated if they had seen an object, and if so, which object. Lupyan and Ward (2013) found that a valid cue boosted subjective visibility of the object when assessed this way.

While these prior studies suggest that expectations can lower thresholds to conscious access, critical questions remain unanswered. First, can we establish directly whether access to consciousness is accelerated by valid expectations? Melloni et al. (2011) showed changes in neural latency but not in behavioral measures of the timing of subjective access, and the links between these features are complex (McDonald, Teder-Sälejärvi, Di Russo, & Hillyard, 2005). Second, can we exclude priming, or implicit associations, as the cause of these and related effects? Lupyan and Ward's (2013) findings could have depended on implicit associations between words and images (see also Costello, Jiang, Baartman, McGlennen, & He, 2009) rather than on explicit trial-specific expectations. Lastly, it is important to investigate the influence of shifts in attentional set, defined here as the stimulus category made explicitly relevant for behavioral responses, which could also contribute to the pattern of results observed in the studies just mentioned.

Here we report psychophysical data intended to resolve these issues. In four experiments we investigated the effects of expectations on the timing of conscious access. The basic paradigm is shown in Figure 1. In all experiments we investigated the transition to conscious access using a version of continuous flash suppression (CFS; Tsuchiya & Koch, 2004, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006). On each trial we presented a changing Mondrian-like mask to one eye while a target picture (e.g., face or house) was presented to the other. The target picture always started invisible (zero contrast) and slowly increased in contrast, while the contrast of the rivalrous mask simultaneously decreased. By this method, participants experienced a breakthrough into visual awareness of the target picture, signaling conscious access. Note that previous research suggests that this breakthrough can be sudden (the whole image breaks through at once) but also partial (parts of the image break through sequentially, Gayet, Van der Stigchel, & Paffen, 2014; Stein, Hebart, & Sterzer, 2011; Stein & Sterzer, 2014; Yang, Brascamp, Kang, & Blake, 2014). Prior to each CFS episode, visually presented cues were employed to manipulate, on a trial-by-trial basis, expectations about upcoming stimuli. The four experiments involved variations on this basic theme.

Experiment 1: Valid expectations accelerate conscious detection

In Experiment 1 we tested the basic question of the influence of expectations on breakthrough to consciousness. Subjects performed a task with continuous masks on one eye, which started at full visibility and faded out, and a target image on the other eye, which started at zero contrast and slowly faded in. Participants were instructed to make a behavioral response at the time they saw any image break through the mask. Before each trial a (visible) cue appeared. This cue was either predictive, indicating which image would likely be presented, or neutral, in which case the cue was uninformative about the identity of the upcoming image.

Methods

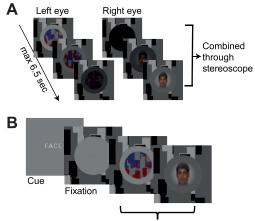
Participants

Thirty-eight healthy observers (26 females, age range: 18–34 years, average 21.7 years, normal or corrected-to-normal vision), naive to the purpose of this experiment, participated in this study after informed consent. The observers participated for monetary compensation (7 Euros per hour) or student credits. The study was approved by the Ethics Committee of the University of Amsterdam.

Materials and stimuli

Stimuli were presented on a 23-in. monitor set to a resolution of 1920 × 1080 at a refresh rate of 60 Hz controlled by a Dell Optiplex 760 computer (Dell, Dallas, TX) running Windows 8. The experiment was programmed in Matlab 7.7.0 (The Mathworks Company, Natick, MA) using the Psychophysics Toolbox routines (Brainard, 1997; Pelli, 1997). Participants viewed the screen through a stereoscope (NVP, La Croix-sur-Lutry, Switzerland), which ensured that each eye only saw either the right or the left half of the screen. The distance between the stereoscope and the screen was 57.4 cm (at this distance, 1 cm on the screen subtends to approximately 1° of visual angle).

The cue word was presented to both eyes (in white, CIE [x, y] coordinates of [0.287, 0.31]), luminance: 37.9



Percept of participant, initially mask, finally face

Figure 1. A typical example of a CFS breakthrough trial involving a valid cue. Participants first saw the cue ("FACE"). Then one eye (the left in Panel A of this example) was presented with changing Mondrian patterns, which were fully visible at the start, but which gradually diminished in contrast/visibility. At the same time, the contrast of the target image in the other eye was gradually increased leading to a transition in interocular suppression and the experience of an image emerging into consciousness (Panel B).

cd/m², on a gray background [0.283, 0.310], luminance: 15.4 cd/m²). This was followed by a background consisting of overlapping white, gray, and black rectangles, which contained a central gray circle (radius: 1.83°, 0.283, 0.310, luminance: 15.4 cd/m²), with a central red fixation spot (radius 0.13°, 0.641, 0.341, luminance: 7.1 cd/m²), again presented to both eyes. On top of the gray circle, but behind the fixation spot, changing Mondrian patterns were presented centrally to one eye (radius: 1.28°), and either a picture (of a face or a house, same radius as the Mondrian patterns) or nothing to the other eye (see Figure 1 for an example). Faces were acquired from the face database from the University of Texas at Dallas (https://pal.utdallas.edu/facedb/request/index). We used neutral faces from the age categories 18–69 years. The house stimuli were obtained from the stimuli database from the Massachusetts Institute for Technology (http://cvcl.mit.edu/MM/stimuli.html). The Mondrian patterns changed at a rate of 3 Hz. The Mondrians started at full visibility, while the picture (or the empty gray circle) was initially invisible (i.e., initially presented at zero contrast). During the trial the contrast of the Mondrians gradually diminished, making them less visible, while the contrast of the central picture (or gray circle) on the other eye gradually increased, making it more visible. The transition from no contrast to full contrast (and vice versa) took 6.5 s, during which the contrast changed linearly. The background on both halves of the display was fully visible during the trial.

Procedure

The experiment consisted of 15 blocks of 25 trials each. The first block was treated as a practice block and was not included in the analysis. Each trial started with a cue presentation (0.7 s, the word "neutral," "house," or "face") to both eyes, followed by the presentation of a static background consisting of randomly overlapping white, gray, and black rectangles, with centrally a gray circle containing a red fixation spot (0.4 s, again identical images were presented to both eyes). Then, changing Mondrian patterns were presented centrally to one eye, and a picture, or in the catch trials no picture, centrally to the other eye. It was randomly determined, per trial, to which eye the Mondrian patterns were presented. The Mondrians started at full contrast, while the picture on the other eye started at zero contrast. Over the next 6.5 s, the Mondrians gradually reached zero contrast, and the picture on the other eye gradually reached full contrast (in both cases the change was linear; see Figure 1). Perceptually, participants experienced this as first viewing changing Mondrians, and after a while an image would appear. The task of the participant was to indicate when the image became visible (by pressing space bar). As mentioned, as a control, on some trials no image was presented: in these catch trials, subjects were instructed to refrain from pressing the space bar. Participants were explicitly instructed to press space bar whenever any picture became visible (we did not specify partially or wholly visible in the instructions).

Importantly, participants were instructed that the word cues "house" and "face" were predictive of which image would follow and that the "neutral" cue was not predictive. They were not instructed of the precise probabilities. A neutral cue was presented on 14% of the trials, a face cue on 43%, and a house cue also on 43% of the trials. After a face cue, a face picture followed on 74% of the trials, a house picture on 10% of the trials, and no picture on 16% of the trials. The percentages were identical (with house and face picture percentages reversed) after a house cue. After a neutral cue, a picture of a face would appear on 42% of the trials, a house picture on 42% of the trials, and no picture on 16% of the trials. Conditions were randomly intermixed throughout the experiment.

Two manipulations were employed in Experiments 1 and 2, which were found to have no effect and which were omitted in Experiments 3 and 4. For completeness we describe these manipulations here. These manipulations were included to test whether precise temporal or pictorial expectations could affect reaction times. Our idea was that when the timing of the image or the specific features of an image were less variable, reaction times should be lower. First, in Experiment 1 (and 2) we added "jitter" for half of the participants. For these participants each trial would start at a randomly

selected moment between 0.4 and 1.9 s after cue offset (for the other participants, each trial would start exactly 0.4 s after cue offset). In both cases the subsequent trial lasted equally long (6.5 s). Since in both Experiments 1 and 2 no differences were found between these two conditions, the results were combined, and this manipulation was no longer employed in Experiments 3 and 4.

Second, the frequency of occurrence of each particular image was manipulated (again only in Experiments 1 and 2). There were four possible face and four possible house images. One face image (randomly assigned per participant) was selected as the familiar image. The familiar image was used as the face image on 50% of the face trials. Two face images (again randomly assigned per participant) were selected to be neutral images. Each of these images was used as the face images on 21% of the face trials. The remaining face image was coded as the unfamiliar image, and was used as the face image on the remaining 8% of the face trials. This means that the familiar face appeared on 50% of the face trials, and the unfamiliar face only on 8% of the face trials. The same familiarity manipulation was applied to the house images. Like the jitter manipulation, the familiarity manipulation had no effect in Experiments 1 and 2—participants responded equally quickly to familiar and unfamiliar images. Therefore the familiarity manipulation was not employed in Experiments 3 and 4. Altogether, the experiment took approximately 60 min.

Data analysis

In this experiment and in Experiment 2, the first block was a practice block and was not included in the analysis. After calculating the accuracy per participant, we excluded those participants with more than 25% false alarms (i.e., pressing space bar on more than 25% of the catch trials), or more than 25% misses (i.e., not responding on more than 25% of the trials where an image eventually appeared). These criteria led to the exclusion of just one participant (this participant produced too many false alarms).

We classified trials into three categories: expected, unexpected, or neutral. Expected trials were those in which a face image followed a face cue or a house image followed a house cue. Unexpected trials were those in which a face image followed a house cue or a house image followed a face cue. Neutral trials were those in which the neutral cue had been presented. We calculated the average reaction time per condition (only for the correct trials; i.e., when participants pressed space bar, and an image of a house or a face had been presented to one eye), and then examined whether expectancy modulated how quickly participants responded.

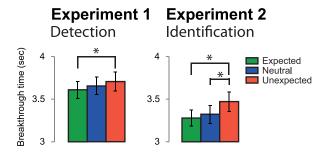


Figure 2. Breakthrough times for expected (green), neutral (blue), and unexpected (red) stimuli in Experiments 1 and 2. Asterisks indicate significant differences between conditions. In both experiments expected stimuli broke through more quickly than neutral and unexpected stimuli. Note that if subjects participated in both experiments (which all but one did), they performed Experiment 1 first. This practice effect was the likely cause of the lower response times in Experiment 2. Error bars indicate between-subjects standard error.

We also tested whether image familiarity (as defined by manipulation of presentation frequency, described above) and jitter affected response times. Both manipulations turned out not to have any effect in this experiment or in the second experiment; jitter: two-way ANOVA, within-subject factor expectation (expected, neutral, and unexpected) and between-subject factor of jitter (jitter or no jitter): no interaction between expectation and jitter: $F(2, 72) = 0.82, p = 0.45, \eta^2 =$ 0.02; Experiment 2: F(2, 62) = 0.18, p = 0.84, $\eta^2 = 0.006$; familiarity: one-way ANOVA, within-subject factor frequency (often, neutral, or rare): F(2, 72) = 0.79, p =0.46, $\eta^2 = 0.02$; Experiment 2: F(2, 62) = 0.28, p = 0.76, $\eta^2 = 0.008$. Therefore, in the analyses of Experiments 1 and 2, we collapsed the results across jitter and familiarity conditions.

Results

A main effect of expectation was observed, F(2, 72) =3.87, p = 0.03, $\eta^2 = 0.097$. Next we investigated whether there was an expectation benefit, which we defined as difference between response times to expected stimuli and response times to unexpected stimuli. Post hoc planned t tests (two tailed) revealed that participants responded to expected stimuli faster than to unexpected stimuli, t(36) = 2.53, p = 0.02, Cohen's d = 0.84, demonstrating an expectation benefit. Furthermore participants tended to respond to expected stimuli faster than to neutral stimuli, t(36) = 1.93, p = 0.06, Cohen's d = 0.64 (see Figure 2, left panel). Finally, we investigated rates of false alarms and misses after either a predictive or a neutral cue. This revealed no significant differences in either misses or false alarms [misses, predictive: 1.7%, neutral: 1.4%, t(36) = 1.04, p = 0.31, Cohen's d = 0.34; false alarms, predictive: 3.8%, neutral: 2.9%, t(36) = 0.71, p = 0.48, Cohen's d = 0.24].

These results indicate that valid expectations accelerated conscious *detection* of target stimuli. However, they do not indicate whether conscious *identification* is affected by expectations (detection and identification are known to involve distinct mechanisms; see Pinto, Scholte, & Lamme, 2012). Specifically, the data so far did not establish whether acceleration of conscious access could occur when *identification* of the target image (rather than *detection* of any image) is required. We therefore performed Experiment 2 to test whether expectations can accelerate the formation of content-specific conscious percepts, (i.e., those requiring identification as well as detection).

Experiment 2: Valid expectations accelerate conscious identification

In Experiment 1, subjects indicated when they saw any image break through masking (detection). In Experiment 2 subjects had to additionally identify the image before responding. Specifically, they were instructed to make one response whenever a house *or* a face became visible, and to make a different response when any other image became visible. The cues in Experiment 2 were identical to the cues in Experiment 1. So the word "face" predicted a face image would appear, the word "house" that a house image would appear, and the word "neutral" was unpredictive. Importantly, the cue predicted whether a house or a face would appear, but the response to a house and a face was the same, making it less likely that any effect on reaction time would be due to response priming.

Methods

Experiment 2 was the same as Experiment 1, except for the following changes.

Participants

Thirty-six participants (24 female, age range: 18–34 years, average 22.03 years) participated in Experiment 2.

Procedure

The ratio of which cues preceded which images were identical to Experiment 1; however, catch trials were different in Experiment 2 than in Experiment 1: Trials on which no image appeared were replaced by trials where another image than a face or a house appeared (either an animal or an object; the stimuli again came

from the stimuli selected from the stimuli database from the Massachusetts Institute for Technology). The task was also changed: Instead of pressing the space bar, whenever an image broke through the Mondrians, participants had to press 1 when a house or a face image broke through, or 2 when any other image broke through.

Data analysis

One participant was excluded based on unusually high false alarm rates (i.e., pressing 2, when no face or house was presented; false alarm rate was higher than 50%). Furthermore, thre participants were excluded because they employed an eye switching strategy (as reported in an informal interview after the experiment)—that is, they checked on which eye the Mondrians were presented, and then continued to watch the trial with that eye closed.

Results

In this identification experiment, similar results were obtained as in Experiment 1. There was an overall effect of expectation on response times, F(2, 62) = 7.74, p = 0.001, $\eta^2 = 0.2$ (see Figure 2, right panel). Post hoc planned (two-tailed) t tests revealed that both expected stimuli and neutral stimuli were responded to faster than unexpected stimuli [expected vs. unexpected: t(31)= 3.46, p = 0.002, Cohen's d = 0.33; neutral vs. unexpected: t(31) = 2.65, p = 0.01, Cohen's d = 0.24], so we again observed an expectation benefit. Again there was no significant difference in misses or false alarms when comparing predictive and neutral cues [misses, predictive: 2.4%, neutral: 2.4%, t(31) = 0.11, p = 0.91, Cohen's d = 0.04; false alarms, predictive: 13.2%, neutral: 11.6%, t(31) = 0.94, p = 0.36, Cohen's d = 0.34]. This suggests that expected images were consciously identified more rapidly than unexpected images.

Taken together, Experiments 1 and 2 suggest that the expectation benefit defined above applies to both conscious *detection* and *identification* of visual stimuli. In both experiments participants gave the same behavioral response to expected, neutral, and unexpected stimuli, suggesting that response priming was not responsible for the expectation benefit. However, the results of Experiments 1 and 2 do not reveal what *type* of expectations caused these effects. Does the word "face" accelerate conscious access of a face image, simply because of pre-existing associations between the word "face" and images of faces? Or did our effects depend on the word cues explicitly predicting the occurrence of a specific image (i.e., the word "face" explicitly, and thus reliably, indicated that the most

likely image to appear was a face image). We investigated this issue in Experiment 3.

Experiment 3: Explicit expectations accelerate conscious access, but pre-existing associations do not

To investigate what type of expectations affect timing of conscious access, we tested three separate groups with three different types of cues: 3a, explicitly predictive word cues (e.g., the word "face" explicitly and reliably predicts the appearance of a face image); 3b, explicitly predictive symbol cues (e.g., a square reliably predicts the appearance of a house); or 3c, nonpredictive, but associative cues (e.g., the word "face" appears before a trial, which has a natural association with images of faces, but both a face and a house image are equally likely to appear after this word cue). Subjects in each group were informed whether the cue reliably predicted the appearance of a certain image or not (and if the cue was predictive, how predictive it was).

We reasoned that if explicit, reliable expectations drive our observed expectation benefit, then both predictive words (3a) and predictive symbols (3b) should accelerate response times to expected stimuli, whereas nonpredictive words (3c) should not. Alternatively, if pre-existing associations drive the expectation effect then response times should be accelerated in the word conditions (3a and 3c), but not in the (predictive but nonassociative) symbol condition (3b). Finally, if both explicit predictions and pre-existing associations drive the expectation benefit, then we should observe this benefit in all three cases.

Furthermore, we changed the paradigm (see Figure 3) in two ways. First, we divided the experiment into two sessions, a house and a face session. In each session there were only two cues, one neutral and one predictive cue (as opposed to two predictive cues in Experiments 1 and 2). In the house session, this meant that there was a neutral cue or a house cue, and in the face session, a neutral cue or a face cue. When determining the expectation benefit, we pooled the data of both sessions together (see Figure 3, panel A). Trials where cue and image matched (e.g., a house image following a house cue) were coded as expected trials. When cue and image mismatched (e.g., a face image following a house cue), the trials were coded as unexpected. Trials with a neutral cue were coded as neutral.

Second, in both sessions we had two trial types, recognition trials and breakthrough trials (see Figure 3, panel B). Breakthrough trials were the same as the trials in Experiment 1, where participants indicated whenever any image broke through the Mondrian

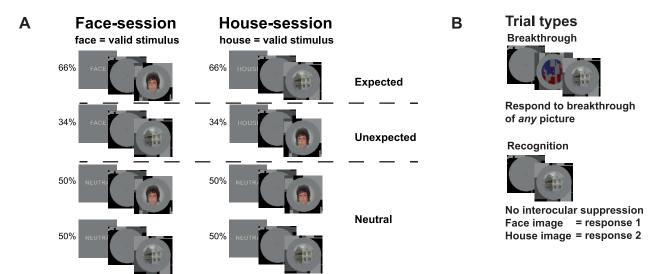


Figure 3. Design for Experiment 3. Panel A shows the two sessions per experiment, a face session and a house session. The order of these sessions was counterbalanced across participants. Trials from both sessions were combined to yield the expected (top), unexpected (middle), and neutral (bottom) conditions. The fraction depicted to the left of the cue indicates how often the shown image followed the cue (so the 66% at the top left means that the face cue in the face session was followed by a face image on 66% of the trials). Note that the percentages given here are for recognition trials. On breakthrough trials, after a predictive cue, 17% of the trials were unexpected, and 17% of the trials contained no image (catch trials). After a neutral cue, again 17% of the trials contained no image, while on the remainder of the trials houses and faces appeared with equal probability. Panel B shows the trial types of Experiment 3. On breakthrough trials, participants indicated whenever any image broke through to consciousness. On recognition trials, there was no interocular suppression; rather, an image was presented at full visibility to one eye, while nothing was presented to the other eye. Participants indicated whether the image was a house or a face.

masks. On recognition trials only one eye was presented with an image; nothing was presented to the other eye (so on recognition trials there was no interocular rivalry). On these trials participants pressed one key for a face image, and another for a house image.

We added these changes for two reasons. First, we wanted to reduce the number of cues per session (from three to two), to facilitate cue use. We reasoned that this could be crucial when employing symbolic cues. Second, the recognition trials allowed us to investigate the effect of a cue, independent of breakthrough against CFS. Suppose a cue type did not affect breakthrough, but it did affect recognition, then we would be able to conclude that the lack of an effect on breakthrough trials was not due to participants simply not processing the cue.

Methods

Experiment 3 was the same as Experiment 1, except for the following changes.

Participants

Experiment 3 was divided into Experiments 3a (40 participants, 34 females, age range: 18–35 years, average 22.2 years), 3b (39 participants, 31 females, age

range: 18–33 years, average 22.1 years), and 3c (47 participants, 36 females, age range 18–35 years, average 22.2 years). Different subjects participated in each subexperiment.

Procedure

Each subexperiment consisted of two sessions (a face session and a house session). Each session contained both recognition and breakthrough trials in equal numbers and randomly intermixed. So when a cue appeared, participants did not know whether a breakthrough trial or a recognition trial would follow—if a Mondrian mask appeared first, they knew it was a breakthrough trial; if a picture of a house or a face appeared without any Mondrian masks, they knew it was a recognition trial. Each session consisted of 10 blocks of 30 trials. The order of the sessions was counterbalanced across participants.

Experiment 3a employed cues that were both predictive and associative, that is, the word "face" reliably predicted (66% validity) that a face image would appear. So, on breakthrough trials, after a predictive cue (the word "face" in the face session, the word "house" in the house session) the predicted image would appear on 66% of the trials. The nonpredicted image (e.g., a house image after a face cue) would appear on 17% of the trials, and on the remainder of

the trials no image was presented after the cue (catch trials, on which participants had to withhold respond). On recognition trials a predictive cue was followed by the predicted image on 66% of the trials, and by the nonpredicted image on 34% of the trials (now catch trials were not needed, because a different response was given to both pictures). After a neutral cue on breakthrough trials, there were again 17% catch trials (on which no image appeared after the cue); on the remainder of the trials, both pictures had an equal chance of appearing. On recognition trials there were no catch trials, so both house and face pictures had a 50% chance of appearing after a neutral cue. Experiment 3b was identical to Experiment 3a, but now the word cues were replaced by symbol cues. For instance a square shape acted as a face cue (reliably predicting the appearance of a face picture), a triangle acted as a house cue, and a circle as a neutral cue. To exclude any effects due to potential pre-existing associations between symbols and images, we counterbalanced, across participants, which symbol predicted which image. Finally, Experiment 3c was the same as Experiment 3a, but now we employed nonpredictive word cues. These cues were only associative, but not predictive. In this case the words "face" or "house" were equally often followed by a house or face stimulus.

For each subexperiment, the ramping up of the contrast of the image (and the ramping down of the contrast of the Mondrian mask) lasted at most 4 s (unlike 6.5 s as in Experiments 1, 2, and 4), leading to faster response times in Experiment 3 than in the other experiments.

Data analysis

We coded face images appearing after a face cue, and house images after a house cue, as expected trials. Face images appearing after a house cue and house images after a face cue were coded as unexpected trials. Finally, face and house images appearing after a neutral cue were coded as neutral trials. In each subexperiment we compared response times on expected, neutral, and unexpected trials, for both breakthrough and recognition trials. In Experiment 3a two participants were excluded from analysis, in Experiment 3b four subjects were excluded, and in Experiment 3c two subjects were excluded, all due to high false alarm rates on breakthrough trials (>25%).

Results

The results of Experiment 3 are shown in Figure 4. First, we investigated response times on recognition trials. For each subexperiment we compared expected, neutral, and unexpected trials. This analysis indicated

that in all cases participants responded fastest on expected trials, and slowest on unexpected trials, indicating that in all subexperiments the cues were successfully processed (for all three cue types, one-way ANOVA with expectation as factor [expected, neutral, and unexpected] and response times as dependent variable: Fs > 13.5, ps < 0.001, $\eta^2 s > 0.23$).

Next we asked in each subexperiment, whether expectation affected response times on breakthrough trials. This analysis revealed that both predictive word and predictive symbol cues significantly affected response times (one-way ANOVA with expectation [expected, neutral, or unexpected]) as factor: predictive word: F(2, 74) = 17.28, p < 0.001, $\eta^2 = 0.32$; predictive symbol: F(2, 68) = 5.91, p = 0.004, $\eta^2 = 0.15$; but unpredictive word cues did not: F(2, 88) = 1.79, p =0.17, $\eta^2 = 0.04$. For both predictive cues (word and symbol), expected stimuli led to faster responses than unexpected stimuli: predictive word: t(37) = 4.71, p <0.001, Cohen's d = 1.55; predictive symbol: t(34) = 2.9, p = 0.007, Cohen's d = 0.99. For breakthrough trials, we performed a between-subjects comparison for the expectation benefit for the three different cue types. First, we calculated the ANOVA with between-subjects factor cue type (predictive word, predictive symbol, or unpredictive word) and within-subjects factor expectation (expected, neutral, or unexpected). This revealed a significant interaction, F(4, 230) = 4.13, p = 0.003, $\eta^2 =$ 0.07, showing that the type of cue mattered for the effects of expectation. Second, we calculated the expectation benefit for each cue type and analyzed whether these were significantly different. This analysis showed that the expectation benefit was significantly larger for predictive words than for unpredictive words, t(37) = 3.49, p < 0.001, Cohen's d = 1.15. However, no other significant differences in expectation benefit were found (other ts < 1.6, ps > 0.12).

Finally, as in Experiments 1 and 2, we compared misses and false alarms following predictive and neutral cues. For all three cue types (predictive words, predictive symbols, and unpredictive words), this revealed no significant differences between misses and false alarms after a predictive or a neutral cue (average misses, predictive cue: 3.2%, neutral: 3%, ts < 1.6, ps > 0.12, ds < 0.46; average false alarms, predictive cue: 5%, neutral: 5.2%, ts < 1.1, ps > 0.31, ds < 0.32).

Summarizing, the analysis of recognition trials revealed that in all subexperiments, participants processed the cues. Importantly, only predictive cues (predictive word or predictive symbol) accelerated response to expected stimuli on breakthrough trials, but unpredictive, associative word cues did not. This indicates that the main factors driving the expectation benefit are not pre-existing associations (in this case between a word and an image), but statistically reliable relations.

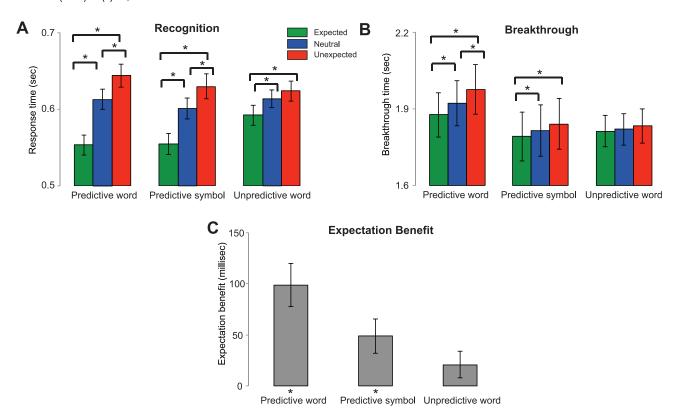


Figure 4. An overview of the results of Experiment 3. Panel A shows results from the recognition trials, Panel B from the breakthrough trials. Panel C shows the expectation benefit per cue type, for breakthrough trials. Asterisks denote significant differences between conditions. Asterisks beneath the *x*-axis indicate that the depicted benefit is significantly different from zero. The main finding is that although participants employed the cue in all conditions (top right panel), expectations only significantly accelerated conscious access when predictive. Error bars in the top panels indicate between-subjects standard errors; error bars in the bottom panel indicate within-subjects standard error.

Altogether, the results of Experiments 1, 2, and 3 suggest that valid expectations accelerate conscious access. However, the data so far have not excluded that our results are caused by the same mechanisms that influence the timing of subjective appearance of stimuli at attended locations. Specifically, attended stimuli can seem to appear before unattended stimuli, even when both stimuli physically appear at the same time (Carrasco & McElree, 2001; Spence & Parise, 2010). To investigate whether a similar effect could account for our results, we performed Experiment 4.

Experiment 4: CFS is required for expectations to accelerate conscious access

Situations in which attention modulates perceived stimulus timing typically involve unambiguous stimulus presentation (e.g., temporal order judgment tasks; Stelmach & Herdman, 1991; Zampini, Guest, Shore, & Spence, 2005). In contrast, expectations likely influence perception most strongly in cases where stimulus presentations are ambiguous, so that prior expectations can aid in resolving uncertainty (Clark, 2013; Howhy, 2013). Indeed, in Experiments 1, 2, and 3 the bottomup input was ambiguous (the stimulus picture was rivaling with flickering Mondrian patterns). We reasoned that if the findings of Experiments 1, 2, and 3 are caused by expectations affecting perception, then this ambiguity is crucial. In contrast, if the same mechanisms that drive temporal orders judgments underlie the current findings, then stimulus ambiguity should not play a significant role. In Experiment 4 we directly assessed the importance of ambiguity in the bottom-up signal by comparing the effect of expectations on trials with and without CFS. We reasoned that if the data of Experiments 1, 2, and 3 is indeed driven by expectations, then cues should affect response times only on CFS trials. However, if our results reflect attentional influences as in standard temporal order judgment tasks, then response times in both CFS and no-CFS trials should be affected by the cues.

To directly compare CFS to no-CFS trials we altered the recognition trials (containing no CFS) of Experiment 3. In Experiment 3, on recognition trials, a different response was given to expected and unexpected stimuli. This raises the possibility that the results of Experiment 3, on recognition trials, could be due to response priming, rather than changes in perception (which was irrelevant for Experiment 3, since in this experiment the recognition trials were only included to verify that the cue had been processed). To directly test whether perception was affected on no-CFS trials, we ensured that the task on CFS and no-CFS trials in Experiment 4 was identical. In both cases participants pressed one key whenever any picture appeared. Thus, we created two types of trials (CFS and no CFS) that were identical, except that only the CFS trials had stimulus ambiguity.

Methods

Experiment 4 was the same as Experiment 1 except for the following changes.

Participants

Thirty-nine healthy observers (30 females, age range: 18–24 years, average 20.3 years, normal or corrected-to-normal vision), naive to the purpose of this experiment, participated in this study after informed consent. The observers participated for monetary compensation (7 Euros per hour) or student credits. The study was approved by the Ethics Committee of the University of Amsterdam.

Procedure

Experiment 4 consisted of two sessions. In one session participants performed detection breakthrough trials. These trials were identical to the trials in Experiment 1. That is, flickering Mondrian patterns were presented to one eye, and an image of a house or a face (or no image) was presented to the other eye. The Mondrian patterns started at full contrast, the image at zero contrast, and over the course of 6.5 s, the Mondrians gradually changed from full contrast to no contrast, and over the same time course, the image gradually reached full contrast. Participants had to press space bar whenever any image broke through CFS, but withhold response when no image broke through. We called these trials CFS trials. In the other session, participants again had to press the space bar whenever any image appeared. However, in this case, when a picture was presented after cue offset, this picture was presented at full visibility to one (randomly chosen) eye 3–4.5 s after offset of the cue, and nothing

was presented to the other eye. We called these trials no-CFS trials. The task was the same as on CFS trials: Participants simply had to press the space bar whenever any image appeared, but withhold response when no image was presented. The order of blocks was counterbalanced across participants. The first session consisted of 11 blocks of 40 trials, and the first block was a practice block (these trials were not included in the analysis). The second session consisted of 10 blocks of 40 trials, so in the second session there was no practice block.

The trial structure was identical in both sessions. Before each trial a cue appeared. This cue could be face, house, or neutral. After each cue, no image appeared on 20% of the trials (catch trials). After a neutral cue there was an equal likelihood of either a face or a house image appearing. After a predictive cue, the indicated image was 3 times as likely to appear as the other stimulus category (so after a face cue, on 60% of the trials a face image would appear, 20% of the trials a house image, and on 20% of the trials no image). The participant pressed space bar whenever any image appeared.

Data analysis

One participant had more than 80% errors on the catch trials in the CFS condition. This participant was excluded from the analysis. We proceeded to analyze the response times for the correct trials in the following manner. Face images appearing after a face cue, and house images after a house cue were coded as expected trials. Face images after a house cue and house images after a face cue were coded as unexpected trials. Images appearing after a neutral cue were coded as neutral trials.

Results

Figure 5 shows an overview of the results of Experiment 4. The findings are straightforward. In line with previous experiments, on CFS trials, participants responded faster to expected images than to unexpected images (one-way ANOVA with expectation as factor [expected, neutral, or unexpected]), F(2, 74) = 4.2, p =0.02, $\eta^2 = 0.1$. A follow-up t test compared expected to unexpected images, t(37) = 2.66, p = 0.01, Cohen's d =0.87. With regards to misses and false alarms, as in Experiments 1, 2, and 3, there was no significant difference after a predictive or a neutral cue in false alarms; however, misses were slightly, but significantly higher after a neutral cue than after a predictive cue [misses, predictive: 1.1%, neutral: 1.4%, t(37) = 2.03, p =0.049, Cohen's d = 0.67; false alarms: predictive: 5.1%, neutral: 4.5%, t(37) = 0.73, p = 0.47, Cohen's d = 0.24].

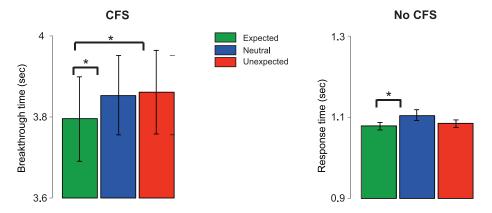


Figure 5. An overview of the results of Experiment 4. The left panel shows the results of the CFS trials; the right panel the no-CFS trials. Asterisks denote significant differences between conditions. The main finding is that expectations only accelerate conscious access, when the bottom-up input is ambiguous, supporting the idea that the "expectation benefit" we have found, across experiments, is driven by predictions. Error bars denote between-subjects standard error.

On no-CFS trials, we found an almost significant effect of expectations on response times (one-way ANOVA with expectation as factor [expected, neutral, or unexpected]), F(2, 74) = 2.98, p = 0.057, $\eta^2 = 0.07$. However, this was almost entirely due to response times being higher on neutral trials, than on expected and unexpected trials. Directly comparing response times on expected to unexpected trials revealed that, without CFS, expected images were not responded to faster than unexpected images, t(37) = 0.53, p = 0.6, Cohen's d = 0.17. Moreover, directly comparing the expectation benefit on CFS trials to the expectation benefit on no-CFS trials revealed a significantly larger expectation benefit on CFS trials, t(37) = 2.1, p = 0.04, Cohen's d = 0.69.

Summarizing, the results of Experiment 4 suggest that expectations only accelerate conscious access when sensory input is ambiguous. This supports the idea that the expectation benefit emerges from predictive effects on conscious perception, and not through mechanisms that underlie attentional influences in temporal order judgment tasks. However, note that reaction times in the no-CFS condition may be showing a floor effect, which could obscure expectation effects. Indeed, because of the pervasiveness of attentional effects in perception, Experiment 4 cannot fully exclude all possible attentional effects. Interactions between expectation and attention are complex and remain incompletely understood (e.g., Kok, Rahney, Jehee, Lau, & de Lange, 2012; Summerfield & Egner, 2009). In other words, we recognize the possibility that attentional effects (perhaps in combination with partial breakthrough) could contribute to the findings of Experiments 1, 2, 3, and 4 (Attarha & Moore, 2015; Stein et al., 2011). However, the most parsimonious interpretation of the results across experiments remains that valid expectations accelerate conscious access.

Aggregate analysis

We investigated whether our results were outlierdriven by examining median rather than mean reaction times. We performed the analysis on the aggregate data of Experiments 1, 2, 3, and 4 (excluding Experiment 3c, because this was the only experiment without predictive effects). For both measures, response times to expected stimuli were faster than to unexpected stimuli, and to neutral stimuli [mean, expected vs. unexpected: t(175) =5.7, p < 0.001, Cohen's d = 0.86; expected vs. neutral: t(175) = 4.52, p < 0.001, Cohen's d = 0.68; median, expected vs. unexpected: t(175) = 5.86, p < 0.001, Cohen's d = 0.89; expected vs. neutral: t(175) = 4.79, p < 0.001, Cohen's d = 0.72]. Moreover, the difference between expected and unexpected or neutral trials was statistically similar for both measures [mean vs. median, difference between expected and unexpected: t(175) = 1.41, p = 0.16, Cohen's d = 0.21; difference between expected and neutral: t(175) = 1.26, p = 0.21, Cohen's d = 0.19].

General discussion

Over four separate psychophysical experiments we have described data indicating that expected visual stimuli gain access to consciousness more rapidly than either neutral or unexpected stimuli. Altogether, our data suggest that this "expectation benefit" holds for both detection and identification, and is not caused by response priming or by attentional influences that drive asynchronous perception of simultaneously presented stimuli in temporal order judgment tasks. Furthermore, the findings of Experiment 3 suggest that our results depend on explicit short-term expectations: Overlearned pre-existing stimulus—stimulus associations produced no expectation benefit. We interpret our

results to support the hypothesis that verification of internally generated predictions determine conscious contents in visual processing. These results are consistent with, but substantially extend, previous findings, most importantly by showing a direct and specific effect of transient expectations on the timing of conscious access.

We recognize that while our current data support the notion that valid expectations accelerate how fast stimuli gain access to consciousness, they do not conclusively prove this. Generally, CFS studies have several important caveats. As mentioned earlier, breakthrough is not necessarily wholesale, but can also be partial (Gayet et al., 2014; Stein & Sterzer, 2014; Stein et al., 2011). This creates the possibility that CFS findings are not solely due to changes in perception, but perhaps (also) due to changes in decision criteria or response biases (Attarha & Moore, 2015; Gayet et al., 2014; Yang et al., 2014). We have tried to control for response biases by having participants give the same response to all stimuli (i.e., in Experiments 1, 3, and 4: Press space bar for *any* stimulus; in Experiment 2: Press 1 for both houses and faces). Furthermore, the absence of significant differences between misses and false alarms after predictive and neutral cues suggests that participants did not change their criterion in response to the cue. However, this does not fully exclude the possibility that subtle response biases or criterion changes, perhaps in combination with partial breakthrough, contributed to the current findings. To further clarify these issues, future neural investigations could play an important role. Such studies may unveil the time course and the primary neural sources of expectation benefits. For instance, it would be highly informative to examine whether expectations have early neural effects, before breakthrough, or whether expectation effects are only observed later in time, during or after breakthrough. In the first scenario, our results are likely perceptually driven. If the second scenario holds, then response biases or criterion shifts may play a role.

Our results are compatible with the extensive literature describing how expectations affect language perception, visual search, and the perception of ambiguous or noisy stimuli (Eger, Henson, Driver, & Dolan, 2007; Sterzer, Frith, & Petrovic, 2008; Summerfield & Egner, 2009). In these studies it is generally found that cognitive ability (language comprehension, search efficiency) is improved by having congruent expectations or context. Our results also follow previous studies showing that ambiguous perception is influenced by expectations. For instance, Sterzer et al. (2008) found that subjects are likely to see ambiguous motion going in the expected direction.

Our data are closely related to, but substantially extend, recent findings presented by Costello et al. (2009) and Lupyan and Ward (2013). Costello et al.

(2009) reported that visual words broke through CFS more quickly, when a semantically associated word was (visually) presented beforehand. For example, after subjects viewed the word "salt," the word "pepper" broke through CFS more rapidly than when the first word lacked semantic association with the suppressed word. This result seems at odds with our Experiment 3, which shows that pre-existing associations do not provide an expectation benefit. However, in the Costello study, participants performed 80 trials, while in our experiment, participants performed 10 blocks of 30 trials (i.e., 300 trials in total). Interestingly, if we only consider the first block of 30 trials in our data, we also find that nonpredictive associations accelerate conscious access (ANOVA with word-image associations [matched, neutral, or unmatched]) as factor: F(2,88) = 4.77, p = 0.011, $\eta^2 = 0.1$; follow-up t test, expected vs. unexpected trials: t(44) = 2.92, p = 0.005, Cohen's d = 0.88. However, this effect quickly disappears with increasing trial numbers, indicating that new associations can quickly be learned, and just as quickly unlearned (Nieuwland & Van Berkum, 2006). Lupyan and Ward (2013) found an effect of a preceding cue on breakthrough against CFS; however, we crucially extended these findings by showing that only explicitly predictive cues affect breakthrough (Experiment 3), that these breakthrough effects are likely not the same as attention affecting temporal order judgments (Experiment 4), and that the effects are similar for detection and discrimination.

A striking discrepancy seems to exist between the main finding of our current study—that valid expectations accelerate conscious access—and the findings of Mudrik et al. (Mudrik, Breska, et al., 2011; Mudrik, Deouell, & Lamy, 2011) and Sklar et al. (2012). In these studies it was found that unexpected scenes (such as a person placing a chess board, instead of a plate of cookies, into an oven) or incongruent short sentences ("I ironed coffee") gained conscious access more quickly under CFS, and that incongruent scenes dominate more frequently during binocular rivalry. However, our study differs from these previous studies in at least two important ways. First, in these previous studies high-level influences were confounded with lowlevel differences (although Mudrick, Breska et al. [2011] did control for several important low-level factors such as contrast and brightness, a plate of cookies still, inevitably, has different low-level properties than a chess board). Yet, even small stimulus changes can influence the effectiveness of an interocular suppressive mask (Yang & Blake, 2012). Second, as acknowledged by Mudrick, Deouell, & Lamy (2011), dominance during binocular rivalry may simply reflect increased attention to a scene or image after it reaches awareness. This altered state of attention may subsequently affect how long an image remains dominant during binocular rivalry (Chong, Tadin, & Blake, 2005).

In summary, our findings indicate that explicit prior expectations can accelerate access of visual stimuli to consciousness in a way that resists explanation by alternative accounts including response bias, response priming, or pre-existing associations. These results have implications for predictive processing accounts of perception (e.g., Clark, 2013; Howhy, 2013) by suggesting that the timing of conscious access depends on validation of perceptual predictions rather than on mismatches between predictions and sensory input. More generally our results suggest that top-down factors can significantly influence the mechanisms that drive the timing of transitions from unconscious to conscious processing.

Keywords: consciousness, predictive coding, continuous flash suppression, expectations, attentional set

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