Research Article

Processing of Invisible Stimuli

Advantage of Upright Faces and Recognizable Words in Overcoming Interocular Suppression

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ABSTRACT—*Familiar and recognizable stimuli enjoy an advantage of predominance during binocular rivalry, and this advantage is usually attributed to their enhanced processing during the dominant phase. However, do familiar and recognizable stimuli have an advantage in breaking suppression? Test images were gradually introduced to one eye to compete against a standard high-contrast dynamic noise pattern presented to the other eye. Results showed that an upright face took less time than an upside-down face to gain dominance against the identical suppression noise. Results also showed that for Chinese readers, Chinese characters were faster to gain dominance than Hebrew words, whereas for Hebrew readers, the reverse was true. These results suggest that familiar and recognizable information, even when suppressed and invisible, is processed differently from unfamiliar information. Apparently, high-level information about visual form does contribute to the strength of a stimulus during its suppressed phase.*

Binocular rivalry refers to the alternations in perception that occur when two different images are presented dichoptically to the two eyes. It is generally believed that rivalry results from the multiple stages of mutual inhibition between neural populations coding for the competing images features, with the neurons generating the dominant image at a given time inhibiting the neurons responding to the suppressed image. Previous studies have shown that perceptual switching occurs when the dominant signal adapts over time and eventually becomes weaker than the signal of the suppressed stimulus (Blake, 1989; Lehky, 1988; Mueller, 1990; Sugie, 1982; Wilson, Blake, & Lee, 2001). It has also been suggested that dominance and suppression rely on distinct neural processes (Blake & Logothetis, 2002). In other words, neural processes that amplify the salience of a dominant target are not necessarily engaged during the suppression phase of rivalry.

Several studies have demonstrated that high-order organizational structures of an image influence its probability of dominance during rivalry. For example, during rivalry, an upright face generally prevails when paired with an inverted face (Engel, 1956). During piecewise rivalry, parts of an object can be grouped into one coherent image through global organizational processes (Kovacs, Papathomas, Yang, & Feher, 1996). It has also been found that the texture patches forming a "Dalmatian Dog" dominate during rivalry more than similar stimuli that cannot be perceptually grouped into a coherent and meaningful object (Yu & Blake, 1992). Remarkably, this effect was obtained even before observers were aware of the embedded "dog," which indicates that the greater dominance of a structured figure does not necessarily depend on actual recognition of that figure. However, all these effects can be interpreted as due to enhancement of the structurally meaningful object during its dominant phases, with or without the observers' awareness of the structure. It is difficult to infer whether the meaningful (familiar) stimuli are processed any differently from their meaningless (unfamiliar) control stimuli during the suppressed phases.

Evidence seems to suggest that the answer to this question is "no," that high-level information is not represented during the suppression phases of rivalry. For example, a number of studies have examined the adaptation and priming effects of a stimulus during rivalry. Low-level features such as stimulus orientation, spatial frequency, and linear motion tend to show a preserved adaptation effect during rivalry (Blake & Fox, 1974; Lehmkuhle & Fox, 1975; Wade & Wenderoth, 1978), although new evidence shows that rivalry suppression can reduce the strength of low-level adaptation (Blake, Tadin, Sobel, Raissian, & Chong, 2006; Tsuchiya & Koch, 2005). However, object or semantic information about the suppressed stimulus is not able to generate an aftereffect (Moradi, Koch, & Shimojo, 2005) or priming effect, a

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result vividly summarized as "out of sight, out of mind" (Zimba & Blake, 1983). The different fates of low- and high-level information during rivalry suppression are consistent with the idea that some visual processing occurs before and other processing occurs after the neural site (or sites) of rivalry. This idea is also consistent with neurophysiological results showing that from primary visual cortex to extrastriate areas to inferior temporal cortex, neuronal responses become increasingly correlated with the alternating perception (Sheinberg & Logothetis, 1997). Neuroimaging studies paint a more complex picture, showing that brain activation is correlated with perceptual alternations from as early as V1 and lateral geniculate nucleus (Tong & Engel, 2001; Wunderlich, Schneider, & Kastner, 2005), and that this correlation carries all the way to the fusiform face and object-sensitive areas (Tong, Nakayama, Vaughan, & Kanwisher, 1998).

However, although some studies suggest that high-level information is not processed and represented during the suppression phase of rivalry, recent neuroimaging studies have demonstrated the contrary, at least for certain types of high-level information. For example, under interocular suppression, emotional faces generate stronger responses in the amygdala than neutral faces (Williams, Morris, McGlone, Abbott, & Mattingley, 2004) and nonface objects (Pasley, Mayes, & Schultz, 2004), and suppressed images of tools can activate dorsal cortical areas (Fang & He, 2005). These findings suggest that considerable information, including object category information about the suppressed stimulus, is processed in cortical and subcortical structures. However, this possibility seems to be at odds with the earlier conclusion that object shape and semantic information do not seem to be extracted and represented during suppression, as they fail to generate an aftereffect or priming effect.

To directly measure the effect of higher-level information such as meaning and familiarity of stimuli during suppression, we adopted a single-trial paradigm measuring the time needed for a stimulus to break from suppression. The critical manipulation was the familiarity (upright vs. inverted face) or recognizability (words in native vs. unknown language) of the test image. Briefly, there were three key components to our approach. First, the test stimuli were competing against the same noise pattern. Second, in each trial, as soon as the observer detected the stimulus or any part of it, the trial stopped. This ensured that the key factor influencing the dependent variable (suppression duration) was operating while the stimulus remained invisible. Third, the dynamic suppression noise was presented immediately at full contrast, whereas the target stimuli were gradually ramped up. This ensured that the noise was the dominant percept at the beginning of each trial.

This approach provided several advantages over the commonly used paradigm, in which average dominance durations are measured for paired stimuli (target vs. control, e.g., an upright face against an inverted face) engaged in many cycles of rivalry. One of the advantages was that our design maximally reduced the influence of a nonexclusive rivalry stage because the observers were asked to make a response as soon as they detected the target stimulus, whether the whole stimulus or just part of it. The second advantage was that the two conditions under comparison (e.g., upright face vs. inverted face) were not competing against each other, in which case it would be difficult if not impossible to determine whether reduced dominance duration of one object compared with the other was due to the effectiveness of the suppressed stimulus or the ineffectiveness of the suppressing stimulus (e.g., stronger upright face or weaker inverted face?). We arranged to have the two stimuli of interest compete against the same noise pattern. This ensured that the suppression times of the target and control stimuli could be interpreted more precisely.

METHOD

Subjects

Ten observers (4 male) participated in Experiment 1. Eight native Chinese speakers (4 male), 8 native English speakers (5 male), and 6 native Hebrew speakers (4 male) participated in Experiment 2. Although they are identified here as native speakers of Chinese, English, and Hebrew, the Chinese speakers and Hebrew speakers were expert readers of Chinese and Hebrew, respectively. Subjects identified as native English speakers could read neither Chinese nor Hebrew. All subjects had college degrees. They had normal or corrected-to-normal vision; their age range was from 23 to 40. Subjects gave written informed consent in accordance with procedures and protocols approved by the human-subjects review committee of the University of Minnesota.

Stimuli and Procedure

Stimuli were generated with MATLAB and presented on a 19-in. Mitsubishi Diamond Pro monitor (1280 × 1024 at 100 Hz) using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). The images presented to the two eyes were displayed side by side on the monitor and fused using a mirror stereoscope mounted on a chin rest. A frame (10.7° × 10.7°) that extended beyond the outer border of the stimulus and fixation point was presented to facilitate stable convergence of the two images. The viewing distance was 40 cm.

Figure 1a shows the general paradigm for the experimental condition. A central cross (0.8° × 0.8°) was always presented to each eye, serving as the fixation point. Briefly, at the beginning of each trial, a standard dynamic noise pattern was presented to one of the observer's eyes at full contrast, and then the test figure (an upright face, an inverted face, a Chinese character, or a Hebrew word) was presented to the other eye at a random location within the region corresponding to the location of the noise. The contrast of the test figure was ramped up gradually from 0 to 100% within a period of 1 s starting from the beginning

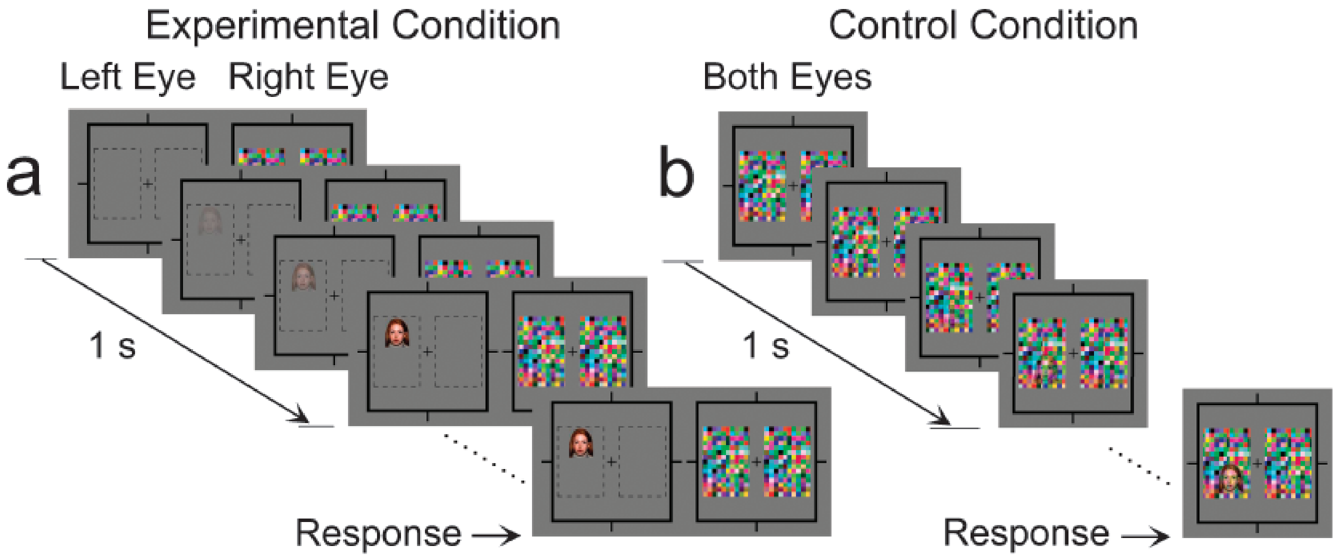

Fig. 1. Schematic representation of the experimental paradigm. In the experimental condition (a), a test figure (e.g., an upright face, as shown) was gradually introduced to one eye to compete with a dynamic noise pattern presented to the other eye. The contrast of the test figure was linearly ramped up from 0 to 100% within a period of 1 s starting from the beginning of the trial, and then remained constant until the observer made a response to indicate the side on which the test figure appeared. In the control condition (b), a test image was presented directly on the noise background with contrast that increased gradually (at a slower rate than in the experimental condition). Subjects viewed the stimulus binocularly and responded to the appearance of the test image as soon as possible.

of the trial and then remained constant until the observer made a button-press response to indicate the figure's location.

In Experiment 1, the test images were 10 upright faces and their inversions. Each test image subtended $2.1^\circ \times 2.6^\circ$ visual angle and was presented in a random position either to the left or to the right of fixation. The horizontal distance between the center of the test image and fixation ranged from 1.9° to 3.9°, and the vertical center of the test image was anywhere between 2.9° above and 2.9° below fixation. At the very beginning of each trial, observers perceived the noise patch and were unaware which side contained the test image. To measure the time it took for the test image to overcome the suppression noise and become dominant, we asked observers to press the left or the right arrow key on a standard keyboard to indicate the side of fixation on which the test image appeared. They were told that they should respond to the appearance of any part of the test image as soon as possible and that they did not need to know the specific content of the image.

Experiment 2 was the same as Experiment 1 except that the test images were 40 Chinese characters and 40 Hebrew words (all nouns, semantically matched between Chinese and Hebrew). Because the Hebrew words had much wider horizontal extension than the Chinese characters, each stimulus was presented either directly above or directly below fixation. The vertical distance between the centers of the words or characters and fixation was fixed at 1.2°. In this experiment, the observers made "up" and "down," instead of "left" and "right," responses.

Each subject in Experiment 1 viewed a total of 120 trials, 60 with upright faces and 60 with inverted faces. Experiment 2 contained 160 trials, 80 with Chinese characters and 80 with Hebrew words. The stimuli were presented in a randomized sequence. Response times (RTs) were calculated based on correct trials only, but very few trials were excluded because accuracy was above 99% for each subject. To reject data outliers, we also excluded trials in which the RT was longer than 10 s (this value was more than 3 standard deviations away from the sample mean). We reasoned that if the test image did not overcome the suppression noise and become dominant within 10 s, then the obtained RT would be likely to reflect some unknown and uncontrolled factors. Overall, fewer than 1% of the trials were excluded from analyses.

To test whether the results obtained in the experimental (rivalry) condition could be explained simply by different recognition speeds or different detection criteria corresponding to the different types of stimuli (upright vs. inverted faces, characters vs. words), we also ran control conditions in which the same test stimuli were blended into the dynamic noise pattern and their contrast was ramped up gradually. Figure 1b shows the paradigm for this condition. Observers viewed the stimuli binocularly (nonrivalry), rather than dichoptically. Their task was exactly the same as in the corresponding experimental condition. Their perceptual experience in this control condition also mimicked the rivalry situation, in which the faces or the words overcame suppression.

The control and experimental conditions were run in separate blocks. Because observers could detect the targets before the test stimuli reached full contrast in the nonrivalry condition, the time course of contrast ramping was modified so that detection time would be in the same range as the suppression time in the experimental condition. The main control conditions were performed with the contrast ramped up at a rate of 10% increment

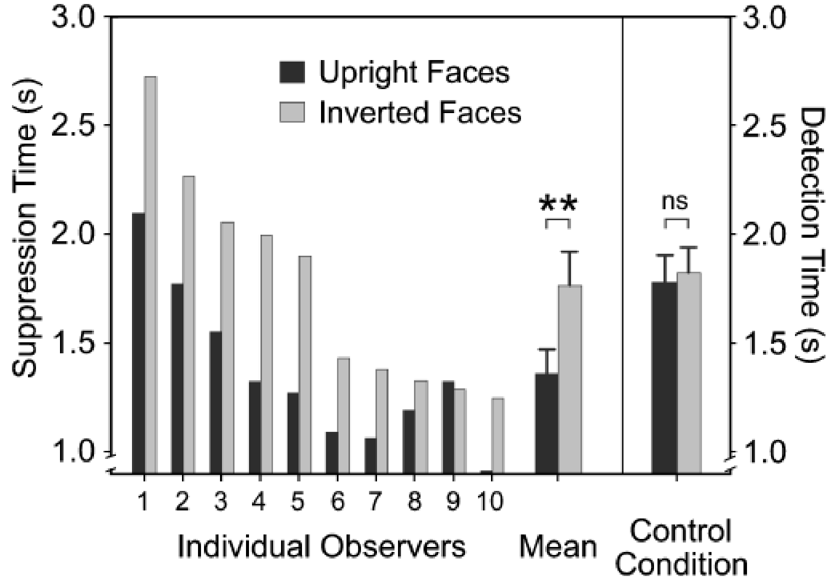

Fig. 2. Suppression and detection times for upright and inverted faces in Experiment 1. The left side of the figure shows the suppression times for 10 individual observers, as well as the averaged suppression times. The two bars on the right show the detection times in the control condition, in which the face images were presented binocularly on the noise background. Asterisks indicate a significant difference between upright and inverted faces, $^{**}p < .001$, $p_{rep} > .985$.

per second, but we also ran the control conditions at larger and smaller contrast increments. Results from different ramping rates were consistent with each other.

RESULTS

We studied the effects of face orientation (upright vs. inverted) and language expertise (Chinese characters vs. Hebrew words for Chinese and Hebrew speakers) on the ability of stimuli to break from noise suppression and become dominant.

Experiment 1: Upright Faces Versus Inverted Faces

In Experiment 1, we tested upright faces and their inverted versions, and we found a significant face-inversion effect: An upright face took less time than an upside-down face to gain dominance against the identical suppression noise (1.36 s vs. 1.76 s), $t(9) = 5.53$, $p < .0005$, $p_{rep} > .99$, $d = 0.92$ (see Fig. 2). This result implies that the suppressed face images were processed to the level where an upright face and upside-down face could be distinguished (i.e., face representation was achieved). One might argue that the difference between upright and inverted faces could have been due to disparate recognition speeds for the two distinct types of test figures as they emerged from noise. In other words, against a noise background, an upright face might be detected more easily than an inverted face, and this difference might have been responsible for the current result. The control condition, in which the same upright and inverted faces were blended into the dynamic noise pattern and their contrast was ramped up gradually, was designed to test this possibility. Observers' perceptual experience in this control condition mimicked their perceptual experience in the rivalry situation, in which the faces overcame suppression.

Results from the control condition showed that there was no significant difference in RT between upright faces and inverted faces (1.78 s vs. 1.82 s), $t(4) = 2.03$, $p > .1$ (see Fig. 2). There was a significant interaction between face orientation (upright vs. inverted) and test condition (experimental vs. control), $F(1, 13) = 11.47$, $p < .005$, $p_{rep} = .97$, $\eta_p^2 = .47$. This pattern of results indicates that the advantage of familiar (upright) faces was specific to the interocular competition, and was not a general advantage in detecting upright faces.

Experiment 2: Chinese Characters Versus Hebrew Words

Faces, especially upright faces, convey rich information that is important for social interactions. Humans are experts at processing facial information, and it is likely that a significant component of human expertise in recognizing faces results from adaptive pressure over the long history of evolution. For this reason, face processing may be privileged, and results of the first experiment may or may not generalize to other categories of objects. In Experiment 2, we explored whether learned familiar visual forms (i.e., words for which people have acquired expertise) also enjoy an advantage in achieving dominance. Two types of test stimuli (Chinese characters and Hebrew words) were dichoptically presented with the dynamic noise to three groups of observers (Chinese, Hebrew, and English speakers). If the result we observed in Experiment 1 was not due solely to

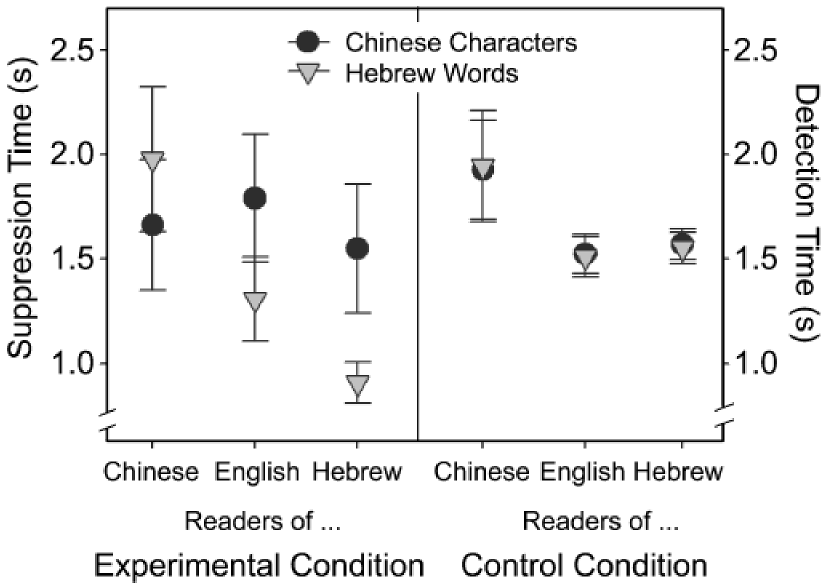

Fig. 3. Mean suppression and detection times for Chinese characters and Hebrew words in the experimental (rivalry) condition (left) and control (nonrivalry) condition (right) of Experiment 2. Results are shown separately for Chinese, English, and Hebrew speakers.

special face-processing mechanisms, then words that are familiar and recognizable to a subject would be expected to have an advantage in overcoming suppression and gaining dominance.

Results indeed showed a significant Observer Group × Stimulus Type interaction, $F(2, 19) = 5.00, p < .02, p_{rep} = .93, \eta_p^2 = .34$ (see Fig. 3): For Chinese speakers, the Chinese characters emerged from suppression sooner than the Hebrew words, whereas for Hebrew speakers, the Hebrew words were faster to gain dominance than the Chinese characters. For English speakers who knew neither Chinese nor Hebrew, the Hebrew words also became dominant faster than the Chinese characters, but the Hebrew words' advantage was larger for Hebrew speakers than for English speakers. Because the Hebrew words occupied a wider horizontal region than the Chinese characters, we believe the effect in English speakers was due to the geometric properties of the stimuli.

In a control condition similar to the one in Experiment 1, we tested whether these results can be explained simply by different recognition speeds or different detection criteria corresponding to the different types of test stimuli. We directly presented the same Chinese characters and Hebrew words on the noise background, gradually ramping up their rate of contrast. For each group of subjects (Chinese, English, and Hebrew speakers), the Chinese characters and Hebrew words were detected equally fast, $F(2, 9) = 0.20, p > .8$, although on average English and Hebrew speakers had shorter RTs than Chinese speakers (see Fig. 3).

Taken together with previous findings regarding binocular rivalry, our results suggest that familiar and recognizable forms, even when suppressed and invisible, are differentially processed compared with unfamiliar and unrecognizable forms and have an advantage in attaining dominance.

DISCUSSION

Early studies showed that when the strength of a stimulus is increased (e.g., by increasing its contrast), the duration of its suppression during binocular rivalry usually decreases (Levelt, 1968). Results from the current study show that changes in high-level shape and form information of the stimuli (i.e., face orientation and language familiarity) also alter their suppression time. Our first experiment shows that when upright and inverted faces are tested against a common suppressing noise, upright faces are "stronger" stimuli. As mentioned in the introduction, it would not be surprising if upright faces were stronger than inverted faces in the dominant phases of rivalry. However, our procedure specifically targeted suppression duration, and the observation that face orientation affected the stimuli's ability to break suppression suggests that at the site (or sites) of rivalry competition, upright and inverted faces are represented differently, with upright faces being stronger. Experiment 2 shows that the effect of high-level information on a stimulus's ability to break suppression is not restricted to faces. In that experiment, the familiarity and recognizability of words contributed to their strength during suppression. For Chinese observers, Chinese characters took less time to become dominant than Hebrew words, but the reverse was true for English and Hebrew speakers, with Hebrew words being fastest to break suppression for Hebrew speakers.

If we took a simplistic view of our data, we might infer that face-orientation representation and visual word-form processing occur before the neural site of rivalry. A recent study suggests that the fusiform face area (FFA) is the neural correlate of the face-inversion effect (Yovel & Kanwisher, 2005), and there is evidence (though controversial) that there is a specialized visual word-form area (VWFA) in the ventral extrastriate areas (McCandliss, Cohen, & Dehaene, 2003; Price & Devlin, 2004). Do our results imply that the site for interocular suppression is later than the FFA and VWFA? The answer is not so simple. Although it is likely that interocular competition starts at V1 when the two eyes' input converges, it is believed that competition is a multistage process (Freeman, 2005; Nguyen, Freeman, & Alais, 2003). In any case, results of the current study suggest that some information from the suppressed image still reaches high-level visual areas (e.g., FFA and VWFA). Further, the information that reaches the high-level areas is strong enough to make a difference in the ability of the stimulus to overcome suppression.

Our study by itself cannot distinguish between two possibilities: First, binocular rivalry may be a process with multistage competition, with some information of the suppressed object still available at high-level stages. Second, object-related information from the suppressed image may not survive interocular competition at the cortical level, but may be processed subcortically and reach cortical object-selective areas via subcortical projections (e.g., through superior colliculus or pulvinar). Furthermore, if the suppressed information has high social or emotional significance (e.g., is relevant to rewards and dangers), it may be able to reach cortical regions via projections through the amygdala. The amygdala responds more strongly to emotional than to neutral images during the suppression phases of rivalry (Pasley et al., 2004; Williams et al., 2004).

Regardless of how information from the suppressed image reaches object-selective regions, the key suggestion from the current results is that such information does reach those areas. In a recent imaging study using a similar interocular suppression paradigm, we showed that even when observers were completely unaware of the nature of the pictures presented, the FFA still reliably showed greater activation for invisible faces than for invisible scrambled faces (Jiang & He, 2006). These findings suggest that suppressed and invisible faces can still be represented in face-specific cortical areas. We believe such object-related representations, however degraded and rudimentary, can and do influence rivalry dynamics via feedback to the early processing stages, such that the feedback signal enhances (strengthens) the input signal associated with a coherent or familiar stimulus. It is possible that the findings reported here are unique to the specific type of interocular suppression we investigated, namely, continuous flash suppression, and cannot be generalized to more typical rivalry conditions in which two stimuli are of similar strength and alternate in dominance. However, existing evidence suggests that, if anything, suppression from continuous flash suppression is more effective than traditional rivalry suppression (Tsuchiya & Koch, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006).

The current study provides strong evidence that substantial information in the suppression phase of binocular rivalry can be processed to the extent that object-related representations can be achieved, either because of incomplete suppression over the multiple stages of rivalry competition or through direct subcortical projections. These object-related representations, in turn, can strengthen the signal of suppressed images, resulting in shortened suppression durations for familiar objects.

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