

Retinotopic and non-retinotopic stimulus encoding in binocular rivalry and the involvement of feedback

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Adaptation is one of the key constituents of the perceptual alternation process during binocular rivalry, as it has been shown that preadapting one of the rivaling pairs before rivalry onset biases perception away from the adapted stimulus during rivalry. We investigated the influence of retinotopic and spatiotopic preadaptation on binocular rivalry. We show that for grating stimuli, preadaptation only influences rivalry when adaptation and rivalry locations are retinotopically matched. With more complex house and face stimuli, effects of preadaptation are found for both retinotopic and spatiotopic preadaptation, showing the importance of spatiotopic encoding in binocular rivalry. We show, furthermore, that adaptation to phase-scrambled faces results in retinotopic effects only, demonstrating the importance of form content for spatiotopic adaptation effects, as opposed to spatial frequency content. Are the spatiotopic adaptation influences on rivalry caused by direct spatiotopic stimulus interactions, or instead are they due to altered feedback from the adapted spatiotopic representations to the retinotopic representations that are involved in rivalry? By using rivaling face and grating stimuli that minimize rivalry between spatiotopic representations while still engaging these representations in stimulus encoding, we show that at least part of the preadaptation effects with face stimuli depend on feedback information.

Keywords: adaptation, spatiotopic representation, retinotopic representation, binocular rivalry, feedback

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Introduction

Binocular rivalry is one of the main tools used to study the formation of visual awareness. To instigate binocular rivalry, one places two conflicting but unchanging images in the two eyes. Despite the fact that the retinal input is unchanging, visual awareness changes from one of the eyes' images to the other. This property means that one has a window on the repeated formation of visual awareness without any change to the external stimuli.

One idea that has become accepted recently is that rivalry takes place at multiple levels within the visual system, and that rivalry strength increases at successive levels (Blake & Logothetis, 2002; Freeman, 2005; Logothetis, Leopold, & Sheinberg, 1996; Logothetis & Schall, 1989; Nguyen, Freeman, & Alais, 2003). The specific interactions between these different levels and the computations that occur within them are still relatively unclear. The present study seeks to clarify aspects of these processes by comparing retinotopic and spatiotopic effects of adaptation.

What causes the internally induced switches from one rival stimulus to the other? According to the general view, one of the key constituents of the rivalry switching process is visual adaptation (e.g., Blake, Sobel, & Gilroy, 2003; Noest, van Ee, Nijs, & van Wezel, 2007). Adaptation is a common neural process that refers to the decrease in sensitivity that occurs among neurons after prolonged stimulation. Critically, adaptation effects persist after the adapting stimulus ceases to be displayed. Psychophysically, this leads to effects such as afterimages (of color or contrast, for example) or to aftereffects such as the motion and the tilt aftereffects. In the context of binocular rivalry, adaptation to one of the rival stimuli is thought to decrease the sensitivity of the responsive neural population and cause a shift in inhibitory interactions in favor of the competing neural population, resulting in a perceptual switch to the less adapted stimulus (Blake et al., 2003; Laing & Chow, 2002; Noest et al., 2007).

One of the useful characteristics of adaptation is that it is selective to a particular group of “tuned” neurons. This specificity can be seen in the variety of forms of adaptation that have been reported. For example, adaptation can occur

to image contrast (Crowder et al., 2006; Solomon, Peirce, Dhruv, & Lennie, 2004), to orientation (e.g., Blakemore & Campbell, 1969), to motion (Mather, Verstraten, & Anstis, 1998), to spatial (Blakemore, Nachmias, & Sutton, 1970) and temporal (Saul & Cynader, 1989) frequency, to depth cues (Knapen & van Ee, 2006), and even to object content such as face identity (Leopold, O'Toole, Vetter, & Blanz, 2001; Webster & MacLin, 1999). Adaptation therefore is often used as a probe to try to identify the locus of particular visual processes, sometimes known as psychoanatomy (Julesz, 1971). Consequently, the neural loci of adaptation to various visual stimuli are better known than those for binocular rivalry. For this reason, manipulating the visual system's state of adaptation to various stimuli offers great potential for revealing otherwise hidden aspects of the neural processes underlying binocular rivalry and for dissecting the visual hierarchy thought to underlie binocular rivalry.

Apart from stimulus specificity, another interesting aspect of adaptation concerns the spatial frame of reference in which it occurs. Traditionally, the effects of adaptation are measured by adapting locally to a particular stimulus and then presenting a subsequent test image at the same retinal location. However, if the observer makes an eye movement between adaptation and testing so that their gaze is directed to another location in the outside world, it is possible to separate retinotopic adaptation from spatiotopic adaptation. When the effects of adaptation are measurable at the same retinal location, it is said to be retinotopic adaptation.¹ In contrast, when the effects of adaptation are measurable at the spot in the outside world where the adaptation stimulus was presented, it is said to be spatiotopic adaptation. Both types of adaptation can be demonstrated (Melcher, 2005; Nishida, Motoyoshi, Andersen, & Shimojo, 2003). In general, the more complex the adapting image, the more spatiotopic adaptation occurs (Melcher, 2005).

In this paper, we will compare retinotopic and spatiotopic adaptation effects on binocular rivalry. The usual manner for investigating the influence of adaptation on rivalry has been to preadapt to one of the rival stimuli before the rivalry measurements begin. This is thought to desensitize neurons responsive to that stimulus and bias perception toward the other stimulus during rivalry (Blake & Overton, 1979; Nawrot & Blake, 1989; Wade & de Weert, 1986), showing a causal role for adaptation in determining rivalry alternations. In these previous studies, however, retinotopic and spatiotopic adaptation were confounded, and the possible influences of image complexity were not studied. In this report, we will disentangle retinotopic and spatiotopic adaptation processes by separately testing retinotopically matched and spatiotopically matched locations. We will also compare the relative importance of these different types of adaptation for both simple grating stimuli and more complex house–face stimuli. In a final experiment, we will report on the effects of feedback of adaptation to lower

levels, as feedback is a likely means of communication between the different levels of processing involved in binocular rivalry.

Methods

Subjects

Nine subjects participated in [Experiment 1](#), 9 in [Experiment 2](#) (6 had also participated in [Experiment 1](#)), 6 in [Experiment 3](#) (5 of them participated in [Experiment 1](#), and 5 also participated in [Experiment 2](#)), and 8 in [Experiment 4](#) (7 of which had participated in one or more of the preceding experiments).

Apparatus

The first two experiments were performed in different countries and therefore with different equipment. Three of the 9 subjects in [Experiment 1](#) and 4 of the 9 subjects in [Experiment 2](#) were shown stimuli on an Iiyama Monitor (1280 × 1024 pix at 75 Hz) in ambient daylight. The other subjects were shown stimuli on a gamma-corrected 22-in. LaCie electron22blueIV monitor (1600 × 1200 pix, refreshed at 75 Hz). No difference was observed between the two groups of subjects, and the data was therefore combined. To create binocular rivalry, we employed a conventional stereoscope with a septum dividing the screen into two equal parts.

Stimuli

In [Experiment 1](#), a circular grating with a diameter of 1.6 degrees, 2.5 cycles/deg was displayed at 100% contrast during adaptation, and gratings had a 30% contrast during rivalry. The adaptor grating was always tilted 45 degrees left from vertical, the rivalrous gratings were both 45 degrees from vertical. The gratings in all experiments had a sine wave profile, i.e., background luminance at the center of the stimulus. In [Experiment 2](#), house and face stimuli (see [Figure 1C](#)) were viewed through a vertically oriented oval window (long axis ~2.4 deg, short axis ~1.2 deg). House and face stimuli, both during adaptation and rivalry, were equated in RMS contrast (contrast was 45%). In [Experiment 3](#), house-grating rivalry was studied. [Figure 1C](#) displays the face stimulus that was used. The grating in [Experiment 3](#) had the same contrast during adaptation and rivalry, which was set per subject to obtain about equal dominance durations for the grating and face stimuli. The grating was oriented 45 degrees from vertical and was seen through an oval window with a size identical to the face stimulus. In this experiment, the grating contained

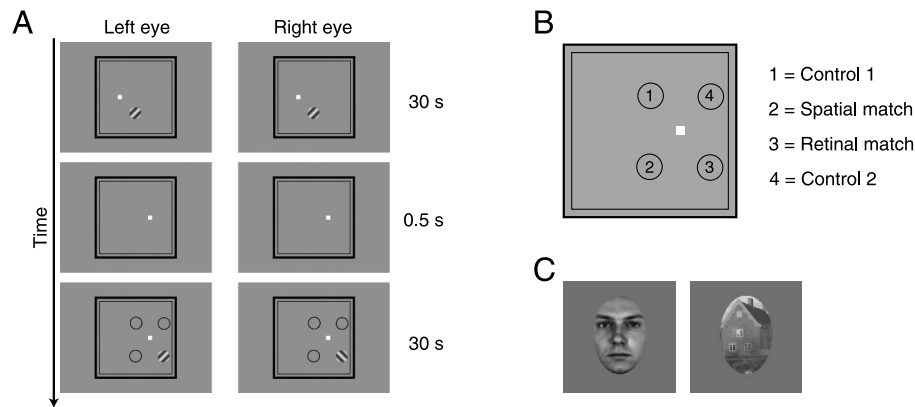


Figure 1. Stimuli and experimental protocol. (A) A trial started with a 30-s adaptation phase. During this phase, subjects fixated a bright fixation point, while a non-rivalrous stimulus was presented in the periphery. After the adaptation phase, the fixation point jumped to its new location. After 0.5 s, a rivalrous stimulus appeared for 30 s in one of four locations indicated by a circle in this schematic. The circles were not presented in the real stimulus. During the rivalry phase subjects indicated their dominant percept. (B) The four possible locations of the rivalry stimulus comprised two control conditions (indicated by 1 and 4, which are called Control 1, and Control 2), one location that was retinotopically matched to the adaptation condition (location 3), and one location that was spatiotopically matched to the adaptation conditions (location 2). (C) The house and face stimulus used in Experiments 2 and 3.

10 cycles (~ 4 cycles/deg). All stimuli were displayed on a mean-luminance background (6.4 cd/m^2 on the LaCie monitor, 31 cd/m^2 , on the Iiyama monitor). A 9×9 degree box, that functioned as a fusion aid, and a spatiotopic reference surrounded the area in which stimuli could be displayed.

In Experiment 4, we pitted gratings against phase-scrambled faces, after adaptation to the phase-scrambled face. The grating stimuli were identical to those of Experiment 3. The competing stimulus was a phase-scrambled version of the face in Figure 1C, seen through an oval window.

Protocol

Each trial started with the appearance of a fixation dot, 1.52 deg left of the center of the display. When the subject pressed a button, a period of binocular adaptation to one of the two stimuli was started (see Figure 1A). The adaptation period lasted 60 s for the first trial and 30 s for all subsequent trials. During this adaptation period, the subject was asked to keep fixation on the fixation mark only. At the end of the adaptation period, the fixation mark jumped to a position 1.52 deg right of the center of the display, and the subject was required to saccade quickly to the new fixation mark. After 0.5 s, the rivalrous stimulus was displayed for 30 s, during which period the subject continually indicated the dominance of the two images using two buttons assigned to the two percepts. Subjects were told to press buttons whenever one or the other stimulus was more pronounced. When both stimuli were equally salient, or when the percept was difficult to interpret, the subjects were asked not to press any button. The rivalrous stimuli could appear at 1 of 4 locations (see

Figure 1B). One of these was in retinotopic correspondence to the adaptation stimulus, one location was in spatiotopic correspondence, and two locations functioned as control conditions (as illustrated in Figure 1B; see Control 1 and Control 2). Image locations were 2.15 degrees from fixation, located at 45 degrees, 135 degrees, 225 degrees, and 315 degrees from vertical upward (see Figure 1). Within sessions, a single adaptation stimulus was used. House and face adaptation in Experiment 2 and face and grating adaptation in Experiment 3 were balanced within each subject, but adaptation sessions to houses and faces always took place on different days. Within one session, each condition was repeated three times.

Results

Experiment 1—Grating adaptation

During the adaptation phase, subjects viewed a tilted grating. After saccading to a new fixation location, a rivalrous stimulus was placed in 1 of 4 spots, matching the adaptation location either in retinal coordinates, spatial coordinates, or neither (see Figure 1). Rivalry took place between two gratings and subjects reported their changing percept during the entire 30 s. We measured the average dominance duration of both the adapted grating and its rivaling partner grating. To quantify the effect of adaptation, we divided the average duration of the adapted grating by the average duration the orthogonal partner grating, normalized by any bias observed in the Control 1 condition shown in Figure 1B. Measures smaller than

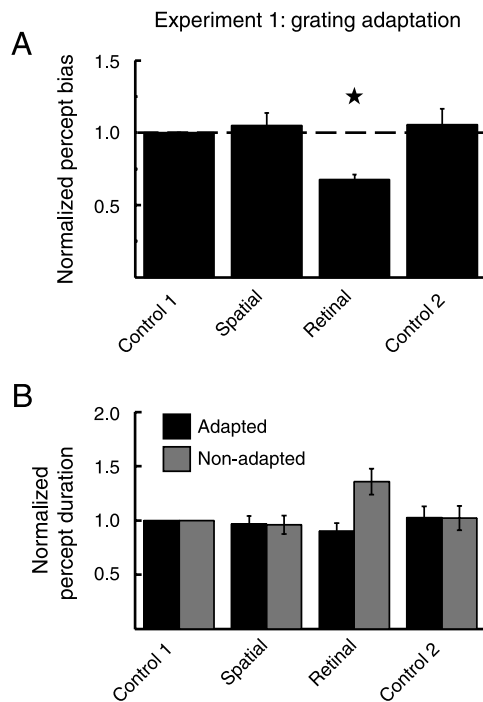


Figure 2. The influence of grating adaptation on grating rivalry. (A) Normalized percept biases (i.e., average percept duration of the adapted stimulus divided by the average percept duration of the non-adapted stimulus, normalized by the bias of Control 1). Adaptation only influenced the bias for retinotopically matched locations. (B) Average normalized percept durations per percept-type (i.e., adapted and non-adapted stimulus), normalized relative to Control 1. The effect of adaptation is evident as an increase in percept durations for the non-adapted stimulus (the conditions retinotopic non-adapted percept duration is significantly different from 1, $p < 0.02$, all other $p > 0.05$). The non-normalized durations are 2.44 s and 2.53 s (Control 1), 2.24 s and 2.31 s (Spatial), 2.08 s and 3.19 s (Retinal), and 2.29 s and 2.44 s (Control 2).

unity indicate that adaptation biased predominance away from the adapted stimulus.

In Figure 2A, we plot the adaptation influence for the four tested rivalry positions. For the grating stimuli used in this experiment, adaptation does not bias perception for either of the control conditions nor for the spatiotopic test spot. It was only in the retinotopic condition that adaptation led to a significant bias (i.e., a difference from 1) toward the non-adapted grating ($p < 10^{-5}$; when not further specified p -values are derived from two-tailed t -tests). The bias, 0.68 (range: 0.52–0.82), is of a strength comparable to previous research (Blake & Overton, 1979, reported biases between 0.5 and ~ 0.75 for their subjects).

Experiment 2—House–face rivalry

Consistent with what was observed with grating adaptation in Experiment 1, house and face adaptation led to strong adaptation effects on rivalry at retinotopically

matched locations (averaged over face and house adaptation: $p < 0.0002$; see Figure 3). More interestingly, adaptation to house and face also influenced house–face rivalry occurring at the spatiotopically matched location ($p < 0.002$), although the spatiotopic effect was smaller than the retinotopic effect ($p < 0.01$, paired t -test). Importantly, the Control 2 condition (see Figure 1B) did not show any systematic bias. As this control condition was located the same distance from the retinotopic location as the spatiotopic condition, the absence of bias in Control 2 indicates that the observed bias in rivalry competition at the spatiotopic location is not caused by adaptation that may have spread from retinotopic adaptation (for example, due to the large receptive fields of face-selective cells).

We also calculated the time course of the influence of preadaptation on house–face rivalry. This is plotted in Figure 4 (with trial-time binned into three intervals) as the cumulative dominance duration of the adapted stimulus divided by the cumulative dominance duration of both

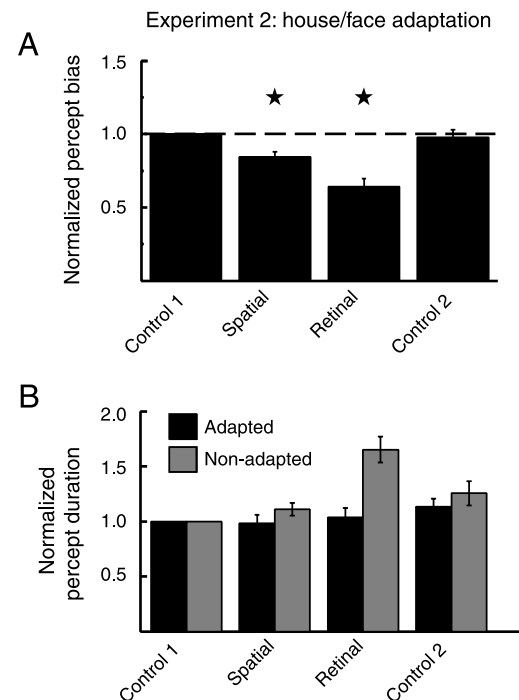


Figure 3. The influence of house or face adaptation on house–face rivalry. (A) Normalized percept biases (see Figure 2A), averaged over house and face adaptation conditions. Adaptation influenced the bias for both retinotopically matched and spatiotopically matched locations. (B) Average normalized percept durations per percept-type (i.e., adapted and non-adapted stimulus), normalized relative to Control 1. The effect of adaptation is evident as an increase in percept durations for the non-adapted stimulus. This effect is significant for retinotopically matched locations ($p < 0.0006$; all other $p > 0.05$). The non-normalized percept durations are 2.28 s and 2.40 s (Control 1), 2.27 s and 2.69 s (Spatial), 2.37 s and 3.95 s (Retinal), and 2.55 s and 2.95 s (Control 2).

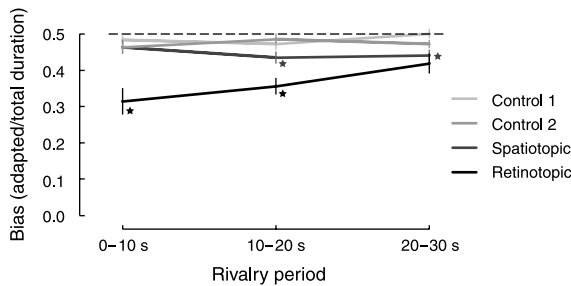


Figure 4. The time course of adaptation influences during house–face rivalry. Each 30-s trial has been divided into three 10-s periods (x-axis), and average predominance of the adapted stimulus has been calculated for each period. Adaptation has a strong retinotopic influence that gradually decreases over the course of the trial. The influence of adaptation on the spatiotopically matched rivalry location is weaker than for retinotopically matched locations but is nevertheless sustained throughout the trial. No significant biases are found for the two control conditions. Stars indicate a significantly lower bias than 0.5 (one-tailed *t*-test with Bonferroni correction).

stimuli. This analysis reveals that retinotopic adaptation has a large initial effect that gradually decreases over the course of the trial, whereas spatiotopic adaptation has a smaller effect but one that is consistently present throughout the trial or even seems to grow over time (i.e., no significant effect in the first part of the trial).

Discussion: Experiments 1 and 2

Experiment 1 confirmed a previous observation (Blake & Overton, 1979) that preadaptation to one of the stimuli from a rival pair will bias subsequent rivalry to favor the other, non-adapted stimulus. Using grating stimuli, the comparison between retinotopic and spatiotopic conditions clearly revealed that the effects of grating adaptation on rivalry are limited to the retinotopically matched location. For rivalry occurring at a spatiotopically matched location, preadaptation to a grating has no influence on rivalry.

This contrasts with **Experiment 2**, which examined rivalry between more complex stimuli that were recognizable visual objects—a house and a face. In this case, while we again observed that preadaptation led to a rivalry bias favoring the other stimulus when rivalry was tested at the retinotopically matched location, we also found a rivalry bias when rivalry was tested at the spatiotopically matched location. In both cases, the direction of the bias was the same—toward the unadapted stimulus. This bias could be due to either a decrease in dominance of the adapted grating or an increase in the dominance of the non-adapted grating. Plotting the average percept durations of both competing patterns separately for both experiments (see **Figures 2B** and **3B**) revealed that the bias resulted from an increase in the dominance durations

of the non-adapted grating. This result is consistent with the finding that adaptation reduces the sensitivity of the adapted neuronal population (Blakemore & Campbell, 1969), which may be compared to physically reducing the stimulus contrast (Blake & Overton, 1979), which in turn is known to increase the dominance duration of a *non-adapted* stimulus (Levelt, 1965). By disentangling the retinotopic and the spatiotopic components of adaptation, we show that this finding is true for both retinotopic (**Figure 2B**) and spatiotopic (**Figure 3B**) adaptation.

Experiment 3—Face-grating rivalry

In **Experiment 3**, we test for a possible influence of feedback on the biased competition. As mentioned in the **Introduction** section, rivalry is generally thought to be initiated at early visual levels and subsequently enhanced at higher levels of processing. This formulation does not explicitly invoke feedback from higher to lower levels as an important contributor to the rivalry process; however, several studies have suggested that feedback during rivalry is important (Alais & Blake, 1998; Alais & Melcher, 2007; Alais & Parker, 2006; Wiesenfelder & Blake, 1990). We sought to investigate the importance of feedback signals in establishing the biased competition by adaptation.

In principle, the effects we observed in **Experiments 1** and **2** could be explained in one of two ways, one which requires feedback to early processes and one which does not. According to the “no feedback” account, it would be assumed that low-level rivalry and high-level rivalry exist independently, and that the observed bias in rivalry following house–face adaptation was strictly due to high-level interactions between neuronal pools sensitive to houses and faces, respectively. An alternative account involving feedback assumes that even though high-level areas processing visual objects may contribute to rivalry, their role is to feedback to early inhibitory processes which are the primary drivers of rivalry (Alais & Melcher, 2007; Alais & Parker, 2006). On this account, the rivalry bias that arises following house–face adaptation would be caused by decreased feedback to early visual levels from the adapted high-level neuronal pool.

In order to investigate the importance of feedback, we instigated rivalry between a face and a grating stimulus and measured separately the effect of preadaptation to the face and the grating. The mismatch in stimulus complexity should preclude high-level rivalry between visual objects but maintain low-level rivalry due to the abundant local image conflict (Alais & Melcher, 2007). We therefore expect that any rivalry bias following face adaptation would be due to an attenuation of feedback signals from extrastriate face-selective neurons. This should be especially so when rivalry is tested at the spatiotopically matched location, as differences between the stimuli in low-level retinotopic adaptation would have no influence in this condition.

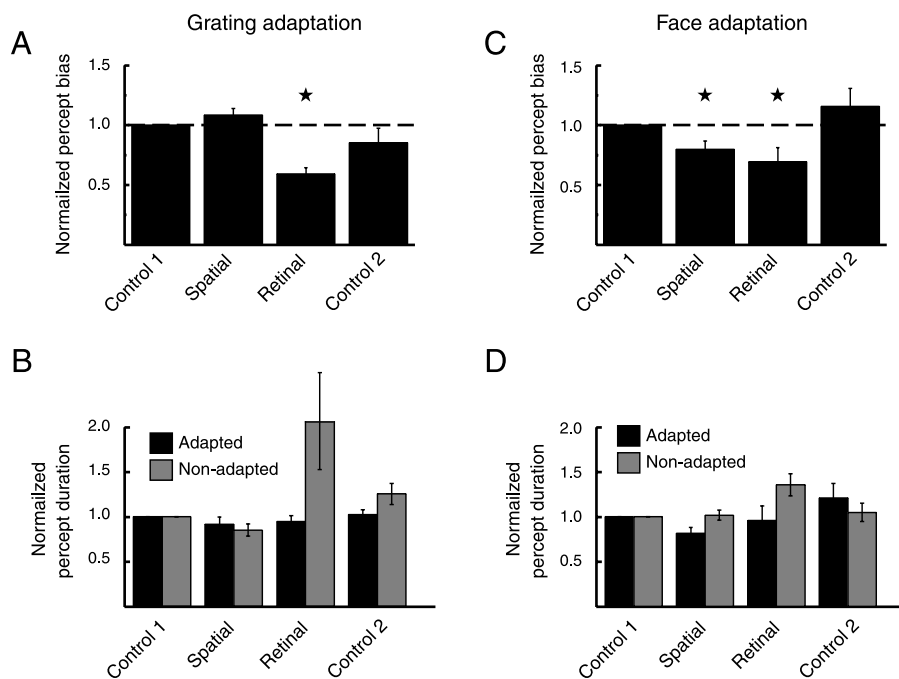


Figure 5. Influences of grating adaptation and face adaptation on face-grating rivalry. (A) Grating adaptation influences only retinotopically matched rivalry stimuli (cf. Figure 2A). (B) The grating adaptation mainly affects the dominance durations of the non-adapted stimuli (although all $p > 0.05$). (C) Face adaptation influences rivalry through feedback both for retinotopically and spatiotopically matched locations (cf. Figure 3A). (D) For spatiotopically matched locations the dominance durations of the adapted stimulus are reduced ($p < 0.04$), while for retinotopically matched locations the dominance durations of the non-adapted stimulus are lengthened ($p < 0.04$). All other $p > 0.1$.

As expected from Experiment 1, adaptation to grating stimuli only biased face-grating rivalry at the retinotopically matched location (Figure 5A). However, for the same rivalry stimuli, adaptation to face stimuli caused a bias for both retinotopic and spatiotopic conditions (Figure 5C). These findings indicate that feedback from spatiotopic areas, activated by the face stimulus, makes an important contribution to the rivalry process at earlier visual areas. As observed before in Experiment 1, the retinotopic bias following grating adaptation was caused by an increase in dominance duration of the non-adapted grating (Figure 5B). However, following face adaptation, the rivalry bias at the spatiotopically matched location that we attribute to attenuated feedback was primarily caused by a decrease in the duration of the adapted face stimulus.

Experiment 4—Scrambled face-grating rivalry

The results in Experiment 3 point to the importance of complex form (e.g., face) information for spatiotopic adaptation influences on rivalry. However, the face and the grating stimuli do not only differ in form content but also contain very different spatial frequency content. Possibly, the spatiotopic effects we measured in Experiment 3 were due to the broader spatial frequency content of face stimuli compared to grating stimuli and not the form information.

A stimulus that contains the same spatial frequency content but not the form content of a face is a phase-scrambled face stimulus. Therefore, to investigate whether form or spatial frequency content *per se* was important, we induced rivalry between grating and phase-scrambled faces after adaptation to the phase-scrambled face. Figure 6 shows that adaptation to a phase-scrambled face only influences the rivalry behavior at retinotopically matched locations ($p < 0.02$). These results therefore show that the spatiotopic adaptation

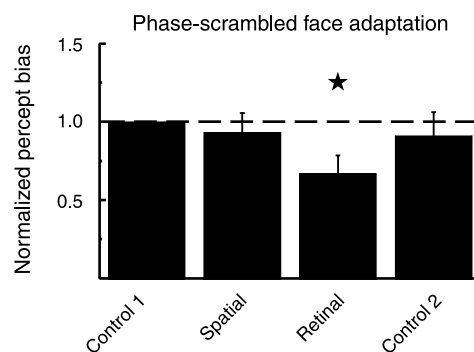


Figure 6. The influence of phase-scrambled face adaptation on rivalry. (A) Normalized percept biases. Adaptation only influenced the bias for retinotopically matched locations ($p < 0.02$, all other $p > 0.25$).

effect of [Experiment 3](#) is not due to a broad spatial frequency content of the stimulus, but instead is due to form content.

General discussion

Accumulating evidence suggests that binocular rivalry is a multi-level process (Blake & Logothetis, 2002), although much remains unknown about the degree of interaction and independence between these different levels. Preadaptation provides a useful tool in this respect for two reasons. First, adaptation is a key factor in determining the dynamics of the rivalry process (Blake & Overton, 1979; Blake et al., 2003; Noest et al., 2007), and second, the neural loci of selective adaptation are far better understood than those of the rivalry process (see [Introduction](#)). There is therefore great potential for adaptation to elucidate the neural processes underlying rivalry. In this report, we have shown that preadaptation to simple and complex stimuli affect rivalry dynamics in different ways. Specifically, we have shown that the effects of adaptation to simple grating stimuli on rivalry dynamics are limited to retinotopically matched locations, whereas the effects of adaptation to more complex stimuli such as houses and faces are observed spatiotopically (in addition to retinotopically).² This last effect is not due to the fact the complex stimuli have a broader spatial frequency content, as we have shown in [Experiment 4](#) that adaptation to phase-scrambled faces does not influence rivalry behavior at locations that are spatiotopically matched to the adaptation location.

We found that retinotopic and, when it occurs, spatiotopic adaptation have qualitatively similar influences on rivalry dynamics. Retinotopic adaptation predominantly influences the dominance durations of the non-adapted stimulus, and we show that this rule also holds for spatiotopic adaptation, indicating that these processes may operate through similar mechanisms. Interestingly, however, the time courses of these adaptation influences on rivalry differ. As shown in [Figure 4](#), the time course for the retinotopic adaptation effect was initially strong but dissipated over time, although it remained stronger than the spatiotopic effect even during the final third of the rivalry observation period (i.e., 20–30 s after adaptation). In contrast, the spatiotopic effect is smaller but still significant and remains largely unchanged over the course of the 30-s trial. This suggests that adaptation not only builds up more quickly for complex stimuli (as suggested by Alais & Melcher, 2007) but may also last longer than adaptation to simple stimuli. These long time windows are perhaps further support that the spatiotopic effects are due to feedback and possibly attentional influences (see below).

The origin of the spatiotopic adaptation

The spatiotopic effects of adaptation we report have at least two possible origins. First, we may have measured a truly spatiotopic effect, in that the adaptation is linked to the spatial position at which it occurred before an eye movement was made. A second possibility, however, is that the spatiotopy we observed could be artifactual, being simply a consequence of the large receptive fields in higher visual areas. According to the second hypothesis, the spatiotopic effects we measured during the test period would arise from the same neurons adapted during the preadaptation phase but are simply expressed at a different position in their receptive field. Neurophysiological data show that receptive-field sizes are far larger for cells in higher visual areas responsive to visual objects than they are for orientation-selective cells in V1 (Gattass et al., 2005). It would therefore appear to be consistent with the second hypothesis that spatiotopic adaptation effects were greater for house and face stimuli than for gratings. However, we can discount this possibility on the basis of our Control 2 condition (see [Figure 1](#)). In this condition, we measured adaptation effects at a location that was the same distance from the retinotopic location as the spatiotopic test location was. The second hypothesis would therefore predict the same adaptation effects should occur at both locations. However, we only found adaptation effects at the spatiotopic location ([Figure 3A](#)), and we therefore believe that this represents a truly spatiotopic adaptation effect.

In order to obtain a spatiotopic representation, a decoupling from retinal stimulation needs to occur. Such decoupling requires information from extra-retinal sources. In our experiment, the only source of extra-retinal information comes from eye-movement-related signals. One of two main sources of extra-retinal information is the efferent copy, which is a copy of the motor command that instructs the muscle to act. This copy of the motor command is thought to inform sensory areas of upcoming changes in visual input due to self-motion (Wexler & van Boxtel, 2005; Wolpert & Flanagan, 2001). Neurons in these areas may react by changing the position of their receptive fields (see below). The other main source is proprioceptive information, which provides postural information, e.g., the position of the eye in the head. Proprioceptive information is necessarily more sluggish than the efferent copy, but eye-position signals can still provide useful information in certain conditions such as in depth perception (see e.g., Backus, Banks, van Ee, & Crowell, 1999). Indeed, eye-position signals could have played a role in our experiments because the adaptation and test phases were relatively long, although the efferent copy from the eye movement is likely to be the most potent source informing spatiotopy (see e.g., von Helmholtz, 1925).

Eye movements also give rise to many other effects. For example, neurons in a multitude of cortical areas are known to change their firing patterns and even their receptive-field locations (e.g., Andersen, 1997; Duhamel, Colby, & Goldberg, 1992; Wexler & van Boxtel, 2005) as a consequence of saccadic eye movements. These receptive-field changes occur just before the start of a saccade and are important in spatiotopy because they ensure space is remapped from the initial eye position to the new position, so that spatial correspondence is maintained across saccades (Duhamel et al., 1992). If a neuron whose receptive field is remapped in this way is preadapted prior to the eye movement, its adapted state should be able to be tapped equally well in its new (spatiotopically matched) receptive-field location. Such a mechanism would explain our results. Interestingly, the remapping of receptive fields seems to be much stronger in higher visual areas than in lower areas and is nearly absent in V1 (Nakamura & Colby, 2002). This ties in well with our finding that spatiotopic adaptation occurred for complex stimuli such as faces and houses but did not occur for simple grating stimuli.

The influence of feedback

In [Experiment 3](#), we looked more closely at the origin of the spatiotopic effects of adaptation. As noted above, rivalry may take place at multiple levels in the visual system, and one of our motives in this study is to find out how these levels interact. The results from [Experiment 2](#) were ambiguous regarding the origin of house–face rivalry: Adaptation could have biased rivalry at a high level (where rivalry-related activity changes have been measured; Tong, Nakayama, Vaughan, & Kanwisher, 1998) by specifically desensitizing one of the two competing neural populations representing the visual objects, or it could have biased low-level rivalry as a result of decreased feedback from the desensitized high-level area (Alais & Melcher, 2007).³ [Experiment 3](#) demonstrates that at least part of the spatiotopic, and likely also retinotopic, influences are caused by feedback from high- to low-visual areas. It has been suggested previously that feedback helps in coordinating perceptual coherence over many local rivalry zones (Alais & Melcher, 2007) and specifically biases perceptual interpretations that are consistent with context (Alais & Blake, 1998; Alais, Blake, & Lee, 1998). [Experiment 3](#) shows that feedback not only provides an interpretation bias, but that this feedback bias is stable despite the occurrence of eye movements. This mechanism would provide the visual system with a cost-effective way of processing ambiguous information: Instead of trying to solve ambiguities anew after each eye movement, it could quickly determine whether the previous interpretation can be maintained before searching for alternatives.

In line with previous findings showing influences of feedback from spatial context (see, e.g., Blake & Logothetis, 2002), we find that the feedback imposed by temporal context (i.e., adaptation) specifically influences the time of suppression of the adapted stimulus ([Figure 5D](#)). This adaptation effect should be most evident (as it is in our data) when testing at a spatiotopically matched location, as this would be free from non-feedback-related effects such as retinotopic adaptation. However, feedback cannot be the only factor involved in the rivalry process because it operates mainly on the dominance durations of the adapted stimulus, while the adaptation bias mainly affected the dominance of the non-adapted stimulus (see [Experiments 1](#) and [2](#)). It appears therefore that the rivalry system can operate independently of any feedback influence when stimuli are simple, presumably as inhibitory interactions between competing pools of early neurons. In addition, when the stimuli are complex visual objects or when global context is provided, feedback from higher-level areas can influence these low-level interactions. However, because it affects mainly the adapted stimulus rather than the unadapted one, feedback appears to operate through a different mechanism than rivalry itself (see also Blake & Logothetis, 2002).

Interestingly, the influences of feedback that we find mirror those found previously for attentional control (Chong, Tadin, & Blake, 2005; Meng & Tong, 2004; van Ee, van Dam, & Brouwer, 2005), in that attention increases dominance durations of the attended stimulus, while leaving the dominance durations of the non-attended stimulus largely unaffected. Since attention is also proposed to influence rivalry through feedback (e.g., by increasing subjective contrast; Carrasco, Ling, & Read, 2004; Klink et al., 2008; Reynolds & Chelazzi, 2004), perhaps adaptation-based and attention-based influences take similar routes toward their influence on rivalry. On the other hand, it has been reported that attention on a stimulus reduces the stimulus' negative aftereffect (Suzuki & Grabowecky, 2003) and therefore potentially the influence of the preadaptation procedure on rivalry. In future research, it may therefore be interesting to pit the preadaptation procedure against an attention-based procedure during rivalry and study how they interact.

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Footnotes

¹Note that retinotopic adaptation is not identical to retinal adaptation. Retinotopic adaptation takes place relative to the position on the retina, but not necessary in the retina itself.

²Note that the spatiotopic adaptation effect we show for faces is not necessarily linked to the spatiotopic adaptation previously reported for face identity (Melcher, 2005).

³The final logical alternative—that rivalry is entirely early and local—can be excluded because of observations such as high-coherence and deep suppression of rivaling complex images (Alais & Melcher, 2007; Alais & Parker, 2006; Nguyen et al., 2003) and the spatiotopic adaptation we report above.

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