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Report

The Functional Impact of Mental Imagery on Conscious Perception

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Summary

Mental imagery has been proposed to contribute to a variety of high-level cognitive functions, including memory encoding and retrieval, navigation, spatial planning, and even social communication and language comprehension [1–5]. However, it is debated whether mental imagery relies on the same sensory representations as perception [1, 6–10], and if so, what functional consequences such an overlap might have on perception itself. We report novel evidence that single instances of imagery can have a pronounced facilitatory influence on subsequent conscious perception. Either seeing or imagining a specific pattern could strongly bias which of two competing stimuli reach awareness during binocular rivalry. Effects of imagery and perception were location and orientation specific, accumulated in strength over time, and survived an intervening visual task lasting several seconds prior to presentation of the rivalry display. Interestingly, effects of imagery differed from those of feature-based attention. The results demonstrate that imagery, in the absence of any incoming visual signals, leads to the formation of a short-term sensory trace that can bias future perception, suggesting a means by which high-level processes that support imagination and memory retrieval may shape low-level sensory representations.

Results

We devised a novel paradigm to isolate the phenomenal contents of mental imagery by measuring its impact on subsequent perception. The experiments capitalize on the bistable phenomenon of binocular rivalry, in which conflicting visual patterns, presented one to each eye, lead to competitive interactions in the visual cortex such that only one monocular pattern becomes exclusively dominant in perception [11, 12]. We hypothesized that the impact of visual imagery on conscious perception might be revealed under these bistable perceptual conditions; specifically, imagery might alter the balance of competitive visual interactions in favor of the imagined pattern.

The rivalry display consisted of a green vertical grating shown to the left eye and a red horizontal grating shown to the right eye. We adjusted the relative strength of the two stimuli to minimize any pre-existing eye bias an observer might have (see Supplemental Experimental Procedures available online). In Experiment 1, the rivalry display was briefly shown once every 10.75 s, and observers reported which of the two patterns appeared dominant after each presentation (Figure 1A). Under conditions of passive viewing, observers were more likely to perceive a given pattern if the same pattern appeared dominant on the preceding trial (Figure 1B, gray bar). This persistence of rivalry dominance across successive presentations (i.e., perceptual stabilization) is believed to reflect the automatic formation of a sensory memory that can bias subsequent perception in a facilitatory manner [13, 14]. Here, the level of perceptual stabilization during passive viewing was ~80%, consistent with previous studies [13–16].

To investigate the effects of imagery, observers were instructed to imagine one of the two rivalry patterns during the blank intervening period between presentations, either the pattern that was dominant or the pattern that was suppressed on the preceding rivalry presentation. Imagery of the previously dominant pattern led to somewhat higher levels of perceptual stability relative to passive viewing (Figure 1B, white bar), whereas imagery of the previously suppressed pattern led to much lower levels of perceptual stability (Figure 1B, black bar). Thus, imagery biased subsequent perception in favor of the imagined pattern. These facilitatory effects were reliable in individual observers (Figure S1). A control experiment confirmed that naive observers showed these imagery effects only for rivalry displays and not for catch-trial presentations of mock-rivalry displays (Figure S2). This suggests that the facilitatory effects of imagery are perceptual in nature and unlikely to reflect decisional bias.

In subsequent experiments, we investigated whether these effects of imagery can be mimicked by viewing a faint pattern (experiment 2), enhanced by longer periods of imagery (experiment 3), impaired by the presence of a bright background (experiment 4), and disrupted by changes in orientation or retinotopic location (experiment 5). For experiments 2–4, observers reported which pattern appeared dominant on each rivalry presentation, after which they were shown or instructed to imagine the pattern that had just been suppressed so that its effect on the stability of subsequent rivalry could be determined. If perceptual stability fell significantly below the level found with passive viewing of a blank screen (~80%), this indicated bias in favor of the previously suppressed pattern. Experiment 5 used a different design; the viewed or imagined pattern was randomly selected on each trial, and its impact on subsequent rivalry perception was measured. Perceptual facilitation was indicated if the seen or imagined pattern appeared dominant on the next rivalry presentation more often than 50% of the time.

Weak Visual Stimulation Resembles the Effects of Imagery

In experiment 2, we investigated the consequences of passively viewing a single physical pattern between intermittent rivalry presentations. Shortly after each rivalry presentation, observers were shown the pattern they reported as suppressed for a 4 s period (Figure 2A), and this pattern's influence on subsequent rivalry perception was measured. We hypothesized that imagery might be mimicking the effects of weak visual stimulation and therefore parametrically varied the

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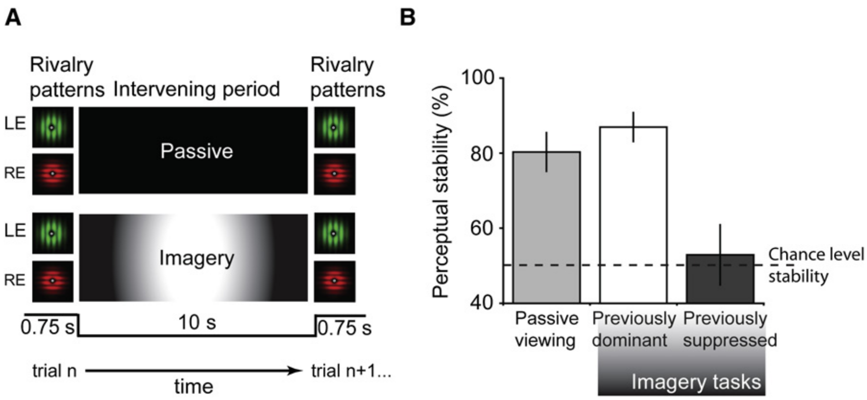

Figure 1. Effects of Mental Imagery on Subsequent Perceptual Dominance in Rivalry

(A) Visual stimuli and timing of events. A rivalry display was presented every 10.75 s, and observers reported which of the two rival patterns appeared dominant. During the 10 s blank interval following each presentation, observers were instructed either to maintain fixation passively or to imagine the pattern that was dominant or suppressed on the previous rivalry presentation.
(B) Results showing perceptual stability across successive rivalry presentations (N = 7). Observers tended to perceive the same pattern across successive presentations during passive viewing (perceptual stability ~ 80%, chance level 50%). Imagery led to significant changes in perceptual stability (F = 21.3, $p < 0.0005$). Whereas imagery of the previously dominant pattern led to somewhat higher levels of perceptual stability than passive viewing (t = *1.9*; $p = 0.10$), imagery of the previous suppressed pattern led to significantly lower levels of perceptual stability (t = 4.5; $p < 0.005$). Error bars represent ±1 SEM.

intensity of this intervening stimulus. Perceptual stability was severely disrupted when the intervening pattern was shown at fairly low luminance levels, corresponding to ~40% of the intensity of the rivalry stimuli (Figure 2B). Further decreases in stimulus luminance led to weaker disruptive effects that eventually reached the level found for passively viewing a blank screen (i.e., 0% luminance). Similar results were obtained for manipulations of stimulus contrast (Figures 2C and 2D), indicating that prior viewing of either a low-luminance or low-contrast pattern can facilitate subsequent perception of that pattern during rivalry.

The facilitatory effects of weak visual stimulation cannot be explained in terms of immediate sensory interactions [17], given the 3 s gap between presentations of the intervening pattern and the subsequent rivalry display. Moreover, these facilitatory effects cannot be explained in terms of neural adaptation or fatigue because prior adaptation to a strong visual pattern is known to weaken both neural responses [18] and subsequent dominance in binocular rivalry [17, 19, 20]. Instead, it seems that passive viewing of a weak physical pattern leads to the formation of a specific perceptual trace, which can facilitate perception of that same pattern at a later time during rivalry. After strong visual stimulation, however, the benefits of this perceptual trace may be masked by counteracting effects of neural adaptation. In the following experiments, we directly compared imagery with passive viewing of faint visual patterns (shown at 40% of the intensity of the rivalry pattern).

Facilitatory Effects of Imagery and Weak Stimulation Accumulate over Time

To what extent does imagery resemble weak visual stimulation, and might both lead to the formation of a short-term perceptual trace? We reasoned that if these short-term facilitation effects resulted from the formation of a physiological trace, then the strength of that trace should increase with prolonged durations of imagery or direct stimulation. Also, if the short-term trace is truly sensory and not dependent on active maintenance [21], then once formed, this trace should persist for brief periods even when the observer must attend to another visual task.

Experiment 3 had the following design: After each rivalry presentation, observers viewed or imagined the previously suppressed pattern for a variable duration of 1–15 s (Figure 3A). Next they performed a challenging discrimination task,

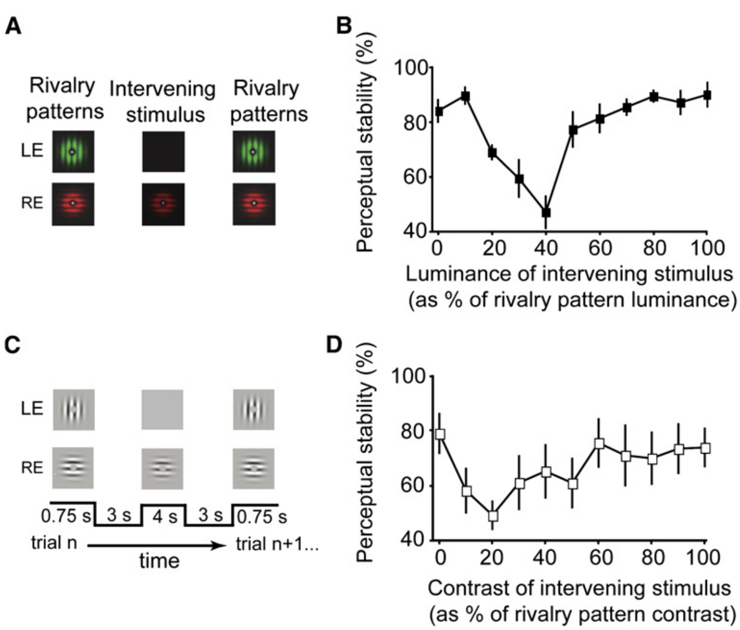

Figure 2. Effects of Weak Visual Stimuli on Subsequent Dominance in Rivalry

(A) Rivalry displays were presented every 10.75 s. An intervening stimulus was presented for a 4 s period between rivalry presentations, consisting of the oriented pattern that was suppressed on the previous rivalry presentation. Luminance of the intervening stimulus was varied across blocks of trials.
(B) Perceptual stability across successive rivalry presentations, plotted as a function of the luminance of the intervening stimulus (N = 5). The intervening stimulus was most effective at disrupting perceptual stability at modest luminance levels, corresponding to ~40% of the mean luminance of the rivalry patterns. Note that lower levels of perceptual stability indicate that rivalry dominance is biased in favor of the intervening pattern.
(C) Same experimental design as in (A), but with luminance-defined Gabor gratings presented on a mean luminance background.
(D) Perceptual stability across successive rivalry presentations, plotted as a function of contrast (N = 5). Contrast values are reported relative to the full contrast of the rivalry patterns, which was 70% Michelson contrast. Errors bars represent ± 1 SEM.

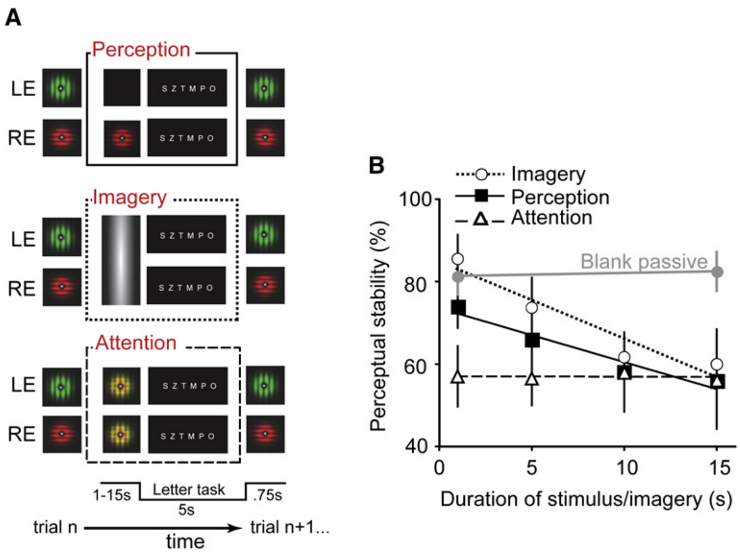

Figure 3. Effects of Task Duration for Perception, Imagery, and Attention

(A) Experimental design. After each rivalry presentation, observers viewed, imagined, or attended to the previously suppressed rivalry pattern for a variable duration (1–15 s), then performed a challenging letter-discrimination task.

(B) Perceptual stability across successive rivalry presentations, plotted as a function of task duration (N = 5). Disruptive effects of perception and imagery significantly increased over time, as indicated by repeated-measures ANOVA ($F = 9.8$, $p < 0.001$), with no reliable difference found between these two conditions (main effect, $F = 3.4$, $p = 0.138$; task × duration interaction, $F = 1.4$, $p = 0.30$). By contrast, feature-based attention strongly disrupted perceptual stability after just 1 s of viewing the plaid stimulus and did not change in strength as a function of task duration ($F = 0.03$, $p = 0.99$). Effects of feature-based attention over time differed from those of imagery and perception, as indicated by a significant interaction effect ($F = 2.77$, $p < 0.05$). In the blank passive condition (gray circles), each rivalry presentation was followed by passive viewing of a blank screen for 1 or 15 s and then the letter-discrimination task. Perceptual stability was unaffected by varying the duration of passive viewing of a blank screen. Plots show linear fits to the data. Errors bars represent ±1 SEM.

identifying letters presented rapidly at fixation over a 5 s period (performance accuracy ~ 70% correct), until the following rivalry display appeared: We designed the letter task to prevent active maintenance of the imagined pattern, thereby allowing us to determine whether the underlying trace could be passively maintained over this delay period.

Longer periods of viewing the physical pattern led to lower levels of perceptual stability (Figure 3B, perception condition), indicating enhanced facilitation and a build-up in the strength of the underlying perceptual trace. (Control experiments revealed no change in perceptual stability when observers passively viewed a blank screen for variable durations.) Longer periods of imagery also led to stronger facilitatory effects (Figure 3B, dotted line), and remarkably, these effects were comparable in strength to those obtained by viewing the physical pattern. The results imply that prolonged mental imagery leads to the gradual accumulation of a perceptual trace, much like the effect of weak perception. After this trace is formed, it can persist for short periods while the observer is actively engaged in another visual task.

Differential Effects of Imagery and Feature-Based Attention

In experiment 3, we also tested for facilitatory effects of feature-based attention, which has been found to modulate rivalry perception to some extent [22–25]. By feature-based attention, we refer to the ability to attend selectively to one of multiple overlapping features occupying a common region of space. Between rivalry presentations, the physical sum of both rivalry patterns was presented to both eyes as a stable composite plaid (see Figure 3A, bottom), and observers were instructed to attend to one of the patterns. An initial experiment revealed facilitatory effects of attention (Figure S3) similar to the imagery effects found in experiment 1.

For experiment 3, the plaid stimulus was presented for 1–15 s, and the letter-discrimination task and the subsequent rivalry display followed. Facilitatory effects of feature-based attention emerged in full strength after just 1 s of performing this task (Figure 3B), unlike the gradual build-up found for imagery and weak visual stimulation. This difference in the time needed for attention to bias rivalry indicates that the effects of imagery can be distinguished from those of feature-based attention.

We also explored whether manipulations of background luminance might reveal differences between the top-down effects of imagery and attention. In early pilot studies, some observers reported difficulty with forming a vivid mental image while viewing a lit background, so we switched to a dark background instead. In experiment 4, however, we purposely manipulated the luminance of the background while subjects performed the imagery or feature-based attention task. Background luminance was set to 0, 25, 50, or 100% of the mean luminance of the rivalry patterns on separate blocks of trials.

Feature-based attention could strongly disrupt perceptual stability at all luminance levels, with no reliable difference between conditions (Figure 4). By contrast, imagery became less effective at disrupting rivalry at higher luminance levels, such that perceptual stability in the 100% luminance condition was no different from control conditions of passive viewing ($t = 0.34$; $p = 0.76$). Given that subjects attempted to perform the same imagery task across variations in background

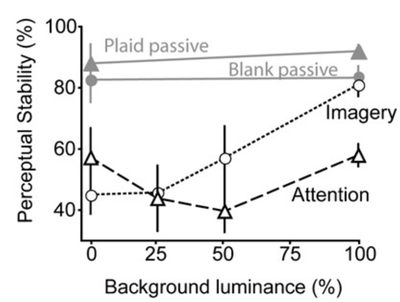

Figure 4. Influence of Background Luminance on Disruptive Effects of Imagery and Feature-Based Attention

Observers either imagined or attended to the pattern that was suppressed on the previous rivalry presentation (N = 4), and the luminance of the background varied across different blocks of trials. Bias effects of imagery were disrupted at higher luminance levels ($F = 5.2$, $p < 0.05$) and thereby significantly differed from bias effects of feature-based attention (ANOVA interaction effect, $F = 5.55$, $p < 0.05$; effect of condition $F = 16.8$, $p < 0.05$). In comparison, perceptual stability of rivalry remained high when observers passively viewed a blank screen (filled circles) or a plaid stimulus (filled triangles) between rivalry presentations, independent of background luminance level. Thus, variations in luminance level alone do not affect the stability of rivalry perception. Error bars represent ±SEM.

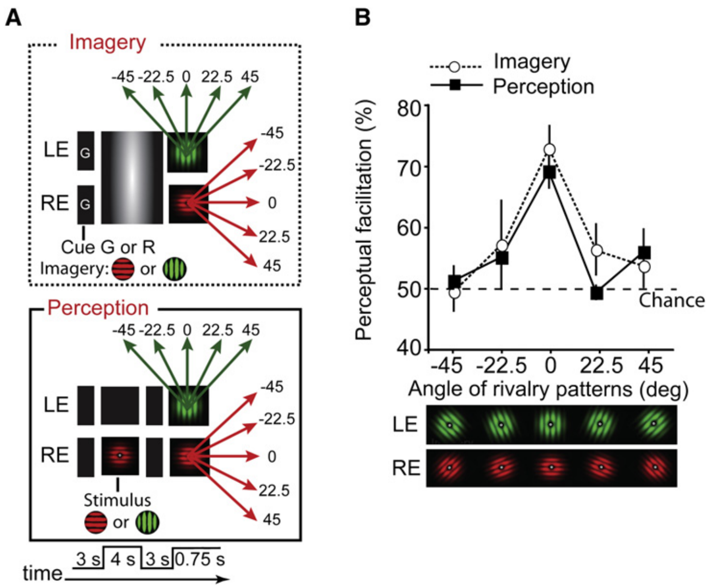

Figure 5. Orientation-Specific Bias of Rivalry Perception

(A) Experimental design and stimuli. In the imagery condition, observers were randomly cued to imagine either a vertical green or a horizontal red grating, and then two orthogonal rivaling patterns were presented 7 s later. On each trial, the rivalry display was rotated by −45°, −22.5°, 0°, +22.5°, or +45°. Both patterns were always rotated the same amount, thereby maintaining orthogonality. In the perception condition, either a vertical green grating or a horizontal red grating was shown for 4 s, a 3 s delay followed, and then the rivalry display was shown at one of the 5 possible angles.

(B) Rivalry dominance was most strongly biased in favor of the previously seen or imagined pattern for rivalry displays sharing the same orientation (N = 5, data sorted by angular difference between cued grating and rivalry test pattern). Analysis of variance revealed reliable effects of orientation bias for imagery ($F = 4.4$, $p < 0.05$) and perception ($F = 6.2$, $p < 0.005$), with no statistical difference between these conditions ($p = 0.66$). Error bars represent ±1 SEM.

luminance, such interference by a uniformly lit background implies that these bias effects are attributable to imagery per se, rather than other aspects of the task instructions.

Orientation Specificity of Imagery

Finally, we investigated the visual specificity of imagery by probing the effects of orientation, a property that is strongly represented in early visual areas [26, 27]. We hypothesized that if mental imagery can activate orientation-selective neurons and lead to the formation of an orientation-selective trace, then subsequent perception should be facilitated only when the imagined orientation closely matches the physical orientation of one of the rivaling patterns.

Experiment 5 introduced a randomized-trial design. On each trial, the grating to be seen or imagined was randomly determined and its influence on subsequent rivalry dominance was measured (Figure 5A). For the imagery task, a randomized cue indicated whether to imagine the green vertical grating or red horizontal grating for 4 s. In the perception condition, an actual grating was presented in place of the imagery task. Next, orthogonal rivalry patterns were presented, both rotated by −45°, −22.5°, 0°, +22.5°, or +45° on any given trial. If rivalry perception was biased in favor of the previously seen or imagined pattern on more than 50% of the trials, this indicated a perceptual facilitation effect.

Analysis of individual trials revealed orientation-dependent effects of mental imagery (Figure 5B), with the strongest perceptual facilitation found for matching orientations (average bias 74%, chance level 50%) and progressively weaker effects found for differing orientations. Perception of an intervening physical pattern led to the same orientation-dependent pattern of results.

A further experiment confirmed that facilitatory effects of imagery were specific to retinotopic location. Observers showed strong facilitation when imagery was performed at the same location as the subsequent rivalry patterns but no facilitation when locations differed (Figure S4). (Similar location-specific effects were observed for feature-based attention, indicating local rather than global facilitation of the attended feature [28].) Taken together, the results suggest that imagery leads to the formation of a precise sensory trace that is specific to both orientation and retinotopic location.

Discussion

This study demonstrates that single episodes of mental imagery can have a powerful functional impact on the outcome of conscious perception. Both imagery and perception led to the formation of a visually specific short-term trace that could bias subsequent perception of ambiguous stimuli in a precise manner. These findings are important because they suggest a potential mechanism by which top-down expectations or recollections of previous experiences might shape perception itself.

Our findings provide strong support for perceptually based theories of imagery [1]. Evidence is mixed regarding whether mental images can provide a veridical representation of stimuli after their removal [29–31]. Studies in favor of the perceptual nature of imagery have found that the active maintenance of mental images can sometimes interfere with perception [32–34] or facilitate perception in a stimulus-specific manner [35, 36]. Because imagery and perception tasks were performed concurrently in previous studies, a potential concern is that the imagery task might alter how subjects attend to the test stimulus. If so, then perceptual effects observed during mental imagery might reflect the byproduct of interactions between attention and incoming sensory signals [6, 35–38]. Our study addressed these concerns by separating imagery and perception tasks in time, thereby allowing subjects to perform imagery in the absence of any incoming sensory signals. In addition, we found novel evidence suggesting that the effects of feature-based attention can be distinguished from those of imagery.

This study also reveals how different forms of top-down influence can alter the balance of perceptual competition during rivalry [11, 12]. Binocular rivalry is strongly influenced by the low-level stimulus manipulations [39] but can also be biased by feature-based attention [22–25]. Here, we found novel evidence that top-down effects of mental imagery can bias perceptual competition in rivalry, suggesting that endogenously generated activity may also have a role in resolving perceptual ambiguity.

What type of memory might support these perceptual facilitation effects? Longer periods of imagery or perception led to stronger facilitation effects, which could survive for several seconds while subjects performed another visual task. Thus, the duration of this perceptual trace extends well beyond that of iconic memory, which lasts only a few hundred milliseconds [40]. The graded and automatic nature of this memory also differs from traditional descriptions of working memory, which involves all-or-none encoding of discrete items and their active maintenance to prevent memory decay [21]. Instead, this short-term perceptual facilitation resembles the effects of perceptual priming [41], which can be quite specific to the features and location of a previously seen stimulus [17, 42–44]. It is striking to consider that "perceptual priming" might be elicited without perception, by simply imagining a previous perceptual experience.

Supplemental Data

Experimental procedures and four figures are available at http://www.current-biology.com/cgi/content/full/18/13/982/DC1/.

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Note Added in Proof

This version differs from the one previously published online in that changes in the affiliations and in Dr. Clifford's middle initials, which incorrectly appeared as "W.C.," have been corrected here.