

# Differential effects of visual attention and working memory on binocular rivalry

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The investigation of cognitive influence on binocular rivalry has a long history. However, the effects of visual WM on rivalry have never been studied so far. We examined top-down modulation of rivalry perception in four experiments to compare the effects of visual WM and sustained selective attention: In the first three experiments we failed to observe any sustained effect of the WM content; only the color of the memory probe was found to prime the initially dominant percept. In Experiment 4 we found a clear effect of sustained attention on rivalry both in terms of the first dominant percept and of the overall dominance when participants were involved in a tracking task. Our results provide an example of dissociation between visual WM and selective attention, two phenomena which otherwise functionally overlap to a large extent. Furthermore, our study highlights the importance of the task employed to engage cognitive resources: The observed perceptual epiphenomena of binocular rivalry are indicative of visual competition at an early stage, which is not affected by WM but is still susceptible to attention influence as long as the observer's attention is constrained to one of the two rival images via a specific concomitant task.

## Introduction

Binocular rivalry occurs when incompatible monocular images are displayed at the same retinal location in the two eyes: perception oscillates between the two alternative interpretations, rather than yielding a stable intermingled percept. As the perceptual epiphenomenon keeps changing over time whereas the physical stimulus remains invariant, binocular rivalry can be usefully employed as a tool to explore the dynamical features of visual awareness and how they vary with the state of the observer. Indeed, binocular rivalry can be influenced by a number of cognitive, motivational and affective factors. Stable characteristics of the observers, such as their past experience and even their sociocultural context can affect rivalry dominance: Upright pictures of human faces prevail over inverted ones (Engel, 1956; Hastorf & Myro, 1959), familiar images dominate over novel ones (Goryo, 1960), and emotional facial expressions dominate over neutral expressions (Alpers & Gerdes, 2007); Jewish and Catholic religious images dominate for respectively Jewish and Catholic observers (LoSciuto & Hartley, 1963), pictures depicting violent acts (e.g., rape or murder) are

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perceived more often than are neutral control pictures by policemen and institutionalized offenders than by control observers (Shelley & Toch, 1962; Toch & Schulte, 1961). Binocular rivalry can also be affected by more volatile cognitive factors: Voluntary intention and attention are known to affect observers' ability to increase alternation rate during rivalry (Lack, 1971; Meng & Tong, 2004; van Ee, van Dam, & Brouwer, 2005). However, their effect on rivalry dominance is more controversial (Chong & Blake, 2006; Chong, Tadin, & Blake, 2005; Lack, 1978; Meng & Tong, 2004; Ooi & He, 1999; van Ee et al., 2005). Furthermore, diverting the observer's attention to a concurrent task during rivalry has been shown to slow down alternation rate (Paffen, Alais, & Verstraten, 2006). Finally, Pearson, Clifford, and Tong (2008) found that endogenously generated mental images can exert facilitatory effects on binocular rivalry stabilization: In case of intermittent presentation of rivalry displays, perceptual dominance tends to stick to the same stimulus that appeared dominant on the preceding trial. When observers are required to imagine one of the rivalry stimuli during the blank period between presentations, perception is biased in favor of the imagined stimulus.

The contents of visual working memory (WM) are one of the major, ever-changing aspects that could affect the cognitive and perceptual state of the observer. Indeed, growing experimental evidence supports the notion that holding in WM a visual object not only influences the processing speed of subsequently presented objects (Downing, 2000; Robinson, Manzi, & Triesch, 2008; Pan & Soto, 2010; Soto, Heinke, Humphreys, & Blanco, 2005; Turatto, Vescovi, & Valsecchi, 2008), but can also bias the appearance of the new sensory input (Kang, Hong, Blake, & Woodman, 2011; Scocchia, Cicchini, & Triesch, 2013; Scocchia, Valsecchi, Gegenfurtner, & Triesch, 2013). However, in the long history of binocular rivalry the question of whether visual WM contents can influence perceptual dominance has never been posed: The present study investigates precisely this issue. We had our observers memorize an image and hold it in memory for a few seconds in the context of a delayed match to sample task. In this way, we could test whether voluntarily maintaining a visual representation in WM has an impact on rivalry dominance.

The idea that the contents of WM can modify the appearance of what we see, especially when sensory information is ambiguous enough to generate bistable perception, stems from a host of experimental evidence showing that the same cortical areas that underlie perceptual processing play an important role in maintaining visual information in WM. This overlap between the neural networks that encode the visual input and those responsible for its maintenance in WM for several seconds after its offset has been demonstrated both at late and

early stages of visual processing: Neurons in face-selective areas of inferotemporal cortex showed sustained changes in their activity profile when a monkey observer was retaining a face in WM (Miller, Li, & Desimone, 1993); firing activity in V1, MT, and V4 neurons was also observed during the WM retention interval when the animal memorized location, motion, and color (or luminance) information respectively (Bisley, Zaksas, Droll, & Pasternak, 2004; Motter, 1994; Supèr, Spekreijse, & Lamme, 2001). Along the same lines, human studies indicated that activation patterns in V1 during WM retention reflected the specific attributes that observers were required to memorize (Serences, Ester, Vogel, & Awh, 2009), that activity in areas V1 to V4 could predict which of two oriented gratings was held in WM (Harrison & Tong, 2009), and that motion information held in WM could modulate phosphene report when TMS was applied to human V5 (Silvanto & Cattaneo, 2010).

If we hypothesize that WM contents can impact rivalry perception via the recruitment of sensory areas that mediate visual processing, we could expect two possible outcomes. On one hand, prolonged engagement of sensory networks could lead to satiation processes (neural fatigue) in those networks and therefore produce a dominance shift to the rival image *least* overlapping with the memory sample. Such an outcome would be consistent with recent evidence of repulsive effects observed in non-ambiguous conditions. Kang et al. (2011) employed moving random dots configurations as stimuli and asked observers to memorize their direction for delayed discrimination: They found that the direction of motion of the stimulus displayed during the retention interval was biased away from the memorized one. Scocchia, Cicchini, and Triesch (2013) required participants to memorize oriented gratings and involved them in an orientation discrimination task during the retention interval: Perceived orientation was repelled away from the memorized one across two subsequent discrimination judgments. On the other hand, sustained engagement of sensory networks could lower their activation threshold during rivalry, thus favoring dominance of the rival image *most* overlapping with the memory sample. Consistent with this view, a recent study of ours (Scocchia, Valsecchi, Gegenfurtner, & Triesch, 2013) showed that the contents of WM can bias bistable perception through facilitation: An ambiguously rotating sphere was perceived to move in the same direction as a previously presented unambiguous sphere significantly more often when participants memorized its speed than when they merely attended to it.

## Experiment 1

The goal of Experiment 1 was to test whether holding in WM a specific image could bias perception

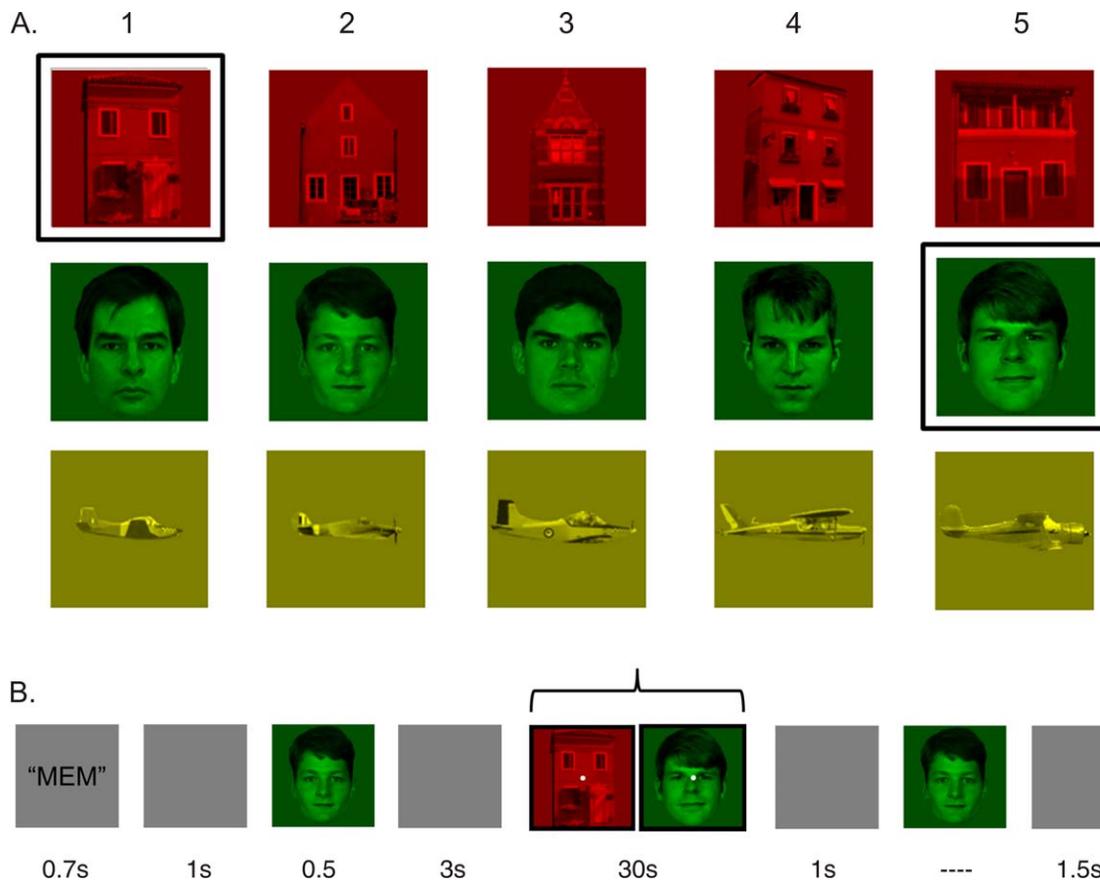


Figure 1. Experiment 1 stimuli and procedure. (A) Stimuli employed in the WM task. A black frame (not displayed during the experiment) identifies the WM stimuli that exactly matched the rivalry stimuli. For clarity, stimuli are numbered within each category. (B) Illustration of a trial sequence of Experiment 1. Observers were required to memorize the initial image, which could belong to one of three different categories (face, house, or airplane, interleaved across trials). Subsequently, they continuously reported the perceived image during rivalry (rival stimuli are indicated by a brace). Finally, they judged whether or not the memory test matched the memory sample. The house-face rivalry stimuli were the same across trials, whereas the memory stimuli were drawn from the image pool in a random order. The memory test belonged to the same category as the memory sample and they matched in 50% of the trials. The display duration is indicated below each stimulus window. Stimuli are not drawn to scale and instructions were presented as actual sentences.

of subsequently presented binocular rivalry stimuli. To this purpose, we employed three categories of stimuli (houses, faces, and airplanes) to test WM performance in a delayed match to sample task and a classical house-face rivalry display to be presented during the retention interval (see Figure 1A). Importantly, one of the rivalry stimuli could match the memorized stimulus (memory sample) from trial to trial. If WM top-down modulation can exert its influence over binocular rivalry via a direct recruitment of neural networks that underpin perception itself, we could expect two possible scenarios:

(a) The visual WM load may lead to *saturation* of those networks. As a result, we should observe prolonged suppression of the memory sample during rivalry. If, for instance, the observer memorized a face, sustained activity in the fusiform face area due to

WM maintenance could lead to a greater dominance of the opposite stimulus, the house, and even more so when the rivalry face exactly matches the memorized one.

(b) The WM load may *prime* the perceptual networks during WM maintenance, without overloading them. If the observer memorized a face, perception of the face rival stimulus would prevail in case of category match and even more so in case of exact stimulus match.

## Methods

### Observers

Observers consisted of 14 undergraduate students from Giessen University who received payment for participation. All observers had normal or corrected-

to-normal visual acuity, and were naïve to the purpose of the experiment. The experiment was conducted in accordance with the Declaration of Helsinki.

### **Apparatus and stimuli**

Stimuli were created using Matlab in conjunction with the Psychophysics Toolbox (Brainard, 1997) and were displayed on two 19-in. LCD color monitors (Dell™ UltraSharp 1907FP) at a viewing distance of 55.5 cm. Stimuli for the left eye were presented on the left monitor screen and stimuli for the right eye on the right monitor screen. Observers viewed the monitors through a Wheatstone mirror stereoscope, consisting of two First Surface Mirrors (169 × 194 mm) to bring the two views into alignment. Physical luminance equivalence between the left and the right display was checked through the mirrors with a Photo Research PR-650 spectroradiometer. The observer's head was stabilized by a chin and forehead rest.

Rivalry stimuli consisted of a red image of a house and a green image of a face subtending  $3.98^\circ \times 3.93^\circ$  of visual angle and were displayed on a gray background ( $30.0 \text{ cd/m}^2$ ). During rivalry, a white fixation dot ( $0.09^\circ \times 0.09^\circ$ ) was placed at the center of each image and a black frame ( $0.18^\circ$  thick) surrounded each monocular image to aid binocular fusion. Rivalry stimuli, memory samples, and memory tests were drawn from a set of five stimuli for each of the three categories. Whereas the memory sample and test images varied across trials, rivalry stimuli were fixed. Stimuli were displayed as individual objects, in the absence of background information. House and airplane stimuli were created on the basis of public images downloaded from the [www.flickr.com](http://www.flickr.com) website, whereas face images were drawn from the Georgia Tech face database (Nefian, 1999), after removal of background information. Illustrative representations of the stimuli are displayed in Figure 1A.

Faces, houses, and airplanes were presented on a green, red, and yellow background, respectively. Stimuli had the same mean luminance, and the root mean square contrast within each figure was fixed at 20%.

### **Calibration procedure**

Each participant underwent a preliminary calibration procedure of the rivalry stimuli in order to identify the RMS contrast that yielded equivalent subjective dominance rates for the two stimuli during a baseline rivalry task. This procedure served to determine the contrast at which the face stimulus should be displayed to match the house stimulus in baseline exclusive dominance during the main experiment. The calibration procedure was conducted before every experiment

employing house-face rivalry presented from then on. On the basis of pilot data, we tested seven levels of RMS contrast for the face stimulus (18.3%, 16.7%, 15%, 13.3%, 11.7%, 10%, and 8.3%) against a fixed 20% RMS contrast for the house stimulus. Each face contrast was presented five times to each eye in a counterbalanced fashion, over 70 trials. Each trial started with the presentation of a white fixation dot ( $0.09^\circ \times 0.09^\circ$ ) for 0.5 s, followed by the display of the rivalry stimuli for 30 s. Participants were required to keep fixation on the white dot and to press the left or the right arrow key only when they exclusively perceived the house or the face, respectively, as long as exclusive perception lasted. They were asked to release the button in case of mixed dominance. Participants' responses were sampled at 100 Hz. At the end of the rivalry stimulus presentation, a blank gray window was displayed until the observer pressed a key to proceed to the next trial. Individual proportions of "face dominant" responses were computed at each level of face stimulus contrast. For each observer, face dominance proportions were linearly regressed over stimulus contrast to find the contrast level at which baseline dominance for house and face were equal. Participants who at this stage reported problems with fusing the two images, whose pattern of responses clearly deviated from linearity or direct proportionality, or for whom the interpolation procedure yielded values below 5% of RMS contrast were excluded from the main experiment. On this basis, two participants were excluded and the experiment was conducted on the remaining 12 participants.

### **Experimental procedure**

Participants were instructed to memorize an image that could belong to one of three different categories (face, house, or airplane) for a 2AFC delayed match to sample. Figure 1B illustrates a trial sequence of Experiment 1. At the beginning of each trial, the instruction to memorize the stimulus was presented for 0.7 s, followed by a 1 s blank interval and then by the memory sample, which was displayed for 0.5 s. Afterwards, the fixation dot was shown for 3 s, followed by the 30 s rivalry stimulus. During its presentation, participants were required to monitor subjective dominance by pressing the left or the right arrow key (as they did during the calibration session). After a 1 s blank interval, the memory test was displayed until participants provided their response: They pressed the up arrow key to indicate that the memory test matched the memory sample and the down arrow key to indicate that they were different. The WM test matched the sample in 50% of cases; in the remaining 50% it was randomly selected from the same category set. A 1.5 s blank interval followed

participants' response before the next trial began: Observers were allowed to take a break every five trials.

Each WM sample was presented 16 times, for a total amount of 240 trials. Since the two rivalry stimuli were driven from the same image pool as the memory and the test stimuli, the memory sample matched one of the rival images in 32 trials. Individual data were collected over five sessions (including calibration session) lasting about one hour each.

## Data analysis

In the four experiments reported in this study, we calculated dominance proportions for each participant and each experimental factor as the ratio of mutually exclusive responses (e.g., “house” or “face,” sampled at 100 Hz) over periods of exclusive dominance, collapsed across trials. In other words, all the instantaneous keypresses relative to a particular observer and experimental factor yielded a single proportion dominance value that was computed after excluding periods of mixed dominance. The use of dominance proportion has the advantage of combining the effects of the number of episodes of exclusive perceptual dominance across trials and of their average duration. These measures are known to show a large intersubjective variability (Levelt, 1965). Instead, the employment of a comprehensive measure as dominance proportion was meant to control for individual differences in alternation rate and to improve statistical sensitivity to possible differences between conditions. We analyzed the observers' reports in terms of dominance proportion rather than of dominance durations: Dominance durations are not a robust measure in our paradigm since single episodes were often truncated (between 3% and 23% of the times, depending on participant and experimental condition), because the display time of the rivalry stimulus was considerably shorter in our experiments than what is typically reported in the literature, where rivalry is displayed for 1 min or longer (e.g., Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006; Chong et al., 2005; Levelt, 1965; Meng & Tong, 2004). However, results do not change significantly when the analyses are conducted on normalized dominance durations.<sup>1</sup> For sake of clarity, we will report dominance proportions in terms of prevalence of house responses from now on. In order to distinguish between sustained and immediate effects of the WM sample presentation on perceptual dominance during rivalry, we also analyzed the first percepts of each trial: We reported the number of trials where “house” was perceived first over the total number of trials for each participant, WM identity and category.

## Results and discussion

Participants understood and adequately performed the task, scoring on average 93.4% correct responses at the memory test. On average, observers reported seeing the house for 53.1% of time during exclusive dominance and they perceived exclusive dominance for 40.85% of the time during rivalry. The left panel of Figure 2 shows the proportion of “house” responses averaged across observers, separately for each WM stimulus and category. A one-way, repeated-measures ANOVA on the proportion of relative dominance across categories failed to highlight any significant effect,  $F(2, 22) = 1.76$ ,  $p = 0.2$ . We also compared the proportion of “house” responses given when the WM stimulus matched the rivalry image and the average of the other stimuli within the same category in order to test the effects of stimulus identity. Dominance proportion did not differ according to identity match both within the house,  $t(11) = 1.01$ ,  $p = 0.33$ , and the face category,  $t(11) = 0.73$ ,  $p = 0.48$ . The right panel of Figure 2 illustrates the proportion of trials where participants reported the house as the first dominant percept. Data are averaged across the 12 observers and presented separately for WM stimulus category and identity. A one-way, repeated-measures ANOVA on the proportion of “house first” responses highlighted a significant difference across categories,  $F(2, 22) = 4.92$ ,  $p = 0.017$ . The Duncan post-hoc tests further showed that observers were more likely to report “house” as a first percept after memorizing a house as opposed to both a face ( $p < 0.01$ ) and an airplane ( $p < 0.05$ ). Direct comparisons of the proportion of “house first” responses between the WM stimulus that matched the rivalry image and the average of the other stimuli within category also failed to highlight any effect of stimulus identity,  $t(11) = 1.3$ ,  $p = 0.22$  for the house category;  $t(11) = -0.22$ ,  $p = 0.83$  for the face category.

Our results point out that the effect of the memory sample on subsequent rivalry dominance is short-lived and can be detected only in terms of the influence of the WM content on the stimulus perceived first during rivalry. Instead, when considering the overall amount of exclusive dominance perceived during rivalry, no differences emerged across conditions. Furthermore, the effect of the WM sample on initial dominance was limited to the WM stimulus category and did not encompass its identity. Although our goal in this experiment was to test the effect of voluntarily holding an object in visual WM on subsequent rivalry perception, we cannot exclude that we actually tackled implicit memory processes, such as priming. This account of Experiment 1 results seems plausible if we consider that the WM task turned out to be relatively easy for participants: As such, it may have posed only limited cognitive demands, which would not require

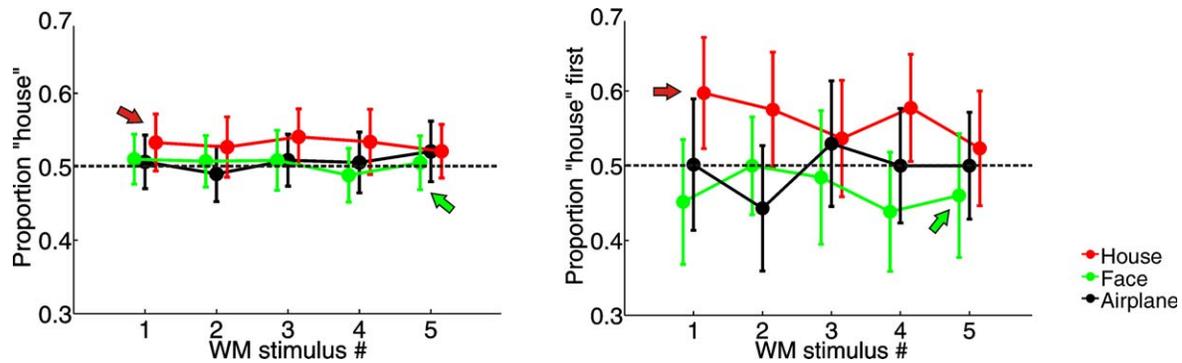


Figure 2. Results of Experiment 1. Left panel: proportion of “house” responses as a function of memory sample. Right panel: the proportion of trials participants reported the house as the first percept during rivalry is plotted as a function of the WM sample, separately for each stimulus category. Red and green arrows indicate respectively the house and the face WM sample that corresponded to the rival stimulus. WM stimuli within each category are numbered as is in Figure 1. Error bars represent the *SEM*. and black, dashed lines indicate chance level.

holding an active visual representation of the stimulus in WM. However, the experimental outcome seems incompatible with *stimulus priming*, as stimulus identity did not play a role in the observed effect. Rather, we could explain our results in terms of *color priming*, as the WM samples and the rivalry stimuli shared the same color background (see Figure 1) in the case of house and face images. Experiment 2 was designed to better address whether visual WM contents may affect rivalry perception and whether color priming could explain the observed results.

## Experiment 2

In the first experiment we could not detect a clear effect of the WM stimulus identity; nevertheless, we observed an influence of its category on subsequent initial rivalry dominance. The conclusions we can derive from these results are limited for two reasons: First, participants were on average 93.4% accurate at the memory task. Such a ceiling effect indicates that the task was not challenging enough, and it may not have been necessary for participants to hold an active visual representation in WM to solve it. Second, as the house and the face images had the same color background both when used as rivalry and as WM stimuli, the observed effect of category on rivalry initial dominance may be due to color priming. In Experiment 2, we employed a different and larger set of stimuli and a more challenging WM testing procedure, which aimed to favor holistic visual encoding of the WM samples and yielded an average 74.2% memory accuracy. Furthermore, we employed grayscale stimuli for the WM task to exclude the possibility of color priming.

## Methods

### Observers

A new pool of seven paid volunteers participated in this experiment. All of them had normal or corrected-to-normal visual acuity, and were naïve to the purpose of the experiment. The experimental setup was the same as described in Experiment 1.

### Stimuli and procedure

Two hundred and forty different grayscale images of houses, faces, and cars (80 for each category) were employed as WM samples and tests. Face images were a selection from the face database provided by the Max-Planck Institute for Biological Cybernetics in Tuebingen, Germany (Troje & Bühlhoff, 1996): They represented male heads with no hair, glasses, beard, moustaches, or paraphernalia. The head models of the database were obtained by morphing real scans to avoid close resemblances to actual individuals. The cars and houses databases were created ad hoc from the [www.flickr.com](http://www.flickr.com) website. All the stimuli were displayed as single objects, in the absence of any informative background. WM stimuli subtended  $6.12^\circ \times 6^\circ$  of visual angle, whereas rivalry stimuli subtended  $3.98^\circ \times 3.93^\circ$ . Rivalry stimuli were surrounded by a black frame ( $0.18^\circ$  thick) and a white fixation dot ( $0.09^\circ \times 0.09^\circ$ ) was placed at the center of each monocular image. The rival house and face stimuli were displayed on a red and on a green background, respectively, and the baseline contrast for the face stimulus was individually determined via the calibration procedure, as described for Experiment 1.

The experimental procedure is illustrated in Figure 3. The rival stimuli were constant across trials and they were drawn from the same image databases as the

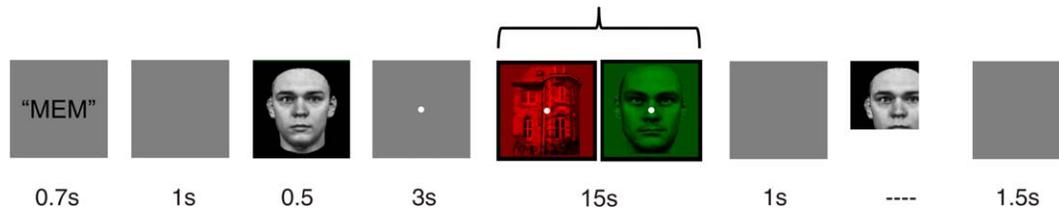


Figure 3. Trial procedure of Experiment 2. Participants were required to memorize the stimulus for a delayed match to sample. During the retention interval, they were presented with the rivalry stimuli and continuously monitored perceptual dominance. The memory test was displayed as the upper left, upper right, lower left, or lower right corner of the test image, covering 49% of its original area. The display duration is indicated below each stimulus window. Stimuli are not drawn to scale and instructions were presented as actual sentences.

house and the face WM stimuli: At variance with Experiment 1, no WM sample matched any of the rival stimuli. On each trial, a new WM sample was presented: The WM test stimulus was equal to the WM sample in 50% of trials; in the remaining 50% it randomly matched one of the other memory samples within the same category.

The WM test display was partially occluded and presented as the upper left, upper right, lower left, or lower right corner of the image, in a counterbalanced and randomly ordered fashion for each category. This measure was taken to render the WM task more challenging and to favor holistic visual encoding of the WM sample. The displayed corner of the WM test covered 49% of the original stimulus (including neutral background): This value was chosen on the basis of a pilot experiment where eight naïve participants were involved in a two-back memory task on the same set of stimuli. The test image was displayed at eight different levels of occlusion (70%, 63%, 56%, 49%, 41%, 34%, 27%, or 20% visible) and the 49% level yielded comparable performance across categories and observers, averaging 73.5% correct. The experimental procedure was the same as in Experiment 1, except that the display time of the rivalry stimulus was limited to 15 s. Altogether, individual data were collected in four sessions (including calibration session) lasting about 45–60 min each.

## Results and discussion

Accuracy at the WM task averaged 74.2% correct responses, implying that the task engaged participants' cognitive resources. On average, observers reported seeing the house for 51.88% of the time during exclusive dominance, and they perceived exclusive dominance 31.84% of the time during rivalry. The left panel of Figure 4 illustrates the relative dominance of "house" responses as a function of stimulus category held in WM. We tested the influence of WM stimulus category on dominance proportion via a one-way, repeated-measures ANOVA and observed no effect,  $F(2, 12) =$

0.41,  $p = 0.67$ . A direct comparison between the house and the face category also failed to reach statistical significance,  $t(6) = 0.73$ ,  $p = .49$ . The right panel of Figure 4 illustrates the proportion of trials where participants reported the house as the first dominant percept, separately for each WM stimulus category.

A one-way, repeated-measures ANOVA on the proportion of "house first" responses also failed to highlight any significant difference between categories,  $F(2, 12) = 1.23$ ,  $p = 0.33$ , as did the direct comparison between the house and the face category,  $t(6) = 1$ ,  $p = 0.35$ .

These results indicate that holding in WM a visual representation does not favor nor hinder perception of the rival stimulus belonging to the same category. Rather, we conclude that Experiment 1 results are better described in terms of color priming, which would also explain why stimulus identity did not play a role in the observed effect.

## Experiment 3

The null result reported in Experiment 2 stands in stark contrast to the findings of our previous study (Scocchia, Valsecchi, Gegenfurtner, et al., 2013), where we showed that WM contents can affect the perceived direction of ambiguous structure-from-motion. In that study, participants had to memorize the speed of an unambiguously rotating sphere and were shown an ambiguous transparent sphere during the retention interval: They reported the perceived direction of motion on a moment-to-moment basis, as in the experiments described here. Dominance systematically shifted towards the direction of motion that matched the memorized stimulus. In Experiments 1 and 2 of the current study, rivalry dominance was not influenced by the memory of object identity (house, face), a much more high-level representation compared to the motion speed which was memorized in our previous study (Scocchia, Valsecchi, Gegenfurtner, et al., 2013). However, it is still possible that if the memorized

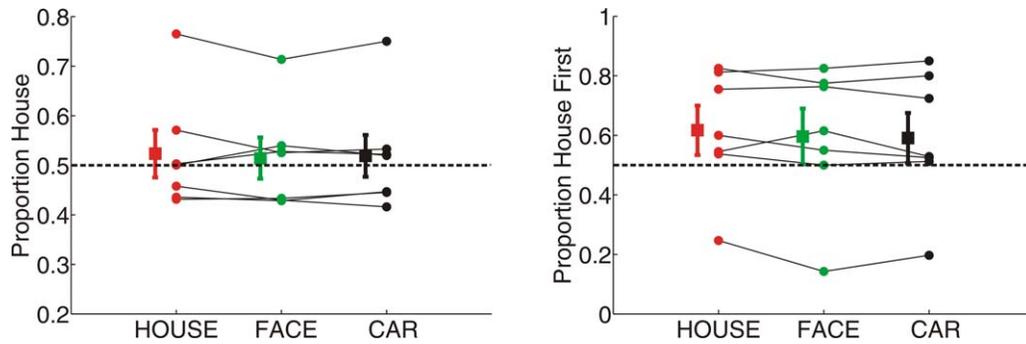


Figure 4. Results of Experiment 2. Left panel: proportion of “house” responses as a function of stimulus category held in WM. Each data point represents the average proportion for one subject. Right panel: proportion of times participants reported the house as the first percept during rivalry as a function of WM category. Error bars represent the *SEM* and black, dashed lines indicate chance level.

stimulus were encoded in terms of low-level features (e.g., speed, spatial frequency, orientation...) rather than face or object identity, binocular rivalry dominance could be affected. Therefore, in Experiment 3 we tested whether a direct match in low-level visual features between the WM and either of the rival stimuli would impact rivalry dominance. We asked participants to memorize the spatial frequency of a grating and displayed two rival orthogonal gratings during the retention interval: The memory sample had the orientation of either rival stimulus. To favor direct comparison, we employed a similar paradigm to the one reported in our previous study (Scocchia, Valsecchi, Gegenfurtner, et al., 2013) and added a control condition where participants attended to, but did not memorize, the first grating stimulus.

## Methods

### Observers

A new pool of 12 paid volunteers participated in this experiment. All of them had normal or corrected-to-normal visual acuity, and were naïve to the purpose of the experiment. The experimental setup was the same as described in Experiment 1.

### Stimuli and procedure

The rivalry stimuli consisted of a green and of a red  $\pm 45^\circ$  sinusoidal gratings at 50% Michelson contrast that subtended  $1^\circ$  of visual angle and were displayed on a grey background. The average luminance of each of the two gratings and of the background was  $13.8 \text{ cd/m}^2$ . The spatial frequency of the gratings was 3.25 cycles per degree (cpd). Eye of presentation, grating color, and orientation were independently manipulated. The non-rival stimuli (i.e.: the memory sample and tests in the WM condition and the attention stimulus in the control condition) were grayscale gratings ( $1^\circ$ ,  $13.8 \text{ cd/}$

$\text{m}^2$ ) that matched the orientation of either rival stimulus, in a counterbalanced fashion with a random presentation order. All the stimuli were displayed within a  $1.5^\circ$  checkerboard frame to aid fixation.

In the WM condition, the memory sample and test had the same orientation within a trial. The spatial frequency of the sample ranged randomly between 1.94 and 4.95 cpd, whereas the spatial frequency of the memory test was determined by a staircase algorithm aiming at 75% of correct responses as participants were involved in a delayed match to sample. The experimental procedure of the WM condition is depicted in Figure 5A: Each trial began with the presentation of the checkerboard, which was displayed thereafter until the rivalry stimulus offset. After 2 s the memory sample was shown for 0.5 s; then the rivalry stimulus was presented for 30 s after a 3 s inter-stimulus interval. Participants monitored perceptual dominance with their right hand as in the previous experiments: They pressed the right or the left arrow key according to the perceived orientation of the stimulus. They were asked to refrain from responding in case they perceived mixed dominance. The memory test appeared after a 1 s blank interval and was displayed until response. Participants judged the test stimulus spatial frequency (i.e.: they were asked whether the distance between the grating bands was the same as in the memory stimulus); they used their left hand to press the “s” or the “d” key to provide “same” or “different” responses, respectively. Afterwards a blank window was presented for 1.5 s; then started the next trial.

The experimental procedure in the attention condition is depicted in Figure 5B; it was the same as in the WM condition, with the following exceptions: First, participants were not required to memorize the unambiguous stimulus but to judge a rapid change in its spatial frequency (i.e.: they were asked whether the distance between the grating bands increased or decreased), thus providing their response after its offset. For this, a 100 ms change in the unambiguous stimulus spatial fre-

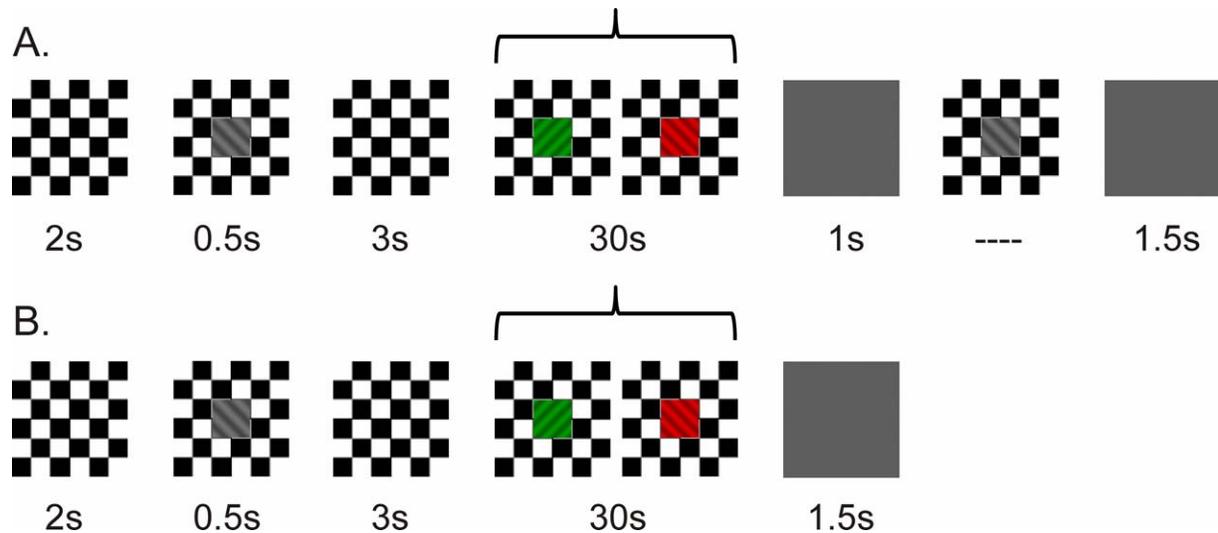


Figure 5. Trial procedure in the WM (A) and attention condition (B) of Experiment 3. In (A) participants were asked to memorize the grating spatial frequency for a delayed match to sample. During the retention interval, they were presented with the rivalry stimuli and reported perceptual dominance on a moment-to-moment basis. In (B) participants were required to judge a 0.1 s change in the unambiguous grating spatial frequency. They provided their responses during the 3 s inter stimulus interval and then monitored rivalry dominance as in (A). The display duration is indicated below each stimulus window.

quency occurred after 400 ms from its onset: Participants pressed the “a” or the “s” key to indicate an increase or a decrease, respectively. The change in spatial frequency was determined by a staircase algorithm aiming at 75% of correct responses. Second, no memory test stimulus was presented, and the rivalry stimulus was immediately followed by a 1.5 s blank interval.

Each experimental condition comprised 32 trials, and participants were allowed to take a break every eight trials. After a brief familiarization with the experimental procedure, participants underwent both conditions, in a counterbalanced order, in a unique experimental session that lasted about 75 min.

## Results and discussion

Participants scored 69.5% correct at the WM and 68.2% at the attention control task, meaning that the task was challenging and of comparable difficulty in the two conditions. The overall proportion of exclusive dominance during rivalry was 82.5% in the WM and 84.5% in the attention condition.

We sorted data by orientation of the unambiguous stimulus: Perception during rivalry was defined to be either congruent or incongruent, depending on whether the reported percept matched the orientation of the unambiguous stimulus or not. By analogy with the previous experiments, we calculated dominance proportion for each participant in the two experimental conditions as the amount of “congruent” and “incon-

gruent” responses (sampled at 100 Hz) over periods of exclusive dominance, collapsed across trials.

The left panel of Figure 6 depicts the relative dominance of “congruent” responses as a function of experimental condition. On average, the dominance proportion of congruent percepts was 49.85% in the WM and 50.34% in the attention condition. Such a difference was not significant at the two-tailed, paired-sample  $t$  test conducted on the data,  $t(11) = -0.66$ ,  $p = 0.52$ . The right panel of Figure 6 represents the proportion of trials where participants reported a congruent percept as the first dominant percept in the two conditions. The first rival percept matched the unambiguous stimulus in 49.2% of the trials in the WM and in 50% in the attention condition, a statistically negligible difference,  $t(11) = -0.48$ ,  $p = 0.5$ .

These results provide no evidence for the hypothesis that holding in WM a low-level visual feature could modulate rivalry perception, at least in this experimental paradigm. Rather, they are in line with the outcome of Experiment 2 which showed no influence of WM on binocular rivalry.

## Experiment 4

Notwithstanding the careful experimental design and the measures taken to engage participants in a challenging WM task based on holistic visual encoding of the memory samples, Experiments 2 and 3 did not highlight any significant effect of visual WM contents

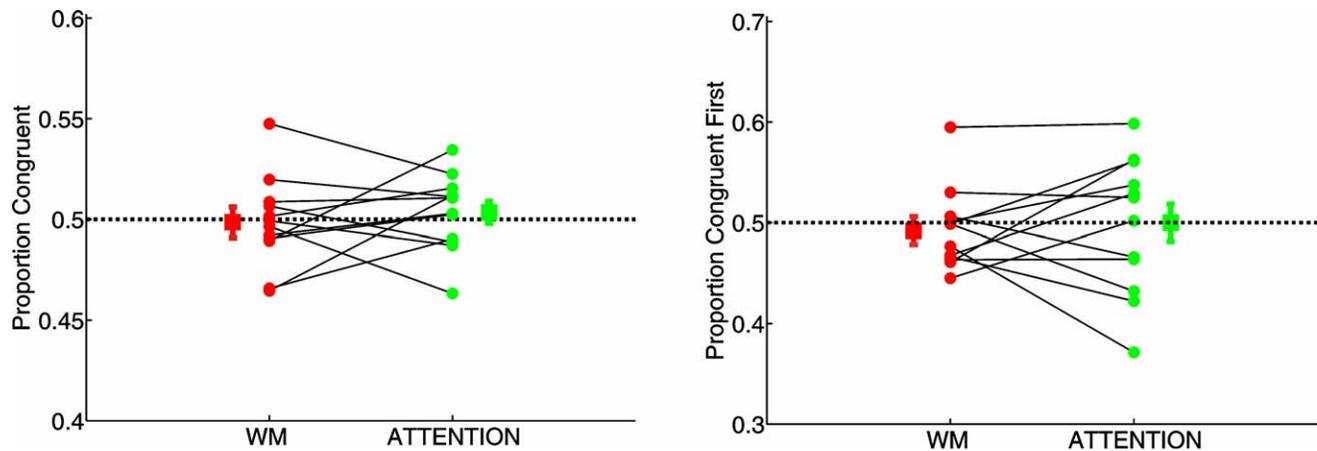


Figure 6. Results of Experiment 3. Left panel: proportion of “congruent” responses as a function of experimental condition. The rival percept is defined to be congruent to the unambiguous stimulus if it shared the same orientation. Each data point represents the results of one subject. Right panel: proportion of times participants reported a congruent percept as the first percept of a trial. Error bars represent the *SEM* and black, dashed lines indicate chance level.

on binocular rivalry. As there is evidence that WM contents can influence perception of structure-from-motion ambiguous stimuli (Scocchia, Valsecchi, Gegenfurtner, et al., 2013), it is possible that the outcome of Experiments 2 and 3 was determined by different mechanisms underlying the two types of bistable percepts, with rivalry being a more automatic form of visual completion and therefore being less susceptible to top-down influence. Indeed, it has been shown that the instruction to attend to one of the two alternative interpretations of the ambiguous stimulus can substantially influence perception of the Necker cube but exerts only a modest effect on face-house rivalry stimuli (Meng & Tong, 2004). On the other hand, endogenous attention strongly affects binocular rivalry when participants are engaged in a tracking task, such as monitoring a continuous change in one of the rival stimuli (Chong et al., 2005; Chong & Blake, 2006).

The discrepancy between the results of Meng and Tong (2004) and the ones of Chong and Blake (2006) and Chong et al. (2006) might be the result of the task employed to elicit endogenous attention (explicit verbal instructions vs. tracking) but also of the difference between the kind of stimuli being used: Whereas Meng and Tong (2004) employed high-level house-face stimuli during rivalry, Chong and Blake (2006) and Chong et al. (2005) made use of gratings or radial checkerboard versus bull’s eye stimuli.

Experiment 4 investigated whether house-face rivalry is susceptible to cognitive influence other than the one exerted by WM. In particular, we tested the effect of sustained endogenous attention with the same type of stimuli whose perception proved not to be affected by the contents of WM.

## Methods

### Observers

A new pool of seven paid volunteers participated in this experiment. All of them had normal or corrected-to-normal visual acuity, and were naïve to the purpose of the experiment. The experimental setup was the same as described in Experiment 1.

### Stimuli and procedure

The rivalry stimuli were the same as in Experiment 2, and all participants underwent the calibration procedure prior to testing, as described above. The experimental procedure is depicted in Figure 7. No WM stimulus was displayed: Instead, participants were asked to monitor either the face or the house rival image, in a blocked fashion, in order to detect a rapid change in its appearance. The change consisted of a 1

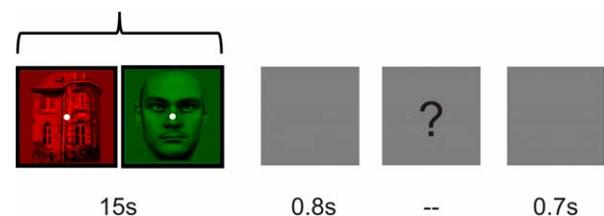


Figure 7. Trial procedure of Experiment 4. Participants were required to report the dominant percept while tracking one of the rival images in order to detect a 200 ms change. 0.8 s after rivalry offset, an instruction window prompted participants to judge whether a change occurred in the target image. The display duration is indicated below each stimulus window. Stimuli are not drawn to scale, and instructions were presented as actual sentences.

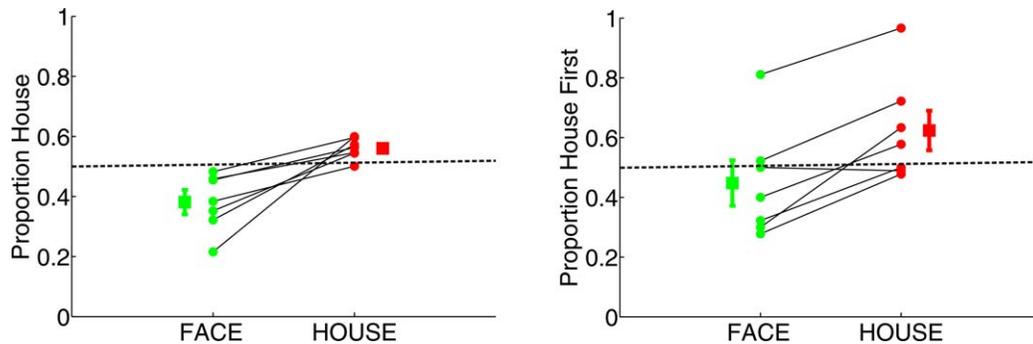


Figure 8. Results of Experiment 4. Left panel: proportion of “house” responses as a function of the stimulus tracked during rivalry. Each data point represents the results of one subject. Right panel: proportion of times participants reported the house as the first percept as a function of the tracked stimulus. Error bars represent the *SEM* and black, dashed lines indicate chance level.

pixel horizontal stretch displayed for 200 ms, which could occur at any time of stimulus presentation apart from the first and last second. Participants were required to report subjective dominance while monitoring one of the two images in order to detect the change. The trial procedure is depicted in Figure 7: At the beginning the rivalry stimulus was displayed for 15 s, followed by a blank window for 0.8 s and then by a prompt window that signaled participants to report whether a change occurred in the face (or in the house) stimulus. Once participants entered their response, a blank window was displayed for 0.7 s and the trial sequence resumed from the beginning. The experimental trials were divided into three sessions of 100 trials each: There were 40 catch trials per session, where the change actually occurred 20 times on the house and 20 on the face stimulus. Half of the participants were required to monitor the house during the first 50 trials of each experimental session and the face during the last 50 trials; the other half did the opposite. An instruction window reminded participants which stimulus to track at the beginning and at the middle of the experimental session, after they took a compulsory break. Furthermore, participants were allowed to take a break every five trials. Participants were tested in four separate sessions (including calibration session) held on different days, and the whole procedure lasted approximately 3.5 hr. As exogenous transients in the rivalry display are known to affect subjective dominance (Walker & Powell, 1979; Wilson, Blake, & Lee, 2001), catch trials were not included in the analyses.

## Results and discussion

Overall accuracy in the two tracking tasks was 87.71%, indicating that the task was sufficiently difficult to require sustained attention. On average, observers perceived exclusive dominance for 48.33% of the time during rivalry. When they tracked the face image, house relative dominance decreased by about

30% compared to when they tracked the house image. This difference proved to be significant at the dependent samples, two-tailed *t* test conducted on dominance proportion,  $t(6) = -4.43$ ,  $p = 0.004$ . Results are illustrated in the left panel of Figure 8. The right panel shows the proportion of times participants reported the house as the first percept as a function of the tracked stimulus. Similar to the results on dominance proportion, observers reported “house” as the first percept of a trial about 30% more often when they were tracking the house compared to the face image. The difference between tracking conditions was statistically significant,  $t(6) = -4.61$ ,  $p = 0.004$ .<sup>1</sup>

One might surmise that the increase in relative dominance of the attended image derived from a bias to report intermingled percepts as exclusive ones when parts of the attended stimulus were visible. Although the level of mixed dominance in Experiment 4 was relatively high, we are quite confident that the observed result is not contingent on our specific experimental setup or on the level of mixed dominance, as it has been previously described in the literature (Chong & Blake, 2006; Chong et al., 2005; Ooi & He, 1999). Instead, we did not find any effect of WM content regardless of the level of mixed dominance (which ranged from 68% in Experiment 2 to 17% in Experiment 3).

Our data provide additional evidence for the influence of endogenous attention on rivalry perception (Chong et al., 2005) when attention is engaged by requiring observers to actively perform a task on one of the rival stimuli. Furthermore, they extend the validity of those findings to complex, meaningful stimuli which proved insensitive to attentional influence in previous studies (Meng & Tong, 2004).

## General discussion

In four experiments we assessed the amenability to top-down influence of binocular rivalry using both

complex (houses and faces) and simple stimuli (sinusoidal gratings): We showed that rivalry dominance can be strongly influenced by sustained attention but not by visual working memory load, at least in this experimental paradigm.

In Experiment 1 we tested whether holding in memory the image of a face, of a house, or of a neutral stimulus (airplane) could affect subsequent rivalry perception: We found that when the WM and one of the rival stimuli belonged to the same category, initial dominance of the matching stimulus prevailed. However, category match did not affect the global amount of dominance across trials. Instead, an identity match between the WM sample and either of the rival stimuli had no effect beyond the one of class membership. Experiment 2 suggests that the results of Experiment 1 could be explained in terms of color priming, as no effect of WM was observed when color information was removed from the WM samples. Experiment 3 extended the findings of Experiment 2 to a different kind of visual stimulus: The lack of a WM effect was replicated with grating stimuli, providing additional evidence against the idea that a direct match in low-level visual features between the stimulus held in memory and either of the monocular ones may influence rivalry perception. Finally, Experiment 4 highlighted the effect of sustained attention on both rivalry initial dominance and overall dominance proportion when participants were involved in a tracking task.

Overall, the present results do not support the idea that WM contents can influence binocular rivalry. Caution should be used in drawing conclusions from a null result, which might be limited to the experimental paradigm utilized in this study, however. In a previous study (Scocchia, Valsecchi, Gegenfurtner, et al., 2013), in which we employed a very similar experimental paradigm, we observed antithetical results: WM contents were found to affect the perception of an ambiguously rotating sphere. In that case, observers were required to memorize an unambiguously moving sphere in one condition and to perform a change discrimination task on the sphere in another condition. They tended to perceive the ambiguous stimulus as moving in the same direction as the unambiguous stimulus both in the WM and in the control condition, but consistently more so in the WM one. Furthermore, relative dominance dropped to chance levels towards the end of the trials in the attention condition, whereas the effect in the WM condition was sustained over time. Thus, where a specific WM influence on bistable perception has been observed, it was characterized as a long-lived effect. The fact that in Experiment 1 of the present study the WM stimulus category had only a short-lived effect on rivalry dominance, together with the evidence collected in Experiments 2 and 3, favors an interpretation of the result in terms of priming rather than of WM effects.

A comparison between the results of this and of our previous study (Scocchia, Valsecchi, Gegenfurtner, et al., 2013) highlights two crucial aspects: First, visual WM effects on ambiguous perception depend on the kind of stimulus being used, with binocular rivalry being resistant and ambiguous structure-from-motion perception being amenable to WM modulation. Second, the influence of attention over bistable perception is multi-faceted: Even when focusing on selective visual attention, a clear distinction emerges between the effects of transient and sustained attention. When attention is directed to a specific visual feature and released before the ambiguous stimulus onset (as in the case of the control condition in Experiment 3 and in Scocchia, Valsecchi, Gegenfurtner, et al., 2013), its effect is limited even for those stimuli that prove to be more suitable to cognitive modulation. Instead, attentive tracking can influence the perception of stimuli that typically involve more automatic forms of visual competition, as binocular rivalry, and that prove resistant to transient focusing of attention. (See also Dieter & Tadin, 2011 and Paffen & Alais, 2011 for insightful reviews on the topic of attentional modulation of binocular rivalry).

Previous studies reported diverging evidence on the effects of endogenous selective attention on binocular rivalry (Chong et al., 2005; Meng & Tong, 2004). On one hand, a possible explanation of this discrepancy could rely on the different attention tasks participants performed in the two experimental paradigms: In Meng and Tong (2004) observers were instructed to attend to one of the two stimuli, whereas in Chong et al. (2005) they were actively engaged in a tracking task. On the other hand, the difference between paradigms that led to dissimilar results could be due to the rivalry stimulus complexity: Meng and Tong (2004) employed meaningful, high-level house-face rivalry, whereas Chong and colleagues (2005) used gratings or patterned stimuli. Our experimental results allow unequivocally discarding the account based on stimulus complexity, as we observed a consistent effect of tracking on house-face rivalry: The task employed to engage attentional resources clearly plays a major role in modulating top-down influence over binocular rivalry. Interestingly, Helmholtz (1866/1925) himself observed that he could favor dominance of one of two rival gratings by mentally counting the lines or comparing the spaces within it. As Chong and colleagues (2005) proposed, performing some kind of mental operation on one stimulus during rivalry could be the critical factor underlying cognitive control over its prevalence. When participants' attentional focus is not bound to one of the stimuli via a specific concomitant task, rivalry dominance seems to be constrained by bottom-up (such as RMS contrast, in our experiments) rather than top-down factors.

Importantly, our results show that the effects of WM and of sustained attention on binocular rivalry are not the same. There is no definitive agreement on the distinction between WM and sustained selective attention in the literature, and it has been proposed that visual WM is one and the same thing as visual attention sustained internally over time (Chun, 2011). Indeed, the requirement of holding a visual stimulus in WM for subsequent recall has been commonly shown to act as an endogenous attentional cue: Visuospatial attention is attracted towards the location occupied by a stimulus that corresponds to the WM template (Downing, 2000; Soto et al., 2005, Turatto et al., 2008). Our experiments underscore that sustained visual attention and visual WM have dissimilar effects on the same bistable stimuli, thus suggesting that they rely on distinct operating mechanisms. Although this conclusion should be limited to the experimental paradigm employed in this study, it is in agreement with research indicating that a match between a visual search item and the content of WM do not automatically elicit attention allocation when paying attention to the WM matching item would impair performance (Downing & Dodds, 2004; Woodman & Luck, 2007). Furthermore, other studies showed that feature-based WM and feature-based attention have additive effects on the perception of motion direction (Mendoza, Schneiderman, Kaul, & Martinez-Trujillo, 2011), and that comparable multiple object tracking and visual WM loads pose different dual-task costs to a concurrent visual WM task (Fougnie & Marois, 2006).

To conclude, the fact that visual WM contents bias relative dominance during ambiguous structure-from-motion perception but not during rivalry points to different neural mechanisms implied in the two types of bistable perception, with binocular rivalry involving competition at an earlier stage of visual processing—at least for the stimuli used in our experiments. Our data are in keeping with previous evidence (Meng & Tong, 2004) showing a substantial difference between the effects of selective attention on perceptual dominance during rivalry and other, higher-level kinds of visual competition (i.e., Necker cube). The results are consistent with the idea that binocular rivalry entails a more automatic form of visual competition than ambiguous structure-from-motion, which would be at the origin of the dissimilar effects of visual WM on the two types of bistable stimuli. Indeed, our study supports the notion that the perceptual epiphenomena of binocular rivalry reflect competition at an early stage, where the signals from the two eyes are not yet combined (Blake, 1989; Haynes, Deichmann, & Rees, 2005; Lee, Blake, & Hegeer, 2005; Lunghi, Burr, & Morrone, 2011; Tong & Engel, 2001; Wunderlich et al., 2005). Such a low-level form of visual competition seems resistant to an influence of visual WM contents,

but is still amenable to a top-down modulation as long as the observer's attention is constrained to one of the two rival images via a specific concomitant task.

*Keywords:* binocular rivalry, visual working memory, selective attention, top-down control

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## Footnote

<sup>1</sup> For all the reported experiments, additional analyses on normalized dominance durations were performed: A first analysis examined the durations of all single percepts for each observer; a second analysis focused on the duration of the first percept of each trial. Durations were normalized based on each observer's average duration of all percepts and of all first percepts, respectively. The results of both types of analyses overlapped the ones obtained by analyzing dominance proportions. In particular, no effect whatsoever of WM or of its interactions was found in Experiments 1, 2, and 3. The only significant result observed was an interaction effect in Experiment 4: a 2-way repeated measures ANOVA with Condition (attend house or attend face) and Reported Percept (house or face) as factors revealed that the interaction between Condition and Reported Percept was significant for both the analysis of mean normalized durations ( $F[1, 6] = 29,98$ ,  $p < .01$ ) and for the analysis of first percepts durations ( $F[1, 16] = 12,74$ ,  $p < .05$ ), thus confirming that the attention condition influenced binocular rivalry.

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