# CONSCIOUS AWARENESS DETERMINED BY SELECTIVE GATING OF INFORMATION IN EARLY VISUAL AREAS

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# Abstract

A number of psychophysical methods that suppress retinal input from reaching awareness have been used to isolate and study the neural correlates of visual consciousness. I describe a novel disappearance phenomenon in which a low-contrast peripheral pattern is vividly erased from awareness: after adapting to the pattern for a few seconds, flashing a high-contrast patch over it can elicit the perceptual disappearance of the stimulus. This finding was explained in terms of nonlinear interaction between adaptation to sustained spatial pattern and rapid gain adjustment to transient change. It was next shown that transient changes contingent upon prior adaptation elicit perceptual alternations in structure from motion, binocular rivalry, Necker cube, and ambiguous apparent motion—linking disappearance phenomena and bistable perception. We next used binocular rivalry and inattentional blindness to examine if invisible inputs influence the neuronal mechanisms that adapt to different aspects of the stimuli. The face identity-specific aftereffect was found to be cancelled by binocular suppression or by inattentional blindness of the inducing face. Conversely, the same suppression did not interfere with the orientation-specific aftereffect. Thus, the competition between incompatible or interfering visual inputs to reach awareness is resolved before those aspects of information that are exploited in face identification are processed. Subsequent experiments showed that face identity aftereffect is invariant to eye movements, but fMRI adaptation in face-selective region of the fusiform cortex did not show such invariance. Therefore identity aftereffect originates either at the same level or subsequent to the level of face processing in the fusiform area. Next, we show that recognition of facial emotional expressions occurs after the level of attentional selection: visual search results were incompatible with preattentive processing of emotional categories. We thus suggest that the invisible or unattended faces are suppressed in early visual areas. This conjecture was experimentally confirmed by showing that when a stimulus is not attended, it evoked a weaker and weaker response in fMRI in subsequent stages of visual processing hierarchy. Thus, attention determines how far the visual input is processed and whether or not a high-level representation of the input would be constructed.

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# 1 INTRODUCTION

## 1.1 Disappearance phenomena as a tool for studying consciousness

The following chapters describe a sequence of studies that examine the relationship between neuronal activities evoked by external visual stimulation and the subjective phenomenal experience of the observer. The central thesis in these studies is that the input to the visual system is processed and gated through a hierarchy of visual area and our subjective experiences directly correlate with the activity in late stages of this hierarchy, where high-level representations of the phenomenal world are created and maintained.

The main tool used to study the neural correlates of visual consciousness psychophysically as well as in combination with imaging and electrophysiological techniques is a class of illusions commonly referred to as disappearance phenomena. Binocular rivalry is the exemplar disappearance phenomenon: if two incompatible images are displayed to the two eyes of an observer, e.g., by using a mirror set, then the perceived image is quite often not a fused combination or superposition of the two images. Instead, the brain suppresses the input form one of the retinae, and the image presented to the other eye dominates the percept. The competitive process is automatic, with little or no voluntary control over which of the two images reaches awareness (Blake and Logothetis 2002; Meng and Tong 2004). After a few seconds, the percept might change and the once suppressed image might become dominant for some time before it is suppressed again, and this cycle continues as long as the input remains the same, similar to other bistable phenomena.

The important advantages of binocular suppression and other similar disappearance phenomena over other methods like masking or inattentional blindness are that they can be used to alter the percept without changing the input and they vividly and compellingly suppress a stimulus from awareness for a few seconds or more (up to minutes in the case of continuous flash suppression;  Tsuchiya and Koch 2005). Thus, disappearance phenomena can be used in conjunction with other tools such as selective aftereffects to study consciousness and dissociate it from attentional and memory related effects (Kim and Blake 2005).

## 1.2 Methodological perils and problems

The mechanisms underlying disappearance phenomena are not fully understood, which might make it difficult to interpret the results in paradigms that rely on disappearance phenomena to study consciousness. Binocular rivalry is the most studied disappearance phenomenon. Nonetheless it is unclear where the site of binocular suppression is. FMRI evidence suggest binocular competition and suppression occurs as early as in V1 (Polonsky *et al.* 2000; Tong *et al.* 1998). Suppression might even occur even at the level of LGN (Haynes, Deichmann and Rees 2005; Wunderlich, Schneider and Kastner 2005)—which could only be due to feedback from V1 because LGN neurons receive input from only one eye. Yet, single cell recording studies find little or no effect in LGN (Lehky and Maunsell 1996) and a small effect  in V1 (Leopold and Logothetis 1996), but show robust suppression in later cortical areas such as the inferior temporal cortex and the visual areas in superior temporal sulcus (Sheinberg and Logothetis 1997). Studies using hallucinogenic drugs are compatible with the hypothesis that a brainstem oscillator in the serotonergic pathway underlies disappearance phenomena and other perceptual rivalries (Carter and Pettigrew 2003; Carter *et al.* 2005). Finally, transcranial magnetic stimulation indicates a role of parietal cortex in modulating binocular rivalry and motion induced blindness (Funk and Pettigrew 2003; see also Lumer, Friston and Rees 1998). Much less is known about the site of other disappearance phenomena.

Different chapters in this thesis provide experimental evidence that sheds light onto how these seemingly inconsistent findings could be reconciled. Although direct demonstration of the site or sites of binocular suppression is not the topic of this thesis, we present a framework that can be used to understand how mechanisms underlying disappearance phenomena are related and how they affect visual consciousness.

### 1.3 Linking disappearance phenomena and bistable perception

Chapter 2 describes a novel disappearance illusion: induced disappearance. Induced disappearance is phenomenally similar to the disappearance of low-contrast peripheral targets after prolonged fixation (Troxler 1804). However, unlike Troxler fading, induced disappearance only requires a few seconds of adaptation. In that respect, induced disappearance is more similar to motion-induced blindness (Bonneh, Cooperman and Sagi 2001) and flash-suppression in binocular rivalry (Wolfe 1984) than Troxler fading. These similarities suggest that suppression following adaptation (Troxler fading) and suppression following competition (motion induced blindness and binocular rivalry) are likely to be simply two sides of a single spectrum of disappearance phenomena.

A series of experiment described in chapter 2 illustrate that the interaction between two separate mechanisms which process sustained and transient aspects of the visual input, respectively, underlie the suppression of the retinal input in induced disappearance and possibly other disappearance phenomena. Sustained adaptation is selective and occurs at a level that receives input from both eyes. The effect of transient adaptation is less selective and location specific, is modulated by context (grouping), and is presumably mediated through attentional mechanisms. A simple model that assumes that sustained and transient adaptation modulate respectively the offset and the gain of neuronal response functions can explain the results. This model can also explain why there is evidence for involvement of both topographic selective visual areas and high-level nonspecific attentional mechanisms in binocular rivalry. The model also predicts that if the adaptive local component of binocular rivalry is reduced (either by intermittent presentation or by moving the retinal position of the rivaling stimuli), the percept would become stabilized, a prediction that is in agreement with recently published empirical results (Blake, Sobel and Gilroy 2003; Leopold *et al.* 2002).

Chapter 3 examines the relationship between induced disappearance and perceptual bistability. We show that the same paradigm can induce perceptual alternations in a number of bistable stimuli (Necker cube, structure from motion, ambiguous apparent motion, and binocular rivalry). Moreover, the same conceptual model can quantitatively simulate the behavioral results.

### 1.4 Level of suppression and the fate of invisible faces

Thus, chapters 2 and 3 succeed to link different disappearance phenomena together and to other perceptual alternations via a model that has a gain and an offset component. Nonetheless, the level at which suppression occurs remains to be addressed. Psychophysical evidence suggests that complete suppression in binocular rivalry occurs after the level in which simple features such as orientation, color, and local motion are processed and the corresponding aftereffects originate. Suppression of high contrast stimuli during adaptation results in little reduction of most aftereffects (Blake and Fox 1974; Lehmkuhle and Fox 1975; White *et al.* 1978) (but see Blake et al. 2006). Recent fMRI evidence suggests that substantial information from the suppressed image can reach late stages of the visual hierarchy (Fang and He 2005; Moutoussis and Zeki 2002). These findings immediately raise a more fundamental question: is there a level before which the competition between visible and invisible stimuli is eventually resolved? Or perhaps, is there an ongoing competition at all levels of representation, and the collective behavior of the interconnected network of rivalries determines our phenomenal percept?

Chapter 4 presents experimental evidence that supports the hypothesis that the competition between visible and invisible stimuli is resolved within the visual system (i.e., there are visual areas that do not have access to the information from the suppressed stimulus). To examine this hypothesis, the face identity specific aftereffect, a high-level aftereffect that presumably originates in the late stages of object processing hierarchy (Leopold *et al.* 2001), was used in combination with binocular rivalry. The results show that the face identity aftereffect is cancelled by binocular suppression: in trials in which the face was not seen there was no subsequent aftereffect. Therefore, the information from the suppressed eye must have been entirely suppressed before reaching stages that are involved in processing of face identity. In similar conditions, we showed that binocular suppression has little effect on the magnitude of the orientation selective adaptation, suggesting that most of the suppression occurs somewhere in between orientation selective and face selective stages of the visual processing hierarchy.

The implications of this result for our understanding of the organization of the visual cortices depend on the neuronal sites of adaptation to orientation and adaptation to face identity. Single cell (Barlow and Hill 1963) and fMRI studies (Engel 2005; Fang *et al.* 2005; Larsson, Landy and Heeger 2006) show that orientation selective adaptation occurs as early as in the primary visual cortex, and there is evidence that some adaptation occurs even as early as the level of the retinal ganglion cells (Hosoya, Baccus and Meister 2005). The experiment described in chapter 5 was initially intended to study orientation selective adaptation in the absence of awareness using fMRI based on a paradigm suggested earlier by Tootell et al. (Tootell, Hadjikhani, Vanduffel et al. 1998). However, we instead found that the hemodynamic changes in Tootell's paradigm are driven by top-down attention, not adaptation. Despite our and others (Boynton and Finney 2003) failure to find a V1 fMRI component that could be attributed to orientation-selective adaptation, subsequent published results leave little doubt that considerable orientation selective adaptation occurs at or before V1. The early origin of orientation-selective adaptation thus does not help much in constraining the site of binocular rivalry.

We next set to determine the neural correlate of the face identity-selective aftereffect. It has been suggested that face processing in humans involve a particular regions of the cortex in the fusiform gyrus: the fusiform face are (FFA) (Kanwisher, McDermott and Chun 1997). Numerous studies were able to isolate this area which responds vigorously to faces, and thus seems to be the main site of face selective processing in humans. There are a number of researchers that have suggested that the visual cortex in the fusiform gyrus is a general visual expertise area for subordinate processing (Gauthier et al. 2000; Gauthier and Tarr 2002; Gauthier et al. 1999; Rhodes et al. 2004; Tarr and Gauthier 2000). Regardless of whether this particular view is correct or not (Grill-Spector, Knouf and Kanwisher 2004), we expected that the site of adaptation to face identity reside in FFA (identification is a case of subordinate processing). It has already been shown that FFA responds less to repeated presentation of the same face than to the presentation of a new face (Avidan, Hasson et al. 2002; Grill-Spector and Malach 2001). However, to establish that FFA adaptation in fMRI and psychophysical face aftereffect are one and the same, it is necessary to show that they behave similarly in all conditions.

Chapter 7 examined this hypothesis by measuring the modulation of fMRI and psychophysical aftereffect with the translation of the retinal images of the stimuli. Such translations occur quite frequently during normal vision because of the movements of the eyes. They also occur because objects themselves move. Our ability to have a coherent percept of the object identity in both cases (retina moves or object moves) implies that high-level representations of objects that are immediately available to our conscious awareness have achieved spatial constancy (via position-invariance or transfer with gaze). The question is whether face identity is represented in such a way or not. If adaptation at one retinal location can evoke an aftereffect at a different location that is as strong as the aftereffect at the same location, then the answer is yes: the mechanisms underlying the aftereffect are at or after the stage that achieves spatial constancy.

This was the case for the psychophysical face identity aftereffect. Results were consistent with the view that the face identity aftereffect is a high-level aftereffect closely linked to our conscious awareness (chapter 4). Surprisingly, the fMRI adaptation in FFA did not show full spatial constancy, and dependence of adaptation on the retinal location of the adapting and test stimuli were consistent with an intermediate representation of faces in the FFA. Thus, face aftereffect might occur at a subsequent stage of cortical processing. Since subsequent areas are not purely visual our results suggest for the first time to our knowledge that a visual aftereffect might arises beyond the level of cortical areas dedicated to visual processing. This finding also explains why FFA activation by a suppressed face (Moutoussis and Zeki 2002) does not necessarily lead to some degree of adaptation to its identity.

Following the finding that faces that are not seen are not registered (at least to the extent that is required for producing a measurable aftereffect), chapter 8 examines whether emotional expressions are processed without awareness. A number of studies have recently reported an advantage in visual search consistent with the hypothesis that negative emotional expressions are processed preattentively and direct attention toward the emotional expression (Eastwood and Smilek 2005; Eastwood, Smilek and Merikle 2001; Hansen and Hansen 1988). The alternative account for the facilitation of visual search for negative expressions is that mechanisms independent of those involved in processing the expression of a face (i.e., mechanisms tuned to accidental features or image primitives rather than emotional expressions) attract attention toward the target. We argue that mechanisms involved in registering facial expressions are tuned to emotion categories such as fearful, angry, or neutral. If the facilitation of the search is not categorical, then it cannot be attributed to preattentive processing of facial expressions. Our results show that image differences—but not category differences—between search target and distracters affect the slope of the visual search time as a function of number of items. Furthermore, we show that a patient with profound deficits in recognition of emotional expression due to bilateral amygdala lesions can nonetheless find targets defined by emotional expressions that she fails to recognize correctly, and her pattern of the facilitation of visual search with image and category differences is the same as healthy individuals. Our results suggest that registering facial expressions requires seeing the face.

### 1.5 Gating information in early visual cortex

The above findings illustrate how early gating of information prevents registration of high level representations of the binocularly suppressed or unattended stimuli. We used fMRI to examine how such gating is implemented in the brain. Because of the slow temporal dynamics of hemodynamic changes which are measured in fMRI, it is impossible to directly dissociate activities reflecting intrinsic mechanisms in each cortical area that underlie feedforward processing of information from feedback activities originating in a different area. A particular instance of this issue is the fMRI evidence showing V1 activity correlates with the percept in binocular rivalry (Lee and Blake 2002; Lee, Blake and Heeger 2005; Polonsky *et al.* 2000; Tong and Engel 2001). Without knowing whether this correlation originates in V1 or elsewhere it is impossible to accept or reject an early origin for binocular suppression based on these results.

In chapter 5, we used a change blindness paradigm to study the correlation between activity in early visual areas and attention or awareness. Observed view a display comprising flickering concentric arcs of gratings (figure 23). The orientation of each grating changed at random intervals and observers were asked to report those changes. By using a combination of crowding (Andriessen and Bouma 1976; Bouma 1970) and masking we were able to make the task difficult such that slightly more than half of the changes were not detected. The Blood Oxygenation Level Dependent (BOLD) signal—a measure of neural activity (Logothetis *et al.* 2001; Mukamel *et al.* 2005) in cortex—in V1 and other retinotopic areas showed a significant increase if and when a change was detected, but not when they actually occurred. In subsequent experiments we showed that the component of the BOLD response that correlates with the percept is stimulus independent and is driven by top-down attention.

In a subsequent study (chapter 6), we tried to dissociate the effect of the top-down attention on the stimulus-driven activation and the stimulus-independent effect by comparing two conditions: in the precue condition attention is deployed before the stimulus onset. Thus, it can affect the stimulus-driven component of the activity. In the postcue condition, attention is deployed after the stimulus-driven activity has considerably subsided, thus minimizing the stimulus-driven effect. In both conditions, we expect to find a stimulus independent component. Nonetheless, the stimulus independent effects should be similar (or behave similarly) in both conditions. Consequently the postcue condition reflects the stimulus-independent effects of top-down attention, whereas differences between pre- and postcue conditions reflect the stimulus-dependent effects.

Consistent with the results of chapter 5, the stimulus-independent effects were observed in retinotopic areas: the stimulus-independent component was as strong in V1 as in V4. Contrariwise, little evidence of a stimulus-dependent effect was found in V1, whereas a significant effect was observed in V4. Behavioral and hemodynamic results were consistent with a model in which attention modulate the gain of the feedforward pathway, and cascaded enhancement or decay of activity in a chain of visual areas determine whether or not retinal information is consciously registered (see Tsotsos et al. 1995; Wilson 2003).

## 1.6 Limitations of a feedforward model

The gain-cascade model is based on a conceptually simple feedforward framework in which top-down feedback can bias perception by modulating the gain of the feedforward processing. This model is biologically plausible, it can explain our results, and it reconciles psychophysical, hemodynamic, and electrophysiological studies of disappearance phenomena and visual attention. However, it inherits the problems of feedforward models, which at best explain only a snapshot of neuronal processing underlying conscious perception. Although feedforward mechanisms might be sufficient for crude superordinate categorization of natural images in controlled experimental settings (Fabre-Thorpe, Richard and Thorpe 1998; Thorpe, Fize and Marlot 1996; VanRullen and Thorpe 2001) and perform reasonably well in computer vision (Riesenhuber and Poggio 2000), it has been argued that there are many instances (e.g., figure 1) that purely feedforward models fail to process and the perceptual analysis of the input necessitates a profound interaction between low- and high-level visual processing (Ahissar and Hochstein 2004; Hochstein and Ahissar 2002; Lee *et al.* 1998; Mumford 1992).

There is no doubt that recurrent models are better models for our highly interconnected brains. However, they are much more complex and do not always provide explanatory power. Some of the recurrent models of vision are not consistent with our empirical findings—for example, chapters 4 and 5 indicate that high-level processing is not preattentive as suggested by the reverse hierarchy theory (Ahissar and Hochstein 2004). These models should be rejected or revised to reconcile with the data.

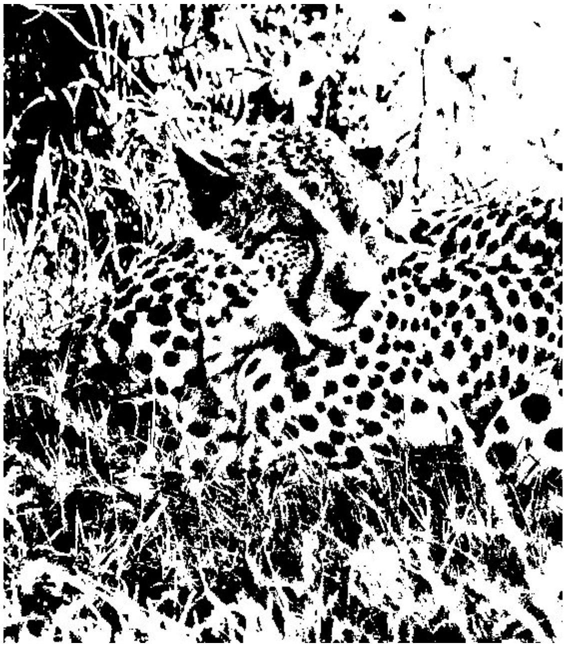

**Figure 1.** The “eureka” effect in vision. Most people who are shown similar figures (Marr's Dalmatian, Marr 1982, p.101; Mooney's faces, Mooney 1957) would not perceive the hidden object immediately, but have little difficulty perceiving it if they use top-down knowledge about the object (e.g., if they guess or are told what the object is). It is also possible to enable some observers to perceive objects that are not actually in the image by providing explicit top-down verbal cues (e.g., a panda bear at the top of the image).

On the other hand, there are perceptual phenomena that are not consistent with a simple feedforward framework and may require a more complicated account. For example, chapter 10 (appendix) presents evidence that perceptual binding is postdictive, i.e., information about events occurring after a target stimulus alters observers’ experience of the target (Eagleman and Sejnowski 2000). Providing a unifying explanatory framework for such phenomena and examining the deviations from the feedforward model in each case are well beyond the scope of this dissertation. Nonetheless, our results suggest that a simple feedforward model—which is an approximation of many biologically plausible models of recurrent visual processing under the experimental conditions in the following chapters—can serve as a simplified framework for understanding and studying the neuronal mechanisms underlying visual consciousness.

# 2 MAKING A STIMULUS INVISIBLE

We observed that presenting a low-contrast Gabor patch (2 cpd, 5 deg eccentricity, contrast = 4%) for 8 seconds and then flashing a 20–30 ms high-contrast patch over it could elicit the perceptual disappearance of a subsequent low-contrast stimulus, whereas neither low-contrast adaptation nor high-contrast flash alone had any considerable effect ( $p < 0.00001$). In other experiments we found: (a) suppressive components are phase-insensitive, (b) the effect transfers between eyes, (c) suppression is selective for orientation, and d) the induction by the transient high-contrast Gabor patch could be transferred to another previously adapted location up to a few degrees. Results indicate synergy between contrast and adaptation through a nonlinear interaction between rapid gain adjustment to transient change and adaptation to sustained spatial patterns. These findings are compatible with non-local mechanisms presumably at the cortical level[1].

## 2.1 Suppressive effect of sustained low contrast adaptation followed by transient high contrast on peripheral target detection

The term "visual disappearance phenomena" groups a spectrum of loosely related circumstances under which salient visual stimuli become perceptually invisible (suppressed). In binocular rivalry, the visual input to each eye is different and one often perceives the input

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[1] This study is published in Vision Research (Moradi, F., and S. Shimojo (2004b). Suppressive effect of sustained low-contrast adaptation followed by transient high-contrast on peripheral target detection. *Vision Res* **44**, 449-460.).

received by one eye alone (Blake and Fox 1974; Wheatstone 1838). After a few seconds, the percept may switch to the other eye. In fading of a low-contrast peripheral target under prolonged strict fixation, suppression follows adaptation rather than rivalry between incompatible stimuli. This phenomenon was described originally in 1804 by Troxler for colored images, and later in 1948 by Cibis for low-contrast gray scale images (Aulhorn and Harms 1972). Troxler fading has been explained in terms of adaptation to the target boundaries (Krauskopf 1963), followed by filling in of the target area with the surrounding background pattern. Unlike rivalry, small eye movements or foveation disrupt Troxler fading.

Recently, visual transients were discovered to trigger disappearance in normal viewing condition. One example is motion-induced blindness (Bonneh *et al.* 2001), where highly liminal targets perceptually disappear and reappear for periods of several seconds when a global moving pattern is presented in the background. Another example was found by Kanai & Kamitani (2003), who demonstrated that a local transient signal such as flashing a ring, apparent motion, or even blinking the target is sufficient to trigger the disappearance of a perceptually salient (but near equiluminance with the background) target. Note that these two phenomena are analogues of masking by moving objects (Grindley and Townsend 1965), and flash suppression (Wolfe 1984) in binocular rivalry, respectively. Only in normal viewing condition, suppression is not in the context of rivalry between two images. Does the transient signal boost earlier adaptation (instead of rivalry), inducing suppression of the subsequent activity?

Foveation can disrupt motion or transient induced blindness, so local adaptation (similar to Troxler fading) might play a role in the aforementioned disappearance phenomena. It is often argued that neither phenomenon requires long steady fixation as opposed to Troxler fading. However, shorter adaptation time can be achieved using high-contrast edge adaptation (Shimojo and Kamitani 2001). These observations motivated us to reexamine the role of adaptation. More specifically, we investigated if transient high-contrast exposure induces disappearance after adaptation to low-contrast spatial patterns, whether there is any interaction between them, and if so, at what level of visual processing the interaction occurs.

We observed that briefly increasing the contrast of a peripheral low-contrast object after a few seconds of strict fixation elicits disappearance of the object, resulting in perceptual filling in of the location with the surround (figure 2a). After a short time—usually around one second or so—the object reappears. Hence, following sustained adaptation to a low-contrast target, transient high-contrast stimulation can induce perceptual disappearance. We refer to this illusion as “induced disappearance,” and will use the term “induction” to refer to the transient high-contrast exposure after sustained adaptation to a low-contrast pattern.

The induced disappearance illusion was equally strong when we inverted the contrast of the high-contrast flash in a subsequent experiment (figure 2b), or when the target was darker than the background. Therefore, the disappearance of the target cannot be explained by light adaptation in retina (see also 2.1.2). We observed that the target reappears after slight eye movements. Note that eye movements result in a visual signal only where luminance is not homogenous (first-order edges). Presumably, induced disappearance is mediated by filling-in following suppression of boundaries. However, we failed to induce disappearance using texture defined targets (second-order edges, see 2.1.7). These observations indicate that induced disappearance predominantly suppresses first-order spatial patterns (luminance defined edges). Therefore, in subsequent experiments we used Gabor patches to study induced disappearance.

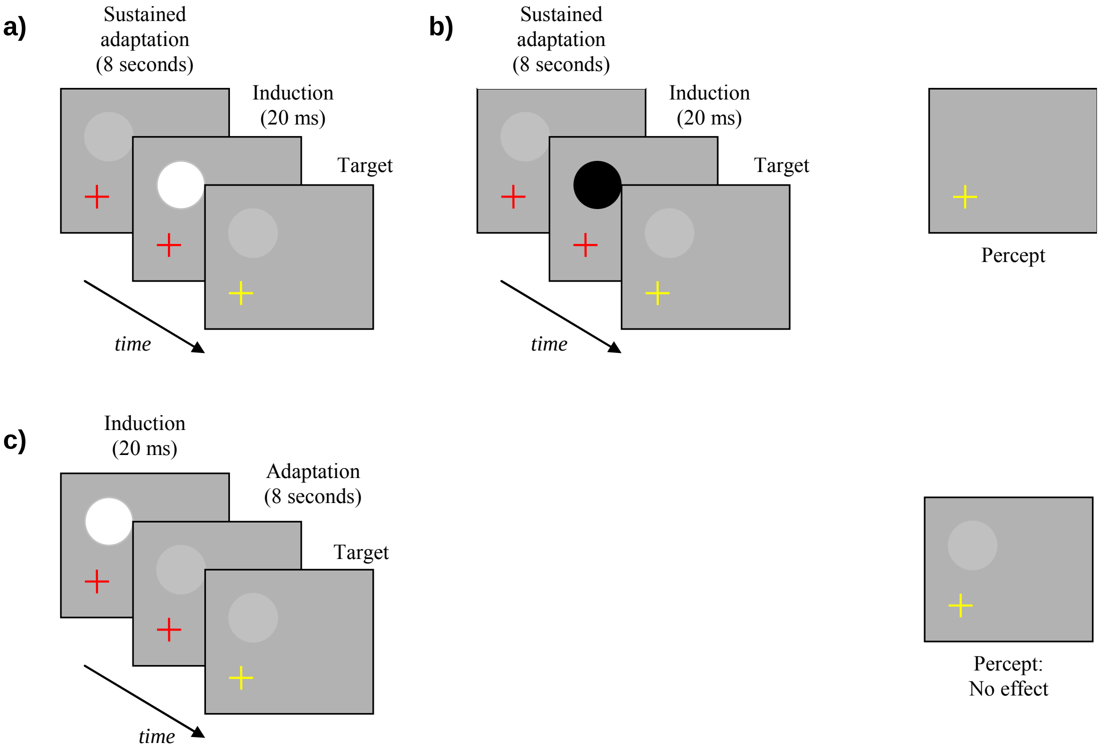

**Figure 2.** Transient induced disappearance.
(a),(b) Induction of disappearance by brief presentation of a high-contrast stimulus after adaptation to a low-contrast pattern.
(c) Reversing the order of the sequence removes the effect.

The main difference between the present study and previous studies is the assessment of the combined effect of the sustained low-contrast and transient high-contrast stimuli. We replicated and quantified our findings using Gabor targets (2.1.2). Inter-ocular transfer of the disappearance and orientation selectivity was studied in 2.1.5 and 2.1.7. In 2.1.8, we showed that the induced disappearance of the target is not local to the site of high-contrast stimulation. Results are discussed in terms of an optimal neural encoder with internal noise.

### 2.1.1 General methods

Volunteers from the California Institute of Technology with normal or corrected to normal vision participated in one or more experiments (2 investigators and 7/3/8 naïve observers for experiment 1/2/3 (respectively), 1 investigator and 5 naïve observers in experiment 4). Experimental sessions were conducted in a dimly lit room, with the monitor as the only light source. The stimuli were presented on the computer screen (Sony Multiscan 20sh, 1024×768). Participants viewed the screen binocularly from 53 cm and were asked to keep their gaze at a red crosshair presented at the center of the screen over the homogenous gray background (36cd/m2) during the whole session. After 30 seconds, trials started. Each trial consisted of an adaptation phase, during which a low-contrast Gabor signal (2 cpd, $\sigma = 1.4$ deg, unless otherwise specified in the description of the experiment, contrast $\approx 4\%$) was randomly presented in one quadrant at 5 deg of eccentricity, followed by a brief (20 ms) high-contrast Gabor signal (induction) with similar spatial parameters (unless mentioned otherwise) at the same location. After 50ms, a low-contrast Gabor signal (target, 80% of the trials), or a blank region (20% of the trials), was displayed for one second, followed by a random-dot mask (figure 3b).

Observers were instructed to press a key to indicate presence or absence of the target stimulus. In about 20% of the trials (catch trials), no target was presented. To avoid confusing adapting and target stimuli, the color of the fixation crosshair was temporarily changed to yellow to indicate the test phase of the trial. The next trial started 2 seconds after the response, always in a different quadrant. Overall, the stimuli were displayed with equal frequency in the four screen quadrants. The phase of the sustained low-contrast Gabor was shifted by $\pi/2$ every 250 ms to reduce the retinal adaptation. In experiment 1a we also used stationary Gabor signals during the sustained adaptation phase.

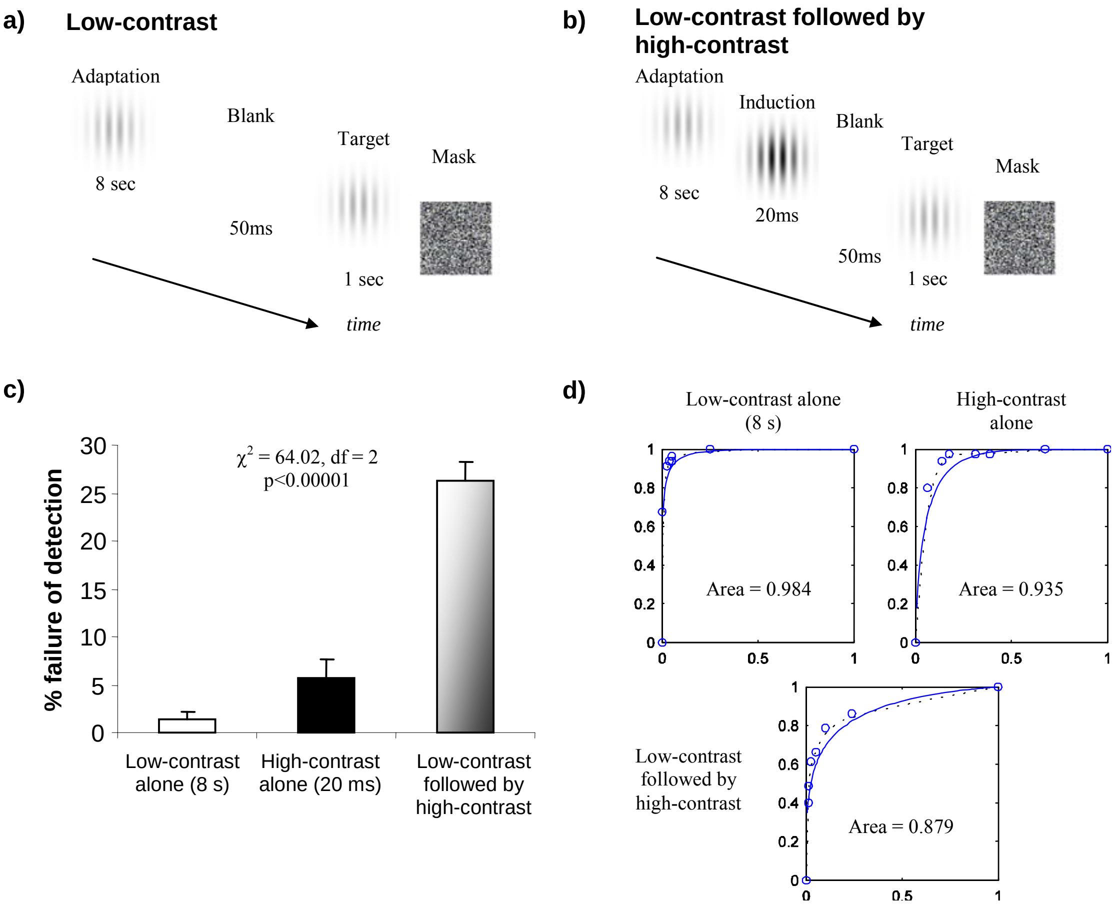

**Figure 3.** Induction of disappearance by brief presentation of high-contrast Gabor after adaptation to low-contrast stimulus.

The experiment paradigm: (a) Low-contrast alone, (b) Low-contrast followed by high-contrast (high-contrast alone condition is not shown).

(c) Results for nine subjects.

(d) ROC-curves for five subjects, same conditions as in c.

In a preliminary experiment, disappearance was successfully induced in eight naïve observers and the two investigators. For three other observers, the frequency of fading was non-selectively too low for a quantitative assessment: the subjects always correctly identified the presence or absence of target in all conditions. However, a result similar to other observers was obtained when we increased the width of the flash ($\sigma$ = 1.87 deg) and increased its duration to 30ms (two subjects) or 50 ms (one subject). For these subjects we used the modified parameters in all experiments. Two of these subjects did not participate in data shown in figure 5 and figure 7 for unrelated reasons.

### 2.1.2 Induced disappearance vs. Adaptation and masking

Under specific circumstances sustained adaptation can elicit disappearance of a low-contrast target. Prolonged adaptation results in the elevation of the contrast threshold that may be enough to suppress the stimulus (Troxler fading). Similarly, transient exposure to a high contrast stimulus can mask a subsequent less salient target stimulus, especially when the target is presented for a short duration (forward masking effect). Adaptation and masking are conceived to involve different circuitries. Is the observed disappearance of the target after sustained adaptation to low-contrast and induction with transient high-contrast a separate effect? Alternatively, is the combination of adaptation and induction more effective than either one alone?

A possible mechanism that may play a role is local (retinal) luminance adaptation. To examine other interactions between the sustained and transient components, we continuously shifted the phase of the Gabor patch during the adaptation phase of the trial. Drifting the stimulus averages out total local absorbed light energy, and reduces the retinal afterimage. We also examined the effect of reversing the contrast polarity of the adapting and inducing stimuli on the disappearance of the target. This part is discussed in section 2.1.4.

#### Methods

The frequency of induced disappearance (8 second adaptation followed by 20ms high-contrast) was compared to the frequency of fading of the target after 8 seconds of adaptation to stationary (1/3 trials) or drifting (2/3 trials) Gabor patch only, and after 20 ms high-contrast Gabor. The paradigm is illustrated in figure 3a,b. The contrast of the Gabor target is 4%, which is considerably above the detection threshold. The null hypothesis is that the probability of failure to detect the target in the combined condition (after adaptation to sustained stimulus followed by transient stimulus) is less than or equal to the sum of the probabilities of detection errors attributable to local peripheral fading (Troxler fading) and forward masking. Participants were asked to report presence or absence of the target. They could also optionally report if the target partially faded, or appeared like a different pattern such as a Gaussian. Those reports (3.7% of the trials) were discarded from the analysis.

#### Results and discussion

For parameters used in this experiment, the proportion of detection failure is significantly higher after the combination of the sustained low-contrast adaptation and transient high-contrast induction than either following sustained adaptation or induction alone ($p < 0.00001$, figure 3c). Furthermore, the disappearance is significantly more frequent than the linear combination of the effects of the two other conditions (26.26% vs. 9.52%, $p < 0.0001$). Hence, induced disappearance cannot be explained in terms of Troxler fading or forward masking.

### 2.1.3 Experiment 1b

To rule out that observers used different cognitive criteria in experiment 1a (response bias) we asked five observers (3 naïve plus two investigators) to report their confidence in presence or absence of the target. They were informed that the target is absent in half of the trials. Each observer finished two sessions of 48 trials (16 trials per condition). The receiver operating characteristic (ROC-curve) was obtained for each condition (figure 3d).

#### Results and discussion

Subjects performed accurately in sustained low-contrast adaptation condition, and nearly as well in brief high-contrast exposure condition (except one subject that confused afterimage of high-contrast Gabor with target). In contrast, participants frequently failed to report the target in the combined condition, even when they were confident about their responses. The ROC-curves suggest that sustained adaptation followed by brief high-contrast induction results in both a lower discriminability and a bias toward failing to report the target. Note that signal detection theory does not have any construct corresponding to subjective awareness of the stimuli (Macmillan and Creelman 1991). However, the ROC-curve is more compatible with a Gaussian model reflecting low-level detection difficulty (solid line) than a high-threshold model reflecting response bias (high-threshold model predicts ROC-curve would be a straight line) (Wickens 2002). Furthermore, since the trials were randomized, it is unlikely that observers could switch between different response criteria for different conditions. Thus the obtained differences among the conditions are unlikely to be attributed to cognitive or response biases.

### 2.1.4 Phase sensitivity and retinal component of induced disappearance

The results in experiment 1a were examined for any effect of contrast polarity. Figure 4a compares induced disappearance following sustained adaptation to stationary vs. drifting Gabor signal (phase shifted by $\pi/2$ every 250 ms). Probability of disappearance was significantly higher following adaptation to drifting Gabor signals compared with the stationary signals ($p < 0.001$). For the stationary condition, the frequency of disappearance after adaptation to stationary Gabor was not affected by reversing its polarity with respect to the target same phase vs. opposite phase ($p = 0.89$). A stronger effect in the drifting condition compared to the stationary conditions is consistent with the idea that reducing adaptation in phase-sensitive stages of visual processing results in stronger activation and consequently more adaptation in subsequent phase-insensitive stages.

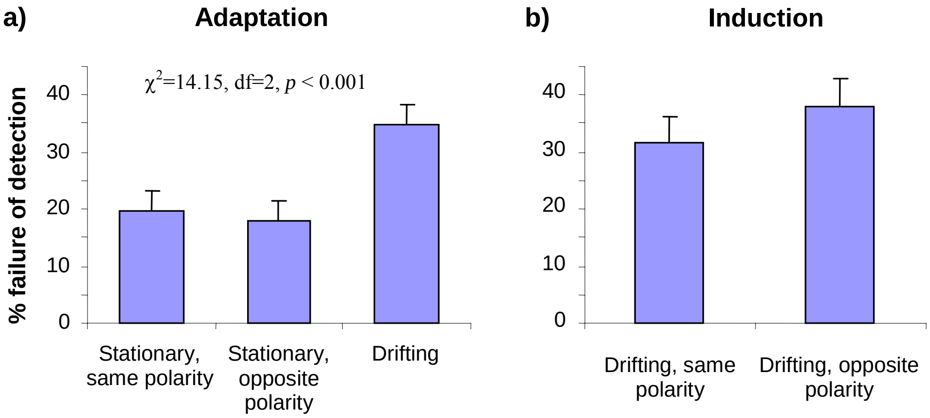

**Figure 4.** Disappearance does not depend on contrast polarity.

(a) Disappearance after sustained adaptation to stationary or drifting low-contrast Gabor for eight seconds, followed by transient induction by high-contrast Gabor (nine subjects, same as figure 3a-c). The stationary low-contrast sustained adaptation had either the same polarity as the target or the opposite polarity. There is no significant effect of contrast polarity for stationary adaptation. In the drifting condition the phase of the Gabor patch was shifted by $\pi/2$ every 250ms to minimize retinal adaptation during the sustained adaptation. This appeared as a slow and relatively smooth motion to the subjects.

(b) Effect of contrast polarity of the high-contrast stimulus (with respect to the target) on induction of disappearance. Same subjects and same experiment as figure 3a-c. High-contrast Gabor patch followed eight seconds of adaptation to a drifting low-contrast stimulus. Error bars indicate S.E.M.

We also looked for any effect of the polarity of the high-contrast inducer with respect to the target, using drifting contrast during the sustained adaptation (figure 4b). The detection was not found to be affected by the polarity of the transient high-contrast Gabor, either ($p > 0.4$).

Neurophysiological evidence indicates that the early representation of visual information (retina, LGN, V1 simple cells) is selective for spatial phase information, but higher areas lose their selectivity. Our results suggest that phase-invariant cortical mechanisms are involved for both adaptation and induction phases of induced disappearance.

### 2.1.5 Induced disappearance as a function of adaptation time

Based on the above results we argue that induced disappearance cannot be explained as fading by visual transients (Kanai and Kamitani 2003). First, removing the sustained low-contrast Gabor alone for 50ms (figure 3a) does not induce disappearance of the target. Second, adaptation appears to be a necessary component (in contrast to Kanai & Kamitani's remark that prolonged adaptation is not necessary).

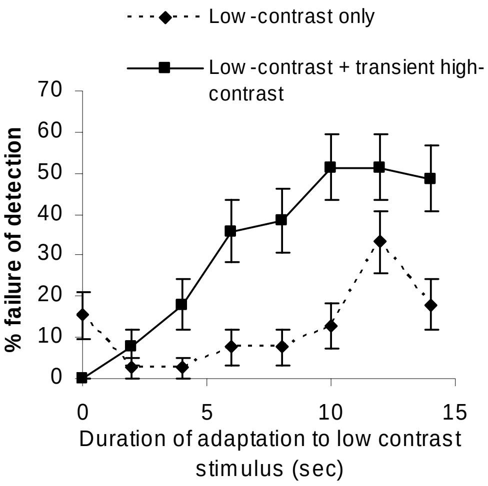

**Figure 5.** Disappearance depends on adaptation time.

The effect of the duration of sustained adaptation to low-contrast Gabor signal followed by induction by brief presentation of high-contrast Gabor on detection of the subsequent target (solid line), compared with adaptation to low-contrast alone (dashed line) (four subjects, pooled data). Error bars indicate S.E.M.

The cumulative nature of the adaptation in induced disappearance can be best illustrated by varying its duration (figure 5). The duration of sustained adaptation (drifting Gabor) was varied between 0 (no adaptation) to 14 seconds in four participants. A 20 ms high-contrast inducer followed adaptation. Half of the trials were conducted without flashing the high-contrast pattern (no induction) and served as control (dotted line).

For both induced disappearance and control conditions the probability of failing to detect the target increases almost monotonically as a function of adaptation time, suggesting temporal integration. For the combined condition the effect starts earlier and rises faster as the duration of adaptation increases compared with the control (adaptation only) condition, indicating synergy between adaptation and induction.

### 2.1.6 Ocular transfer

We examined ocular transfer of induced disappearance using dichoptic stimulation. Observers viewed the monitor through a set of mirrors, such that each eye viewed a separate region of the screen. Adapting low-contrast and brief high-contrast stimuli were presented to one eye. In 40% of the trials, the target was presented to the same eye. In another 40%, the target was presented to the other eye. The target was absent in the rest of the trials. Participants were asked to report if the target was absence or presence. Each participant ran 30 trials.

**Results**

In the monoptic condition (where adapting and test stimuli were presented to the same eye), participants failed to report the target in 35±6.2% of the trials (mean ± S.E.M.), whereas in the dichoptic condition (target was presented to the eye that was not adapted), in 31.7±6% of the trials observers reported target presence as absence. Although the effect is slightly stronger in the former condition, the difference was not significant ($p = 0.81$). We conclude that the site of adaptation is cortical, consistent with results from experiment 1.

### 2.1.7 Orientation selectivity

The disappearance of the target in experiments 1 and 2 does not necessarily indicate suppression of neural activity due to adaptation, as we have suggested. Higher-level mechanisms such as attention (as opposed to specific mechanisms) underlie similar illusions in which an otherwise salient stimulus is not perceptually resolved. For example, in attentional blink paradigm observers are not aware of a target presented in a time window around some nonspecific distracting event. Similarly, in crowding phenomena (He, Cavanagh and Intriligator 1996), the observer is unable to resolve the orientation of the target (although strictly speaking the target is not invisible in this case).

One way to dissociate higher-level and low-level mechanisms is to look at the orientation selectivity of the effect. Adaptation is selective for orientation, at least in early stages of the human visual hierarchy. Result of a preliminary experiment in our lab indicated that sustained adaptation to a Gabor pattern has little effect on the detection threshold for orthogonal orientation. However, a general mechanism such as spatial attention or location-based inhibition of return does not depend on the orientation of the preceding stimuli. Consequently, positive evidence for orientation specificity could imply involvement of low or intermediate level visual mechanisms, namely, adaptation.

### Methods

We compared disappearance induced by high-contrast patterns with same or orthogonal orientation to the target pattern (figure 6a–d). Induction followed 4 or 8 seconds of adaptation.

### Results and discussion

Detection of the target subsequent to adaptation was found to be highly selective for the orientation of the sustained low-contrast stimulus ($p<0.0001$, after both 4 and 8 seconds). There was hardly any disappearance when observers were adapted to a Gabor patch orthogonal to the test (figure 6c).

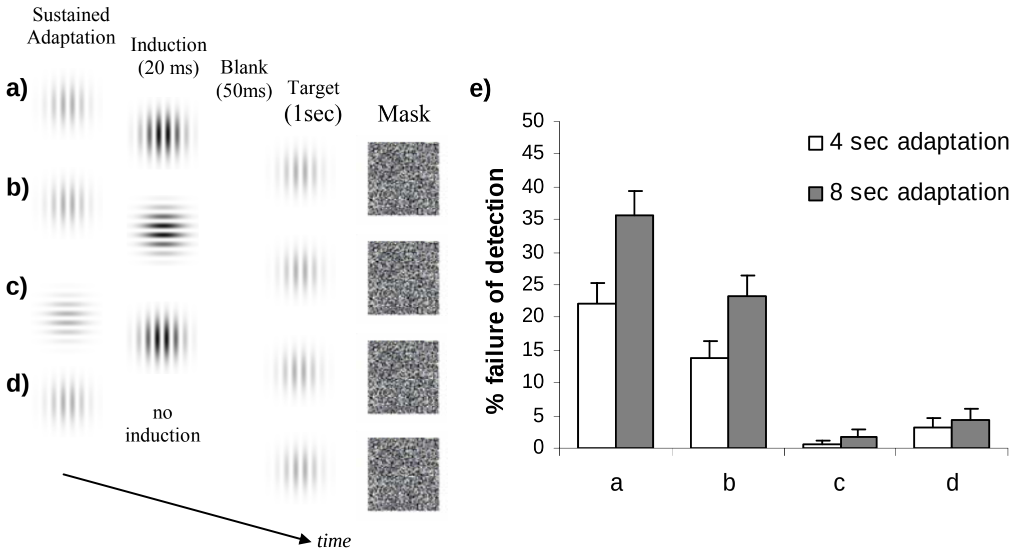

**Figure 6.** Orientation selectivity of the flash-induced disappearance.

(a) Induction using high-contrast Gabor with the same orientation as the low-contrast stimuli.

(b) High-contrast induction with orthogonal orientation to the low-contrast stimuli (adaptation and target).

(c) Sustained adaptation to low-contrast Gabor with orthogonal orientation with the target, induction with same orientation as target,

(d) Low-contrast adaptation without induction with high-contrast (control),

(e) Results: a vs. b: $p > 0.05$ after 4 sec, $p = 0.016$ after 8 sec, b vs. d, $p < 0.01$, after 4 sec, $p < 0.0001$ after 8 sec (10 subjects). The experimental paradigms are depicted on the left side (for trials in which the target was vertical).

Induced disappearance was partially selective for the orientation of the high-contrast inducer. Although there was some effect when inducer had orthogonal orientation (figure 6b), the frequency of disappearance was considerably reduced ($p$=0.054 and 0.016 after 4 and 8 seconds, respectively). Therefore, induced disappearance involves orientation-specific adaptation.

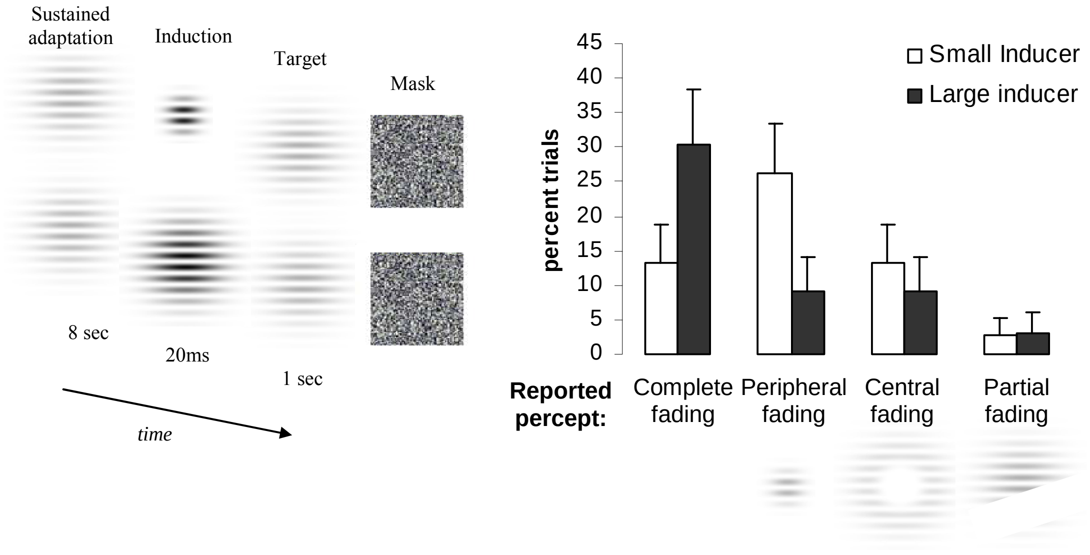

**Figure 7.** Disappearance following local induction.

There is no significant difference between the responses of observers for trials with small inducer compared with trials with larger inducer ($\chi^2 = 4.1095$, df = 4, $p > 0.35$, 4 participants). Participants had to report if they perceived the target or not (complete fading), and if the target was perceived as a smaller Gabor patch (peripheral fading, an illustration was shown in the inset of the graph), as a hollow ring (central fading due to local induction), or anything else (partial fading).

Although all adapting stimuli have the same texture boundaries, disappearance occurs only when the adapting texture has the same orientation as the target. Thus, adaptation to texture boundaries does not underlie induced disappearance. The results suggest involvement of early or intermediate visual processes in induced disappearance. High-level mechanisms lacking orientation selective representations cannot exclusively mediate the effect.

### 2.1.8 Spatial and contextual effects

Adaptation can be specific to the region that the stimuli were presented (as in retinal light adaptation), or it can extend into other parts of the visual field. Non-local effects indicate lateral connections within early cortical areas or secondary mechanisms and involvement of intermediate or high-level areas. Such mechanisms might be affected by grouping and other contextual effects.

In preliminary experiments, we failed to induce disappearance at locations other than where it was adapted to sustained stimulus. In contrast, disappearance could be induced by briefly flashing a high-contrast Gabor in the 2–3 deg vicinity of the adapted location. Induction in the opposite hemi-field had no effect. These findings are comparable to high orientation-selectivity for sustained low-contrast and partial selectivity for transient high-contrast induction (figure 6). In the next two experiments we investigated if a) induction simply depends on distance, and b) there is any contextual effect.

In order to determine whether induced disappearance is a local (location specific) effect or not, a large low-contrast drifting Gabor signal ($\sigma = 2$ deg) was presented on the screen during the adaptation phase (8 sec), followed by either a small ($\sigma = 1.2$ deg) or large ($\sigma = 2$ deg) high-contrast Gabor (20ms). The target was always a large ($\sigma = 2$ deg) Gabor signal. Subjects were asked to press one out of five keys to report what they perceived: (a) large Gabor, (b) small Gabor, (c) ring, (d) parallel lines, or (e) nothing (i.e., complete fading). The paradigm and results are presented in figure 7.

### Results and discussion

Observers experienced complete disappearance of the target more frequently after induction by the larger stimulus than the small one. Partial and incomplete fading of the target were reported more commonly following the small inducer. These results suggest that the size of the transient inducer affects the disappearance of the subsequent target. Nonetheless, the dominant pattern of the incomplete fading is the disappearance of the periphery of the target, which contradicts a purely local effect because only the central portion of the target overlaps the inducer. Observers did not perceive the target as a hollow ring (“Central fading” in figure 7) in the small inducer condition—which is predicted by the local adaptation—more frequently than when the larger inducer was used (*p* > 0.7).

### Experiment 4b

Experiment 4a demonstrates that a transient high-contrast pattern smaller than the target fails to induce a perceivable local disappearance. However, filling-in with the peripheral part of the Gabor pattern may confound the results by masking a small local scotoma. To rule out this explanation and study the possibility of contextual effects, we introduced two separate Gabor signals ($\sigma$ = 1.4 deg, center to center distance = 3 deg, figure 8a,b). During the adaptation phase, both locations experience adaptation to the low-contrast drifting Gabor. The Gabor patches were oriented either parallel (or collinear), or orthogonal to each other. A high-contrast signal with the same orientation was briefly displayed for 20 ms at one of the locations (e.g., location 1). Participants were asked to report presence or absence of subsequent low-contrast targets at both locations by pressing two keys in succession (two 2-AFC tasks). If disappearance is a local effect, observers should experience disappearance only at location 1. On the other hand, if induced disappearance involves global mechanisms, one might experience disappearance at both locations, and particularly at location 2. In 27% of the trials, one or both targets were absent (not included in the analysis).

### Results and discussion

The results are illustrated in figure 8c. Each bar depicts proportion of trials that observers failed to report both (white bars) or one (gray and black bars) of the two targets. The pattern of responses was different for condition a (same orientation, figure 8a) and b (orthogonal orientation, figure 8b) ($p<0.001$). In condition a (left three bars), observers reported both targets as absent in 16% of the trials. In another 15% of the trials, they only failed to report the target at location 1 (same as induction). In 7% of the trials, target 1 was detected, but participants failed to detect target 2 (no induction at location 2). Overall, in 41% of all trials that disappearance was induced, disappearance was induced in both locations. In condition b, disappearance was more isolated to one location. Only in 21% of trials with disappearance, it was reported in both locations (a vs. b: $p < 0.001$).

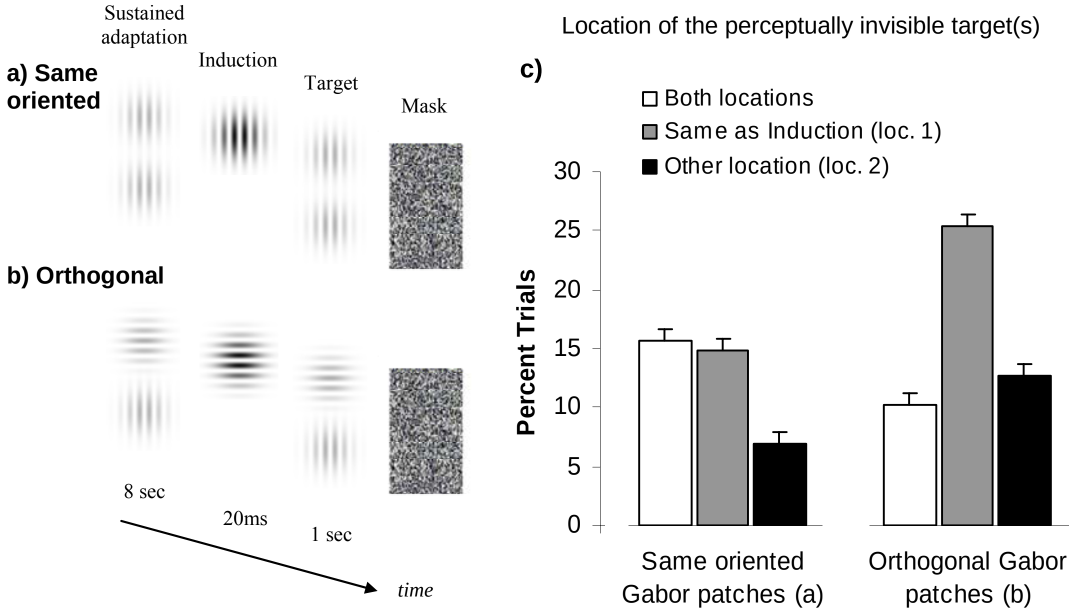

**Figure 8.** Disappearance at one of the two neighbor target locations.

The two targets are either (a) collinear or (b) orthogonal to each other. The transient stimulus (induction) appears only at one of the two locations.

(c) Disappearance is observed in both locations. The effect depends on the orientation similarity between the two locations ($\chi^2$ =16.65, df = 3, $p < 0.001$, six subjects). In some trials, subjects failed to detect any of the two targets. In other trials, subjects failed to detect only one of the targets, which was not always consistent with the location of the transient (same vs. other location).

Results confirm that induction is carried out by non-local mechanisms. In more than 22% of the trials subjects failed to detect the target located where induction had not taken place (location 2), which considerably higher than 5% of trials in experiment 1a for low-contrast adaptation only. We already mentioned that induced disappearance does not transfer following eye movement. What distinguish lack of transfer following eye movement and transfer in experiment 4b and resolve the ostensible inconsistency are the absence of retinal-motion signal in our experiment, and the fact that the effect transfers to a previously low-contrast-adapted location rather than an unadapted location of the retina (following eye movement). Nonetheless, the original target (the same location as the induction) still undergoes disappearance more frequently than the alternative target, indicating that although the effect is not purely local, proximity still plays some role.

Experiment 3 demonstrates that induced disappearance has orientation selective components. Experiment 4b suggests that it might also spread in an orientation selective manner, either because the underlying mechanisms is orientation selective, or because co-linear Gabor patches tend to perceptually group together more often than orthogonal Gabor patches. As mentioned above, when the targets are collinear or parallel, they tend to disappear together, indicating that disappearance obeys perceptual grouping. The overall frequency of the disappearance of the target at the location of the transient is not significantly different between the two conditions, and is similar to the results in experiments 1a. That is, the presence of another stimulus does not weaken the induced disappearance. Notably, the target disappears slightly more often when the other location is adapted to a Gabor patch with orthogonal orientation (35.5% vs. 30%, $p = 0.23$). It is also worth mentioning that in some of the trials subjects could detect the target that followed the transient, but failed to detect the target at location 2, as if the disappearance is induced in the first place and then is transferred to the other location.

## 2.2 General discussion

### Summary

In experiments 1–4, we studied the effect of adaptation on the detection of peripheral low-contrast Gabor patches by using the following paradigm: a low-contrast Gabor patch was presented for several seconds, and then was briefly replaced by a high-contrast patch. Afterwards, subjects were presented with a low-contrast Gabor patch or homogenous background, and were asked to report their percept. In a significant number of trials subjects failed to detect the presence of the target. Both sustained adaptation to the low-contrast stimuli and induction of disappearance by the transient high-contrast stimuli were necessary to get this effect. The target was otherwise easily detectable. Subjects failed to detect the target more frequently when the retinal adaptation during the presentation of the sustained stimulus was minimized by slowly drifting the phase of the Gabor patch than when stationary Gabor patches were used for sustained adaptation. On the other hand, adapting to orthogonal orientations reduced or even eliminated the effect.

Thus, in many of the trials the target stimulus was not consciously registered. Observers failed to detect it either as a consequence of earlier sensory suppression, or alternatively as a result of later removal of the signals by a high-level process. Sensory suppression is often conceived as a mechanism that keeps stimuli from reaching visual awareness by affecting the afferent pathway to the cortex or the cortex itself (Blake 1989; Burbeck and Kelly 1984) Although a pre-cortical component has been suggested for suppression in Troxler fading (Goldstein 1974; Kotulak and Schor 1986), we ruled out retinal and pre-cortical adaptation by demonstrating (a) detection probability does not depend on the contrast polarity of the stationary stimuli (2.1.4), and (b) a substantial degree of interocular transfer occurs (2.1.6). These findings imply that the adaptation component responsible for the current effect occurs at or after complex cells in V1 since opposite contrast polarities are conveyed by different and independent channels in retina and LGN that are not affected by adaptation of the other.

### Induced disappearance and optimal coding of contrast

Suppression following adaptation can be modeled by a threshold-nonlinearity: sustained and transient stimuli both locally increase the threshold, and the results are qualitatively explained in terms of linear summation (or temporal integration) of the threshold increments. Nonetheless, this naïve scheme hardly accounts for the magnitude of the effect of a transient high-contrast stimulus as brief as 20-30 ms. Different selectivity for orientation and location also indicates that sustained and transient stimuli play distinct roles.

Adaptation is viewed as a mechanism that dynamically adjusts the mapping between the range of stimulus intensities and the neural code (Attneave 1954; Brenner, Bialek and de Ruyter van Steveninck 2000; Wainwright 1999). This view can help understanding the illusion. Assume that the mapping (alternatively the psychometric curve) is monotonic in the form of $f$(input/gain – offset), where $f$ is the standard normal cumulative distribution function, and gain reflects the standard deviation of the input, and the observer has some inherent internal noise which is independent of the input. Discriminability of two levels of stimulus intensity is inversely proportional to the slope of $f$ at those values. For efficient coding (in statistical sense), discriminability should be high for events that occur with high frequency, and low for low-frequency events. That is, the mapping (offset, gain) should conform to the distribution (mean, variance) of the inputs (figure 9). As the distribution is not a priori fixed, the ideal observer should estimate and dynamically update distribution parameters. As a side effect of this process, adaptation followed by induction might affect the gain and offset in a way that renders a subsequent low-contrast target below the threshold.

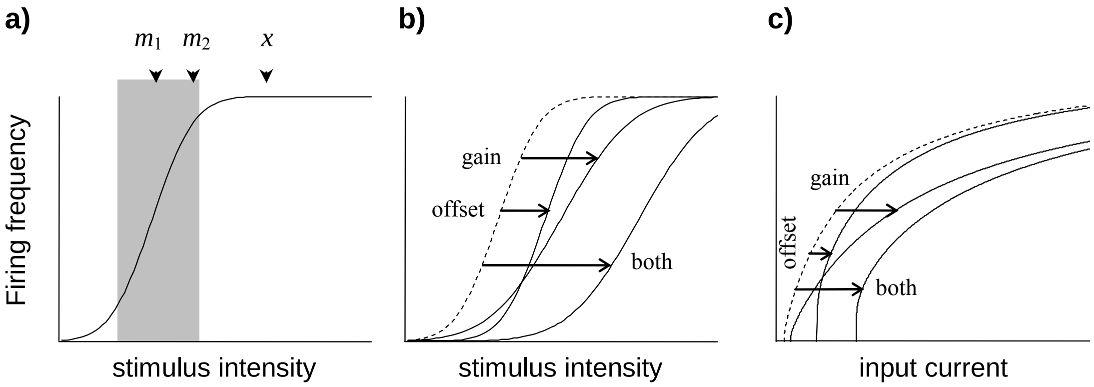

**Figure 9.** Modulations of stimulus-response function after adaptation.

(a) The stimulus-response curve before adaptation. This curve is optimal for intensities around $m_1$ (indicated by a small arrow above the graph). However, this curve is not optimal for stimulus intensities around $m_2$, and the response for $x$ is saturated.

(b) Adaptation may improve coding efficacy by modulating the offset (threshold) of the stimulus-response curve in the case that the mean input intensity is $m_2$ (given a constant variance), or by reducing the gain (slope) when the mean is $m_1$ but some samples are as high as $x$ (increased variance). These conditions respectively correspond to sustained adaptation to low-contrast vs. induction (adaptation to high-contrast). Notably, modulation of both offset and gain has a combinatory effect, causing $m_2$ to fall below the threshold.

(c) Biological plausibility: the input current vs. firing rate curve for a leaky integrate-and-fire model neuron with refractory period. Shunting inhibition elevates the offset whereas increasing the spike threshold (via a hyperpolarizing current) modulates the gain. Again, there is a large combinatory effect when both gain and offset change.

The likelihood of a particular distribution can be estimated from the input using Bayesian inference. The posterior probability is proportional to the probability of the data given the distribution times the prior probability of the distribution. For inputs around the mean (where probability of the data given the distribution is around its maximum), the likelihood changes gradually. Consequently, estimation of the optimal offset for neural code requires temporal integration (deWeese and Zador 1998; Fairhall *et al.* 2001). In contrast, a sudden increase in the range of stimulus intensities dramatically alters posterior probabilities and rapidly modulates the gain (deWeese and Zador 1998; Fairhall *et al.* 2001). In this framework, we propose that sustained low-contrast adaptation gradually increases the offset and the gain, elevating the detection threshold. Then, induction reduces the gain without effectively affecting the offset, causing the target contrast to fall below the range of intensities encoded effectively by neurons, as schematically illustrated in figure 9. The model can explain induced disappearance and is consistent with electrophysiological data (Ohzawa, Sclar and Freeman 1985) and psychophysical experiments that showed that detection threshold (which reflects offset) but not discrimination threshold (which reflects gain) increase after prolonged adaptation to low-contrast stimuli (Maattanen and Koenderink 1991).

### Neural mechanisms involved in induced-disappearance

In terms of neural circuitry, suppression by a transient stimulus may be based on either inhibitory feedbacks from higher-level areas or suppression within the early visual cortices. Induced disappearance cannot be explained by cross-orthogonal suppression (because the effect disappears after adaptation to an orthogonal stimulus) or inter-ocular suppression (because monoptic and dichoptic adaptation are similarly effective) within primary visual cortex. Both cross-orthogonal and inter-ocular suppression are reportedly stronger or equal between orthogonal stimuli than stimuli with the same orientations (Benevento, Creutzfeldt and Kuhnt 1972; Blakemore and Tobin 1972; Freeman *et al.* 2002; Sengpiel and Blakemore 1994; Sengpiel, Freeman and Blakemore 1995). In contrast to monocular rivalry (Campbell *et al.* 1973), disappearance is weakened following exposure to patterns orthogonal to the target. In short, suppression does not seem to be caused by known inhibitory connections within primary visual cortex.

In 2.1.8 we presented two sustained low-contrast adaptation stimuli and two targets, but the transient high-contrast inducer only appeared at one location. In a substantial number of trials subjects failed to detect the target at the other location or both targets disappear at the same time. Colinear targets disappeared together more frequently than orthogonal targets, consistent with mechanisms that involve perceptual grouping and contextual effects. Similar results have also been reported in other disappearance illusions. Disappearance might be induced by stimulating a location other than the targets in fading induced by visual transients (Kanai and Kamitani 2003) and motion-induced blindness (Bonneh *et al.* 2001). Perceptual grouping effects are also observed for motion-induced blindness (Bonneh *et al.* 2001). These findings are in agreement with the view that the target disappears as a result of an active process that involves higher-level selection mechanisms (Logothetis 1998; MacKay 1986). There is evidence of involvement of frontoparietal areas in altering or modulating the percept in related illusions such as motion-induced blindness (Pettigrew and Carter 2002), binocular rivalry (Lumer *et al.* 1998), and crowding phenomena (Afraz *et al.* 2003). It is plausible that the same brain regions be involved in, or modulated, induced disappearance.

Although the results in 2.1.8 and the aforementioned evidence from other disappearance phenomena appear to indicate involvement of extrastriate processes, explanations based solely on nonspecific mechanisms such as the limitation of attentional resources or filling-in induced by secondary (texture defined) edge adaptation are not consistent with our results and cannot explain the orientation specificity of the effect. We failed to induce disappearance by flashing the high-contrast inducer in the opposite visual field, i.e., by covertly shifting attention away from the target. In induced disappearance, both sustained adaptation and transient high-contrast are necessary to induce the effect. Attentional resources at the time that the target is presented should not be affected by previous adaptation. There is also little evidence about the dependence of other related mechanisms such as change-blindness and inhibition of return on the previous history of adaptation to some specific orientation. This is not to say that attention cannot modulate the effect. Attention plays a role in peripheral fading (Lou 1999) and might also affect the performance of the subject in induced disappearance, presumably by increasing the exposure of the neural circuitry that undergoes adaptation to the adapting stimulus. However, taken all together, our results put the underlying mechanism at the interplay between intermediate and early cortical levels of visual processing.

## Conclusion

We dissociated between sustained adaptation to a low-contrast spatial pattern and transient induction with a high-contrast stimulus and demonstrated a combinatory effect that indicates synergy between contrast and adaptation. A phenomenological model that can explain the results in terms of contrast gain and offset was presented based on the idea of optimal neural encoder (Attneave 1954). These results establish cortical origins for both sites of transient and sustained adaptations involved in induced-disappearance phenomenon. The effect is selective for orientation. Furthermore, it was established that the disappearance of the target involves non-local mechanisms, conceivably associated with top-down influence and contextual modulation. Considering the similar characteristics in a wide variety of experimental manipulations, the same mechanisms may also underlie suppression of object boundaries in illusions such as motion-induced blindness or fading induced by visual transient.

# 3 LINKING DISAPPEARANCE PHENOMENA AND OTHER PERCEPTUAL ALTERNATIONS

When our visual system is confronted with ambiguous stimuli, the perceptual interpretation spontaneously alternates between the competing incompatible interpretations. The timing of such perceptual alternations is highly stochastic and the underlying neural mechanisms are poorly understood. Here, we show that perceptual alternations can be triggered by a transient stimulus presented nearby. The induction was tested for four types of bistable stimuli: structure from motion, binocular rivalry, Necker cube, and ambiguous apparent motion. While underlying mechanisms may vary among them, a transient flash induced time-locked perceptual alternations in all cases. The effect showed a dependency on the adaptation to the dominant percept prior to the presentation of a flash. These perceptual alternations show many similarities to perceptual disappearances induced by transient stimuli (Kanai and Kamitani 2003; Moradi and Shimojo 2004b). Mechanisms linking these two transient-induced phenomena are discussed [2].

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[2] This chapter is published in Perception (Kanai, R., F. Moradi, S. Shimojo, and F. A. Verstraten (2005). Perceptual alternation induced by visual transients. *Perception* **34**, 803-822.). The initial idea of the experiments was conceived independently by RK (experiment 1) and FM (experiment 2a). Other experiments were designed by FM and RK and carried out by RK. FM added the computational model and simulation results.

## 3.1 Perceptual alternation induced by visual transients

When we are presented with a stimulus that has multiple perceptual interpretations, we experience a sequence of spontaneous perceptual alternations between the possible interpretations. Such multistable stimuli have been used to dissociate perceptual from stimulus-driven mechanisms to study visual awareness. The timing of the alternations is highly variable, and the underlying mechanisms as well as the neural substrates are poorly understood. Understanding the mechanisms underlying the perceptual alternations is important not only for understanding bistable perception per se, but also for understanding the dynamics of normal vision (Blake and Logothetis 2002).

The perceptual alternations can be explained, to some extent, in terms of passive decays of perceptual signals (or adaptation). Although adaptation indeed increases the probability of alternations, it does not seem to directly cause them (Hock, Schoner and Voss 1997; Köhler and Wallach 1944). That is, an additional factor seems necessary for an alternation to actually occur. Contributions of more active, top-down processes have been suggested to mediate alternations. Imaging studies have shown the involvement of parietal and frontal cortical areas (Kleinschmidt *et al.* 1998; Lumer *et al.* 1998). Also, bottom-up signals following small eye movements have been suggested to be responsible for perceptual alternations (Levelt 1966; Levelt 1967; Murata *et al.* 2003) (but see Blake, Fox and McIntyre 1971; Wade 1973). Since eye movements result in a transient signal due to new retinal input, the visual transient may contribute to or may even be responsible for the induction of perceptual alternation. Surprisingly, to the best of our knowledge, this possibility has not been investigated systematically.

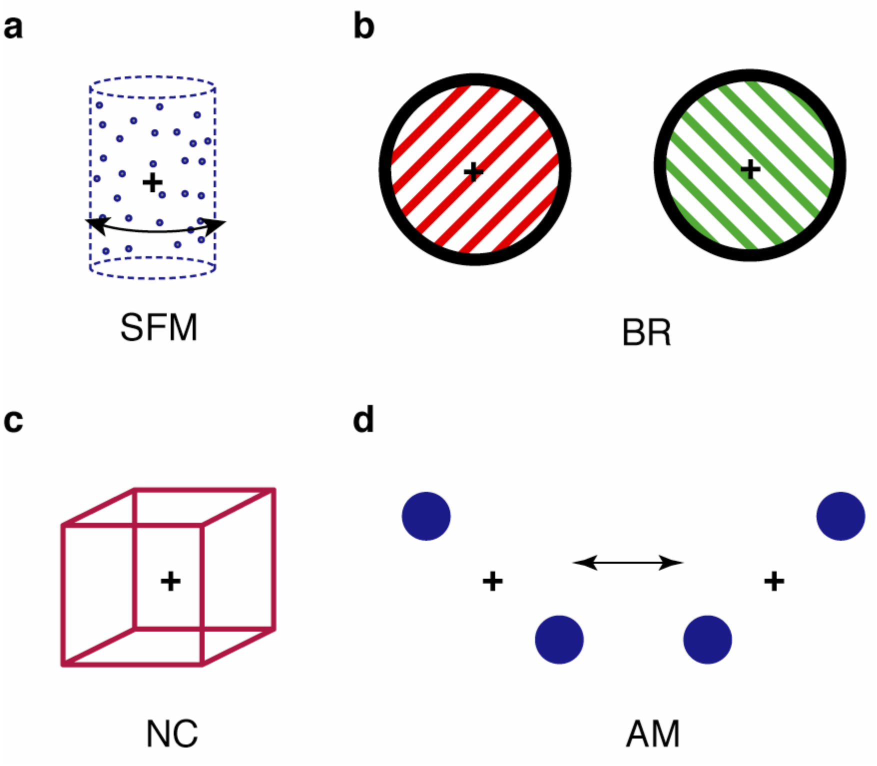

**Figure 10.** The four types of bistable stimuli used in experiment 1.

(a) Structure from motion (SFM). Dots can be perceived as a rotating cylinder and the perceived direction of rotation alternates spontaneously.

(b) Binocular rivalry (BR). Two square gratings (orthogonal to each other) are viewed dichoptically. Percept alternates between the two gratings (eyes).

(c) Necker cube (NC). One surface of the cube appears in front and then the same surface is perceived in rear.

(d) Apparent motion (AM). Two frames are alternately shown. In one frame, two disks are at the upper-left and lower-right positions, and in the other frame, they are at the upper-right and lower-left positions. The correspondence between these disks across the two frames is ambiguous. Therefore, this stimulus is typically perceived as two disks moving along either horizontal or vertical axis, and these two percepts alternate.

In this study, we show that a visual transient can trigger a perceptual alternation. The induced alternations were time locked to the transient, and therefore the timing is highly predictable. We show that presenting a flash behind a bistable figure results in a sudden transition of the current perception into the competing interpretation. This effect, termed Induced Perceptual Alternation (IPA), is demonstrated using a variety of ambiguous stimuli including structure from motion, binocular rivalry, Necker cube, and ambiguous apparent motion. IPA manifests characteristics similar to another transient-induced phenomenon where visual transients induce perceptual disappearance of objects (Kanai and Kamitani 2003; Moradi and Shimojo 2004b). In both cases, transient stimuli cause a drastic change of the percept to a constant visual stimulus. We attempt to offer a schematic model that explains how visual transients produce a drastic perceptual change both in perceptual rivalry and disappearance.

### 3.1.1 Basic effect

In our first experiment, we show that perceptual reversals can be induced by transients in a variety of bistable stimuli; structure-from-motion, binocular rivalry, Necker cube, and bistable apparent motion.

#### Methods

Four naïve observers and one of the investigators (RK) participated. All observers had normal or corrected-to-normal vision. The stimuli were generated on a Macintosh computer using Matlab PsychToolbox (Brainard 1997; Pelli 1997) and presented on a 22-inch CRT monitor (LaCie Blue Electron). The refresh rate of the display was 85 Hz, and the resolution, 1280 X 1024. The viewing distance was 57 cm.

We displayed four types of bistable stimuli. These stimuli were Structure-From-Motion (SFM), Binocular Rivalry (BR), Necker Cube (NC), and bistable Apparent Motion (AM). The details of the stimulus parameters are described below. A fixation cross was placed in the geometric center of each stimulus. At random intervals every 2-4 s, the background was flashed for 47 ms without occluding the bistable stimuli. The flash was white (56 cd/m2).

SFM (figure 10a): The SFM consisted of 400 blue dots with a lifetime of 1 second presented against a black background. The shape of the structure was a cylinder rotating around the vertical axis centered at the fixation cross (red). The size of the cylinder was 3.9o in height and 3.12o in diameter. The rotation speed was 0.2 rps. For this stimulus, the transient was a flash (47 ms) that had a rectangular shape covering the background of the stimulus area of SFM.

BR (figure 10b): Two orthogonal square-wave gratings, red-black vs. green-black (45 deg and 135 deg) were presented in a circular area (diameter 7.8o). The gratings were presented dichoptically using red and green color filters. The gratings had a spatial frequency of 0.8 cpd and the duty cycle was 20%. To support binocular fusion, a white ring (0.4 deg in width) was surrounding the stimulus. The combinations of color (red and green), eye (left and right) and orientation (45 deg and 135 deg) were randomly chosen for each trial. Transient flashes were presented by briefly changing the black part of the gratings (the local background) into white for 47 ms.

NC (figure 10c): The skeletal drawing of a cube was presented in blue against a black background. The length of each edge was 1.95 deg when viewed from a perpendicular angle. The flash (47 ms) was a solid white disk with a diameter of 7.81deg centering at the fixation.

AM (figure 10d): AM was created by presenting a pair of blue disks alternately against a black background. The diameter of each disk was 0.98 deg. In one frame the two disks were presented in the upper-right and lower-left quadrants, and in the other frame, in the upper-left and lower-right quadrants. These two frames were alternated every 200 ms, and there was no blank interval between the frames. The four disk positions were 1.17 deg away from the fixation point along both the horizontal and vertical axes. The flash was a white disk (4.69 deg in diameter) centering at the fixation cross.

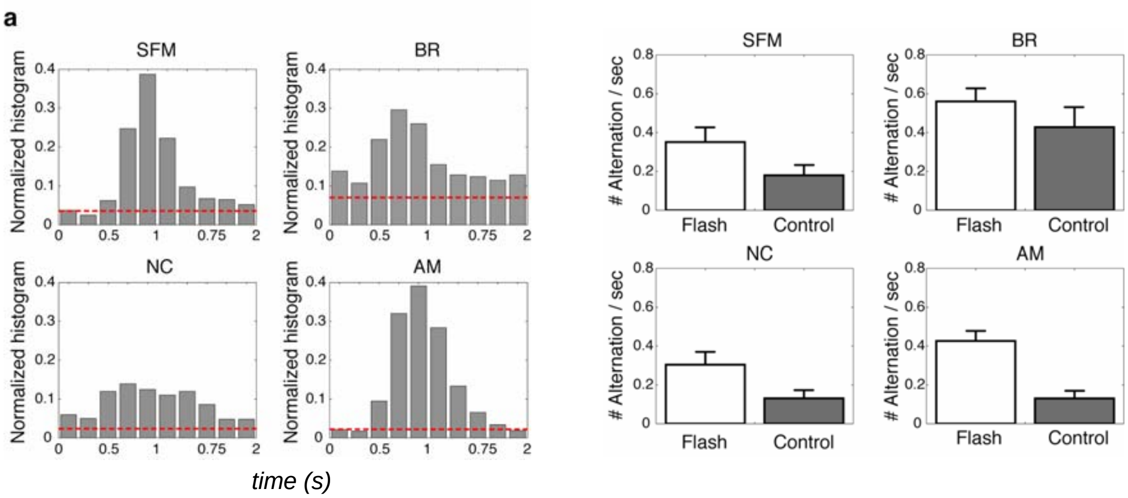

**Figure 11.** The results of experiment 1.

(a) The frequency of perceptual reversals is shown with respect to flash (time zero). All perceptual alternations after a flash are included (not just the first one). The frequency is shown in a normalized scale. That is, the bar height corresponds to the probability that a reversal occurs within a certain bin (200 ms) after a flash, i.e., the number of alternations (within the bin) divided by the total number of flash events. For comparison, dashed lines are drawn to indicate the frequency of reversals in the unit bin width (200 ms) when the alternations rates were estimated without presenting the flash (control). The histograms for the four types of bistable stimuli show that observers' responses to reversals frequently occurred at 0.5–1.0 seconds after a flash. This pattern was evident in all four stimuli. The data are from four observers.

(b) Alternation rate for each condition. The rate was higher in the condition with flash (white bars) than in the control condition (gray bars).

### Procedure

Before starting the experiment, naïve observers were familiarized with bistable stimuli and perceptual reversals. It is known that it can be difficult for naïve observers to experience the first alternation (see Rock and Mitchener 1992). In a trial, the observers viewed a bistable stimulus continuously for 30 seconds, and responded by a key press, when they experienced a perceptual reversal at any time during a trial. A flash (lasting for 47 ms) was presented randomly between 2 and 4 seconds after the previous flash (uniform sampling). The flashes were always presented behind the ambiguous stimuli (by briefly changing the local background to white), without occluding any part of them.

As a control, we conducted the same experiment without the flashes to obtain the spontaneous reversal rates. Thus, there were 8 conditions (the flash and control conditions for each of the four stimulus types). For each condition, the observer performed ten trials in a single session (the total viewing duration was 300 seconds). The order of the conditions was randomized for each observer.

### Results and Discussion

Figure 11 shows the frequency of alternation with respect to the flash onset. Alternations were observed often 500~1000 ms after the flash, indicating that sudden perceptual changes occurred just after the flash. The dashed lines show the frequency of alternation in the control experiment where the same stimuli were viewed but without the flash.

Overall, the frequency of the alternation is significantly higher than the spontaneous alternation rates (t-test: SFM, $p<0.05$; BR, $p<0.01$; NC, $p<0.01$; AM, $p<0.05$). The median of the time to alternation after the flash was presented was 706 ms, 612 ms, 1024 ms, and 824 ms for SFM, BR, NC, and AM, respectively. These values are larger than reaction times for simple detection tasks (<500 ms). This suggests that observers responded to the percept that occurred after the flash, and did not simply react to the sudden flash. Such long reaction times might also suggest that the flash did not directly cause the alternation of the percept, but instead altered the dynamics of bistability. Figure 11b shows the mean alternation rates for each stimulus type. In all stimulus types, the rates were higher in the flash condition compared with the control conditions (SFM, $p<0.01$; BR, $p<0.05$; NC, $p<0.01$; AM, $p<0.01$), the IPA seems more remarkable in the conditions with SFM and AM compared to BR and NC (figure 11a). Why the flash was more effective at inducing alternations in these two types of stimuli is unclear. A difference between SFM/AM and BR/NC is that the former stimuli are dynamic (i.e., continuously moving), whereas the latter stimuli are constant. Thus, IPA may possibly have a stronger effect with dynamic stimuli.

### 3.1.2 Spatial specificity

Thus, a flash indeed induces alternations of the perceptual interpretation of ambiguous stimuli. However, the flash was always presented at the same location as the ambiguous stimuli. In the next experiment, we address the question as to whether the IPA is spatially limited to the location of the flash or caused by any transient stimuli.

We compared two conditions while presenting bistable stimuli in the periphery: (1) flash was presented at the same location as a bistable stimulus, and (2) flash was presented on the other side of the visual field (same eccentricity).

#### Methods

Five new naïve observers participated in the experiment with SFM and four naïve observers in the experiment using NC. Control data were obtained from three observers who participated in both experiments. Stimuli were presented on a CRT monitor with a resolution of 1152 X 864, and a refresh rate of 85 Hz, and were viewed binocularly from 57 cm.

We chose to use two types of bistable stimuli, SFM and NC, as an example of dynamic and static ambiguous stimuli, respectively. We describe the details of the parameters used for these stimuli below.

SFM: An imaginary cylinder consisted of 200 white dots (3.5 arcmin) against a black background. The cylinder subtended 4.4 deg × 4.4 deg, and presented at an eccentricity of 2.93 deg from the nearest edge to fixation on the left visual field (LVF). The cylinder rotated around a horizontal axis at 0.9 rps.

NC: A Necker cube (4.4 deg x 4.4 deg) was displayed in LVF. The edge nearest to the center of the screen was 2.93o away to the left. The NC was presented on a gray background. Steady fixation while viewing a stationary object in the periphery results in a disappearance of the object due to adaptation (Troxler 1804), especially when transient stimuli are presented nearby (Kanai and Kamitani 2003; Moradi and Shimojo 2004b). To avoid retinal adaptation and perceptual disappearance during observation, we had observers track a small dot (7 arcmin from the center) slowly rotating around a fixation cross (at 0.32 rps).

The bistable stimuli were presented in the left visual field. At a random timing between 3 and 5 seconds (uniform sampling), a white flash of the same size was briefly presented for 35 ms. There were two conditions as to the position of the flash. In the ipsilateral condition, the flash was presented at the same location (LVF) as the bistable stimuli. In the contralateral condition (control), the flash was presented at the opposite location in the right visual field (RVF). Other factors—such as eccentricity, the duration of flash, etc.—were similar.

Observers pressed a key to report the percept at the beginning of each session and when a percept switched to another. In a session, a bistable stimulus was shown continuously for 150 seconds. Three observers performed 4 sessions (2 ipsilateral sessions and 2 contralateral sessions). Two observers participated only in the ipsilateral condition. The order of experiments was counterbalanced within and between the observers.

### Results and discussion

The frequency of perceptual alternations is plotted as a function of the time elapsed after the flash was presented (figure 12). It can be seen from the histograms that in the ipsilateral condition, the alternations occurred following the flash. This resulted in a high frequency of reversals around 500 to 1000 ms, both in the SFM (figure 12a) and in the NC condition (figure 12c). This was followed by a reduction of the frequency around 1.5 s.

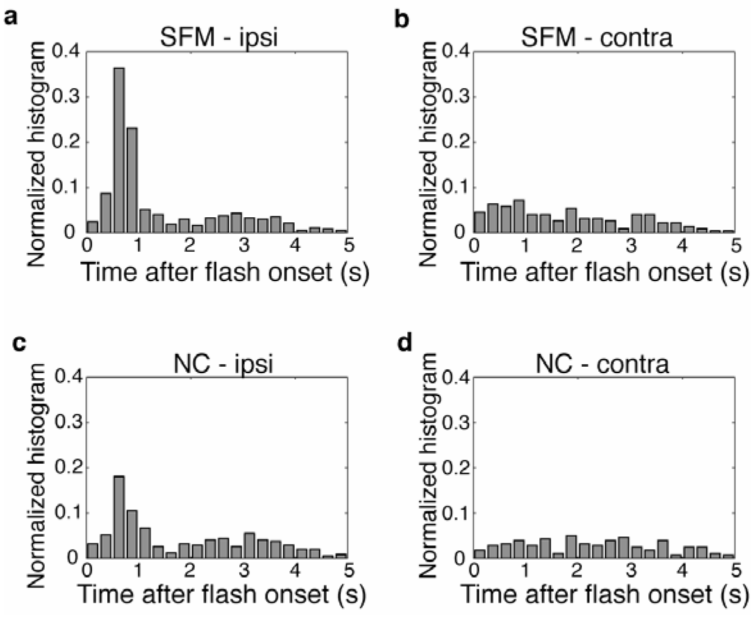

**Figure 12.** The results of experiment 2a.

The frequency of perceptual reversals is shown with respect to flash (time zero). The frequency is shown in a normalized scale, that is, as the probability that a reversal occurs within a certain bin (250ms) after a flash.

(a) The results for the condition where SFM and flash were presented in the same visual field (LVF). Alternations occurred frequently just after the flash (<1000 ms).

(b) The results for the condition where SFM and flash were presented on the different visual field. The peak after the flash is not as evident as the ipsilateral condition.

(c) The result of NC-ipsilateral condition.

(d) The result of NC-contralateral condition.

In contrast, these peaks were not evident in the contralateral condition where the flash was presented in the opposite visual field (figure 12b,d). The mean time of alternations with respect to the flash was significantly smaller in the ipsilateral condition (Kruskal-Wallis ANOVA, $p<0.001$ in both SFM and NC). Also, the probability of reversals—as measured by the number of alternations per flash—was significantly larger in the ipsilateral condition than in the contralateral condition (SFM: 1.133 vs. 0.736, $\chi 2 = 17.28$, $p<0.001$; NC: 0.925 vs. 0.739, $\chi 2 = 7.21$, $p<0.01$).

The results indicate that the IPA retains a certain level of spatial specificity. That is, perceptual alternation is not triggered just by any transient event visible to the observers. The interaction between the flash and bistable stimuli is limited. This spatial specificity is informative as to the level where the flash interacts with the representations for bistable stimuli. It shows that the interaction is presumably occurring at relatively early visual areas where visual inputs are retinotopically organized.

The fact that the flash presented on the opposite side does not induce perceptual alternation also suggests that the IPA is not caused by a secondary effect. For example, the perceptual alternations could be produced by a secondary effect of the peripheral flash like eye movements or eye blinks (but see Tse, Sheinberg and Logothetis 2002). If the flash were to induce eye movements or blinks, perceptual alternations would be expected to occur also in the contralateral condition. However, this was not the case.

Thus, the IPA appears to be mediated via local interactions between a transient stimulus and the representations for bistable stimuli.

### 3.1.3 Spatial specificity

As said, the spatial specificity tells us where the flash interacts with the representations for bistable stimuli. While the previous experiment shows that alternations are not induced by any transient events, it was not sufficient to tell how large the effective range is. Thus, we devised a similar, but more thorough experiment. Instead of comparing the two locations of the flash across visual hemifields, we now used 25 locations surrounding a bistable stimulus in the same hemifield as the target bistable stimulus.

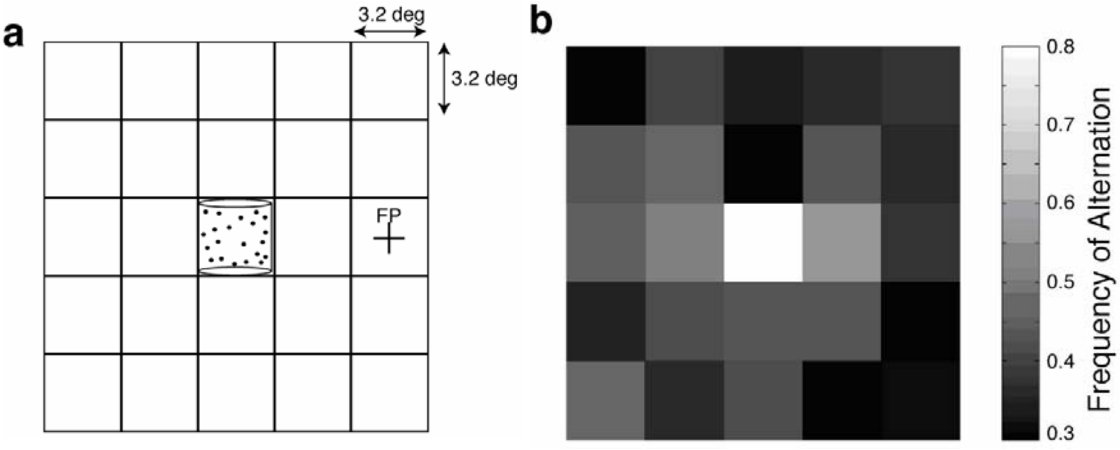

**Figure 13.** The design and results of experiment 2b.

(a) The lines are drawn for illustration purposes, and are not shown during the experiment. A SFM display is shown at the center of the grid pattern which is at an eccentricity of 6.4 deg left of the fixation. A square flash was shown at one of the 25 locations.

(b) The probability that a flash at a given position induces an alternation of the rotation direction is shown by brightness. Brighter color indicates high probability of perceptual alternation, while darker color indicates low probability.

### Methods

Six new naïve observers participated in this experiment. Stimuli were presented on a CRT monitor with a resolution of 1280 X 1024, and a refresh rate of 75 Hz, and were viewed binocularly from 57 cm.

For this experiment, we used a cylinder-shaped SFM consisting of 200 blue dots (2.4 arcmin) against a black background. The cylinder subtended 3.2 deg x 3.2 deg, and presented at an eccentricity of 6.4 deg from the nearest edge to fixation on the left visual field (LVF). The cylinder rotated around a horizontal axis at 1.0 rps.

The stimulus configuration is shown in figure 13a. The display was segmented into 25 regions in a grid fashion. Bistable stimuli were always shown at the central square, and a white square was flashed (67ms) at one of the 25 regions.

In a trial, the observers viewed a bistable stimulus for one second, and then the flash appeared at one of the 25 regions. The size of the flash was 3.2 deg × 3.2 deg. The bistable stimulus was continuously viewed for another one second, and then removed from the display. The observers reported whether alternation occurred during the trial by pressing a key. Twenty samples were made for each flash location. Thus one block consisted of 500 (25 positions × 20) trials.

**Results and discussion**

The results are shown in figure 13b. The probability of perceptual alternation per trial is displayed in brightness. As can be seen from the figure, the highest rate of alternations was observed at the position of SFM. And the effect strength gradually decreased as the distance between the SFM and the flash increased (Spearman r = -0.786, $p<0.001$).

So we can draw two conclusions from these data. First, the IPA is spatially confined to the location of the flash. Second, the specificity is not so strict; in other words, spatial overlap between the flash and a bistable stimulus is not a requirement. Thus, the flash influences on a spatial range which is slightly larger than the flash itself.

### 3.1.4 Location specificity vs. perceptual grouping

Experiment 2a and 2b demonstrate that presenting a flash near the location of a bistable stimulus induces perceptual alternation, whereas a flash distant from the bistable stimulus does not. Is the effective area of transient limited solely by the spatial separation? Here, we are interested in characterizing the nature of this spatial specificity. In particular, the question we address in this experiment is whether the spatial specificity is defined in an object-based manner, or solely based on spatial separation.

We examined whether a flash presented on a distant, but perceptually grouped object can induce an alternation. We presented two SFM cylinders in the LVF, rotating around a vertical axis. In this configuration, both cylinders are perceptually grouped together and often perceived to rotate in the same direction (Eby, Loomis and Solomon 1989; Gillam 1972; Grossmann and Dobbins 2003). Observers were asked to report reversals for just one of the cylinders (target), while a flash was presented either at the target or non-target locations. If perceptual alternation operates in an object-based fashion, then presenting a flash at either location should induce alternations.

In these tasks, attention is conceivably directed only to the target. This attentional bias may disrupt the perceptual grouping of the two cylinders. Therefore, these tasks could possibly undermine the grouping effect. Thus, using the same configuration, we also performed an experiment where observers were asked to report whether both cylinders are moving in the same direction, or in the opposite directions. This task requires the observers to attend both cylinders.

These experiments will tell us whether the effective range of a transient is affected by perceptual grouping, or simply determined by the spatial distance.

### Methods

Eleven naïve observers participated in the experiment. Two SFM stimuli (cylinders) were presented ±0.6 deg apart from the horizontal meridian (figure 14a-d). Thus, the distance between the cylinders (edge-to-edge) was 1.2 deg. At a random timing between 3 and 5 seconds (uniform sampling), a white flash of the same size was presented at the same location as one of the stimuli. The apparatus and stimuli parameters were identical to experiment 2,

Five conditions were tested in separate blocks. In conditions 1-3, the two cylinders were rotating around the vertical axis, and observers were asked to report the reversals of the top (condition 1, n = 10), or bottom cylinder (condition 2, n = 11), or if both cylinders are rotating in the same direction (condition 3, n = 10). In conditions 4-5, the two cylinders had orthogonal axes. Unlike coaxial configuration, spontaneous perceptual alternations are not linked for orthogonal SFM cylinders. Observers were asked to report the reversals of the top (condition 4, n = 7), or bottom cylinder (condition 5, n = 9). The target cylinder was always rotating around the vertical axis.

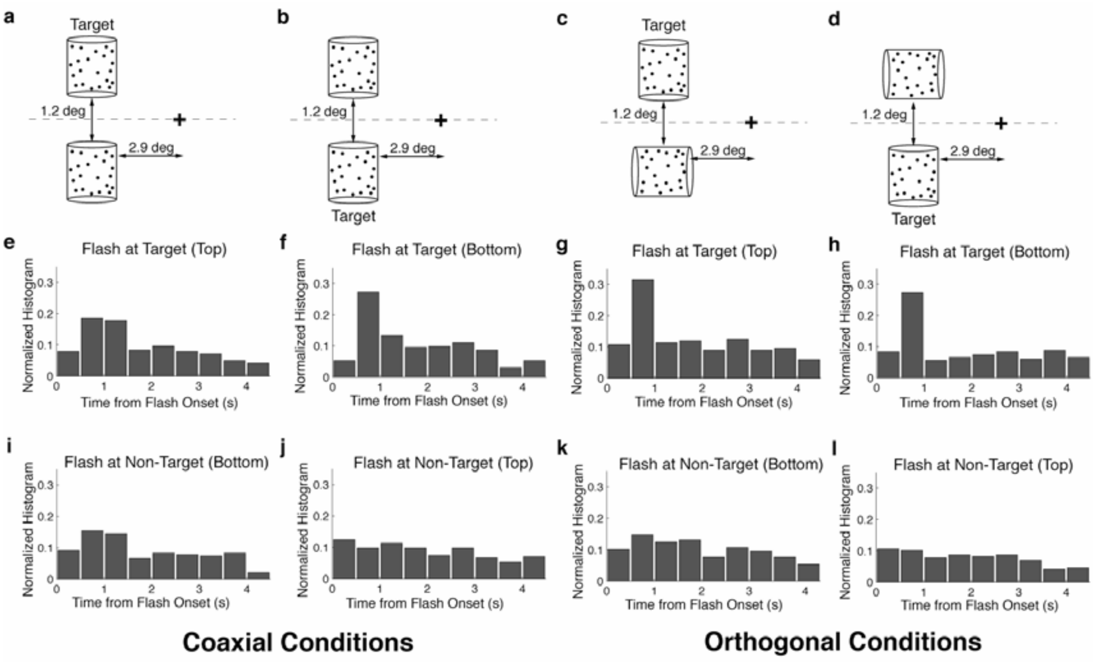

**Figure 14.** The results of experiment 3.

(a) The stimulus used in condition 1 is schematically illustrated. Two SFM cylinders, rotating around the vertical axis, are presented in the LVF 0.6 deg off the horizontal meridian. The observers reported the reversals of the top cylinder (target).

(b) The stimulus used in the condition 2. The configuration is the same as the condition 1, but the target was the bottom cylinder.

c and d). The stimuli used in conditions 4–5, respectively. The non-target cylinder was rotating around the horizontal axis.

(e)-(h) The alternation frequency of the condition shown in a-d in which the flash was presented at the target cylinder. The histogram shows the alternation frequency as a function of the time elapsed after a flash. The bin width is 0.5 s. The histogram is normalized by the total number of flashes.

(i)-(l) The results of the same conditions (a-d) in which the flash was presented at the non-target cylinder (bottom).

**Table 1. Perceptual grouping and induced reversals**

| Condition | *Freq. reversals at target location* | *Freq. reversals at non-target location* | |
|---|---|---|---|
| Coaxial Cylinders | | | |
| Target at the Top (condition 1a) | 18.8 ± 2.5% | 15.4 ± 2.3% | $p$=0.4 |
| Target at the Bottom (condition 2a) | 27.3 ± 2.7% | 9.8 ± 1.8% | *** |
| Orthogonal Cylinders | | | |
| Target at the Top (condition 1b) | 31.5 ± 3.6% | 14.9 ± 2.7% | *** |
| Target at the Bottom (condition 2b) | 27.3 ± 3.0% | 10.2 ± 2.1% | *** |

*** Same location vs. different location: $p<0.001$

The SFM stimuli were presented continuously in each block for 200 s. The order of the experiments was randomized for each observer. In all the conditions, the flash occurred at the target location or the non-target location randomly.

### Results and discussion

The results for each stimulus condition are shown in figure 14a-d, and the number of induced reversals (i.e., reversals occurring within 0.5–1 s after the flash) for each condition is summarized in Table 1. As in the previous experiments, perceptual alternations were successfully induced when the flash was presented at the location of the target (figure 14e-h).

Of interest here is whether an alternation is induced when the flash is presented on a spatially separate, but perceptually grouped stimulus. The results were ambiguous as to this question. In fact, we found an asymmetrical effect between the upper and lower visual fields for coaxial SFM. When the target was the cylinder in the upper visual quadrant (condition 1, figure 14i), there was an effect of perceptual grouping. That is, the flash on the lower cylinder produced a time-locked perceptual alternation of the top cylinder. Indeed, the IPA occurred about equally frequently independent of the flash position (condition 1: same vs. different, *p*=0.92). On the other hand, when the target was the lower cylinder (condition 2, figure 14j), the flash on the upper cylinder did not produce the IPA of the lower cylinder (condition 2, same vs. other: *p*< 0.001, Chi-square test). This shows that the IPA is spatially very specific to the target position, when the target is in the lower visual field.

Why is there such an asymmetry between the upper and lower visual quadrants? Perceptual grouping between the top and bottom cylinder seems to be an important factor, because IPA was confined to the target location for orthogonal configuration of SFM stimuli, regardless of the target being in the upper or lower visual quadrant (figure 14k,l). Another possible factor is attentional resolution, which is also known to manifest an upper-lower asymmetry (He *et al.* 1996). Since attentional resolution is higher in the lower visual field, attention to the bottom cylinder may more effectively individuate the target stimulus from the other cylinder. If so, the perceptual grouping of the two cylinders would be weaker when the lower cylinder is attended.

When the observers were required to attend to both cylinders (condition 3), the flash disrupted the synchronous rotations of the two cylinders (figure 15a), which often took 0-1 s to recover (figure 15b). We did not find a noticeable difference in the effect depending on the flash position (top or bottom) as in the other conditions where the observers were monitoring the rotation direction of either cylinder. Three observers reported that the flash induced anti-rotation quite frequently. This implies that for these observers, the flash had often a local effect. However, other observers experienced the anti-rotation rarely, as if the rotations of both cylinders are always linked. Probably, the difference across observers is due to their tendency to attend either locally or globally without intending to do so. These observations, together with the asymmetry between the upper and lower visual fields, suggest that a flash can have an effect both locally and globally depending on observer's attentional state.

Taken together, the IPA manifests both a spatial specificity and an effect of perceptual grouping depending on the target position. Currently, we cannot specify what other factors determine on which principle the IPA operates. However, as we discussed above, one of the likely candidates is attention. When a local aspect of a stimulus is attended, it will be relatively isolated from the rest. In such a situation, the IPA is limited within this area: a flash outside the attended part does not induce an alternation. On the other hand, when attention is directed to an object as a whole (two cylinders as one grouped object), a transient stimulus presented within this object seems to have a global impact on the entire object including the portions that are not directly stimulated by the transient.

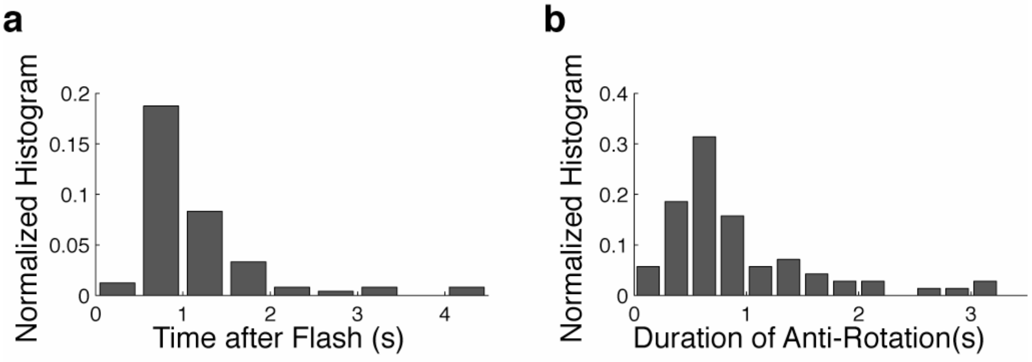

**Figure 15.** The results of experiment 3 (condition 3).

(a) The occurrences of anti-rotation are shown as a function of the time elapsed after a flash. The histogram is normalized by the total number of flashes.

(b) The durations of anti-rotation are shown. The histogram is normalized by the total number of the occurrences of anti-rotation.

### 3.1.5 Effects of adaptation

In the previous experiments, we presented a flash repeatedly and showed that the flash is responsible for the increase in the frequency of perceptual reversals. In bistable perception, adaptation to the dominant percept is widely considered as one of the key factors causing perceptual alternations (Babich and Standing 1981; Blake *et al.* 2003; Cornwell 1976; Köhler and Wallach 1944; Merk and Schnakenberg 2002). How is the effect of a flash related to the adaptation process in bistable percepts? The purpose of the next experiment is to examine the possible interactions between a transient stimulus and adaptation. Prior to a flash, we presented bistable stimuli for a variable duration of time, and examined the dependency of IPA on the adaptation duration.

If the flash directly causes an alternation independent of sensory adaptation to a dominant percept, the alternation frequency will not depend on the adaptation duration. Alternatively, if adaptation does have an effect on the IPA, the frequency of IPA will depend on the adaptation duration.

#### Methods

Six observers including one investigator (RK) participated in this experiment. One observer was excluded from the analysis because he had difficulty in perceiving perceptual alternations in SFM, even when he continuously viewed the stimulus for several minutes. The stimuli were presented on a 22-inch CRT monitor (LaCie Blue Electron). The refresh rate of the display was 60 Hz, and the resolution 1280 X 1024. Viewing distance was 57 cm.

In this experiment, we used SFM and NC. One trial consisted of three phases; adaptation phase, flash phase, and post-flash phase (figure 16a). In all phases, a bistable stimulus was continuously shown on a black background. The duration of adaptation phase was varied between 250 ms, 500 ms, 1000 ms, 2000 ms, and 3000 ms. In the flash phase, the stimulus background turned into white for 82 ms. Subsequently, the same stimulus was observed for another 500 ms so that observers could make a judgment as to whether there was a perceptual reversal or not.

The exact parameters used in this experiment are described below. The center of the stimuli was located 5.9 deg left of the fixation cross.

**SFM:** The cylinder of the SFM-stimulus had a radius of 1.9° of visual angle and a height of 4.5 deg. It consisted of 800 blue dots with a lifetime of 583 ms (35 frames) and rotated at a speed of 0.5 rps.

**NC:** The Necker cube was drawn in blue subtending approximately 2.5 deg of visual angle when viewed from the perpendicular angle.

At the end of each trial, observers reported whether perceptual reversals occurred just after the flash. The observers also reported whether the spontaneous alternation occurred before the flash. In order to avoid the contamination of spontaneous alternations, those trials were not counted and repeated later. Observers were instructed to attend to the initial percept once the trial was started. This manipulation of attention is known to keep spontaneous alternations lower (Pelton and Solley 1968), thus preventing frequent early alternations before the flash. Observers performed 20 trials for each condition.

### Results and discussion

The results for the SFM and NC stimuli are displayed in figure 16. The proportion of trials for which the flash triggered a perceptual alternation is shown as a function of adaptation duration. The results show that the flash was more effective at inducing an alternation when one interpretation had been perceived for a longer time, which results in deeper adaptation. The alternations increased monotonically as the adaptation duration increased (Spearman's rank order correlation: R = 0.79, $p<0.001$ for NC, R = 0.65, $p<0.001$ for SFM). The results indicate that some adaptation is required for an alternation to occur and a flash by itself is not necessarily sufficient.

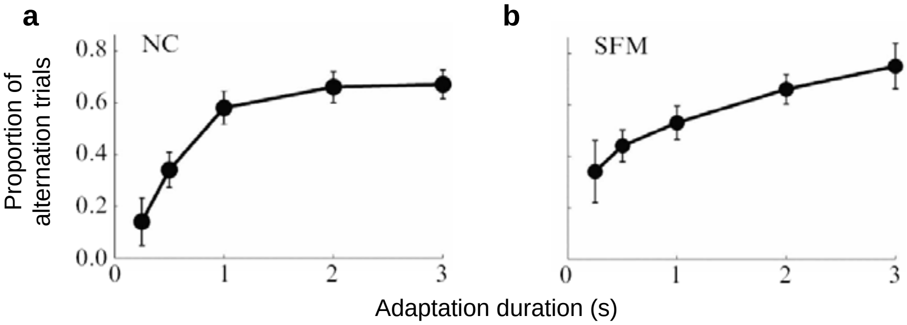

**Figure 16.** The results of the adaptation experiment.

(a) The results of NC condition. Proportion of trials in which observers perceived an alternation is plotted as a function of the adaptation duration.

(b) The results of SFM condition.

### 3.2 General discussion

We have shown that perceptual reversals during the observation of ambiguous stimuli can be induced by a transient stimulus. This induced perceptual alternation (IPA) provides us with a means to investigate the dynamics underlying the perceptual alternation.

Our experiments revealed the basic characteristics of the IPA. First, the reversals are time locked to the flash (in a time scale of a few hundred milliseconds). Second, the effect is largely confined to the location of the flash. That is, the flash needs to be presented near the target stimulus. Third, adaptation to the dominant perceptual interpretation is necessary, and the strength of the effect depends on the depth of adaptation.

These characteristics are shared by another transient-induced phenomenon, where a transient stimulus triggers a fading of an object presented in the periphery (Breitmeyer and Rudd 1981; Kanai and Kamitani 2003; Moradi and Shimojo 2004b; Wilke, Logothetis and Leopold 2003). The fading effect shows a similar time-locked characteristic. It is confined to a limited spatial region near the transient stimulus. Also, pre-adaptation, although brief, is necessary for a fading to be reliably triggered. In addition to the similarities in these basic characteristics, what is common between the perceptual alternations and disappearances, is that conscious perception for a physically constant stimulus is drastically changed by transient stimuli. In fact, results of other studies also suggest that there is a common mechanism underlying both perceptual disappearance and bistable percepts (Bonneh *et al.* 2001; Carter and Pettigrew 2003). Given these similarities between perceptual alternations and fading, we try to understand the function of a visual transient both in the perceptual fading and the IPA in a unified scheme. Here we address this issue in two parts: first, what kind of dynamics can result in such a behavior, and second, what is the possible underlying neural mechanism for such dynamics.

### 3.2.1 Neural model and simulation

We propose a schematic model of the effects of transient input that incorporates both the alternation and fading effects. Perceptual bistability is often considered analogous to the alternation between states or attractors in bi- or multistable neural networks or dynamical systems (Kawamoto and Anderson 1985; Poston and Stewart 1978). Stability can be analyzed in such models by constructing a so-called energy function (or Lyapunov function) such that in the absence of noise the energy always decreases until the system reaches a fixed state or a stable attractor. The stable states of such models are determined by local minima of the energy function. In figure 17, two mutually exclusive percepts for a bistable stimulus are illustrated as two locally stable minima in the energy function (left and right).

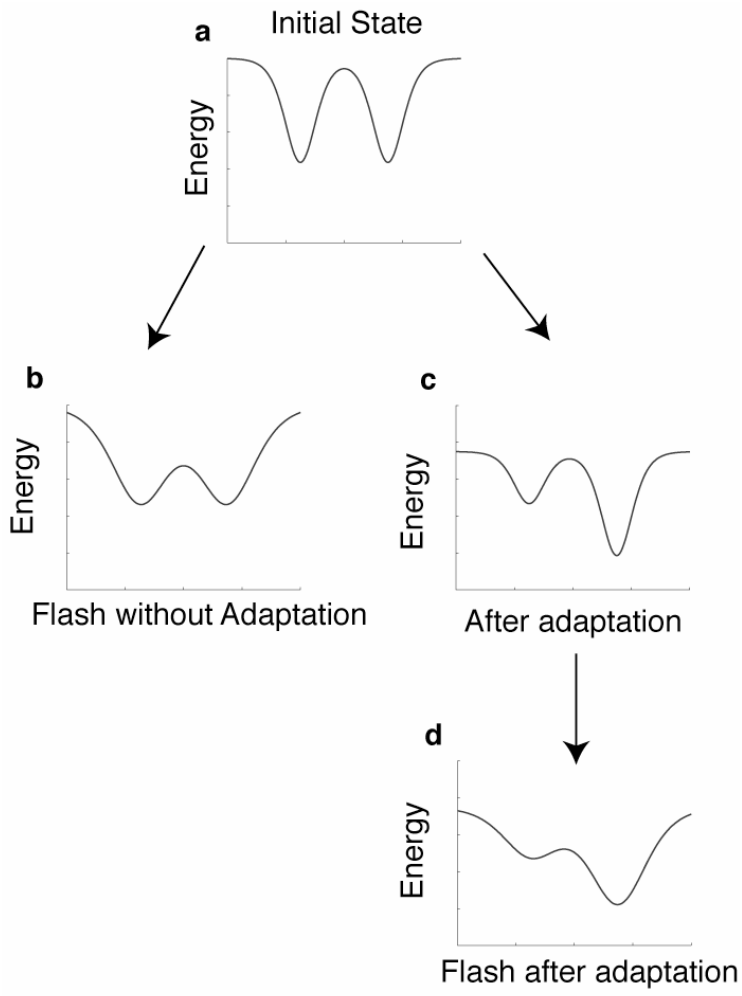

**Figure 17.** A schematic model of the flash-induced alternation.

Two mutually exclusive percepts are illustrated as the two energy wells (left and right).

(a) Upon stimulus onset, energy wells for both percepts are deep.

(b) When a flash is presented without a substantial adaptation, the smoothing effect (see text) is not sufficient to lower the energy barrier enough for perceptual alternation to occur.

(c) After adaptation, the energy well for the dominant percept becomes shallow (here the left well).

(d) When a flash is presented after adaptation, the smoothing effect of the flash lowers the energy barrier for the perceptual state to transit to the other interpretation.

Experimental evidence suggests that prior adaptation can increase the reversal rate from the adapted percept to the unadapted percept (Long, Toppino and Mondin 1992). This finding is consistent with a scheme in which adaptation changes the energy landscape of the system by increasing the energy of the adapted state (figure 17c). Conceivably, a transient stimulus at the same location should induce a reversal either by changing the state of the network, or by modifying the energy landscape.

It has been suggested that a salient transient signal triggers a rapid change in the gain of the input (see 2.2). This type of response is necessary for efficient coding of information in a changing environment. In the absence of the transient signal, the gain gradually returns to the level before the flash. However, the change in the input gain following a flash results in smoothing of the energy landscape (figure 17b). Consequently, our model predicts that the spontaneous reversal rate increases following the flash. However, if a flash follows sufficient adaptation, the combined effect of adaptation and reduction of the gain makes the previous local minima unstable and as a result, induces a perceptual alternation (figure 17d)[3].

Figure 18 demonstrates a minimal implementation of the aforementioned schematic account. We modeled the bistability in our network using opponent neurons (that selectively respond to opposite directions) with symmetric inhibitory connections (figure 18a).

When there is no noise in the network, the state always converges to one of the two stable minima (percepts) and the outcome is determined by the initial condition. In the presence of stochasticity, however, the system occasionally alternates between the two percepts. The rate for switching from one state to another depends on the difference between their energies and noise level, as well as the height of the energy separating the minima.

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[3] The observer who did not perceive any perceptual alternation in the SFM condition in Experiment 4 reported that flash makes the SFM flat temporarily, and the cylinder shape restores after some duration. This observation is consistent with our interpretation that a flash makes the energy landscape smooth. In this observer, energy minimum for one interpretation was predominant, and the smoothing effect could only make the minimum briefly unstable, and was not sufficient to induce an alternation.

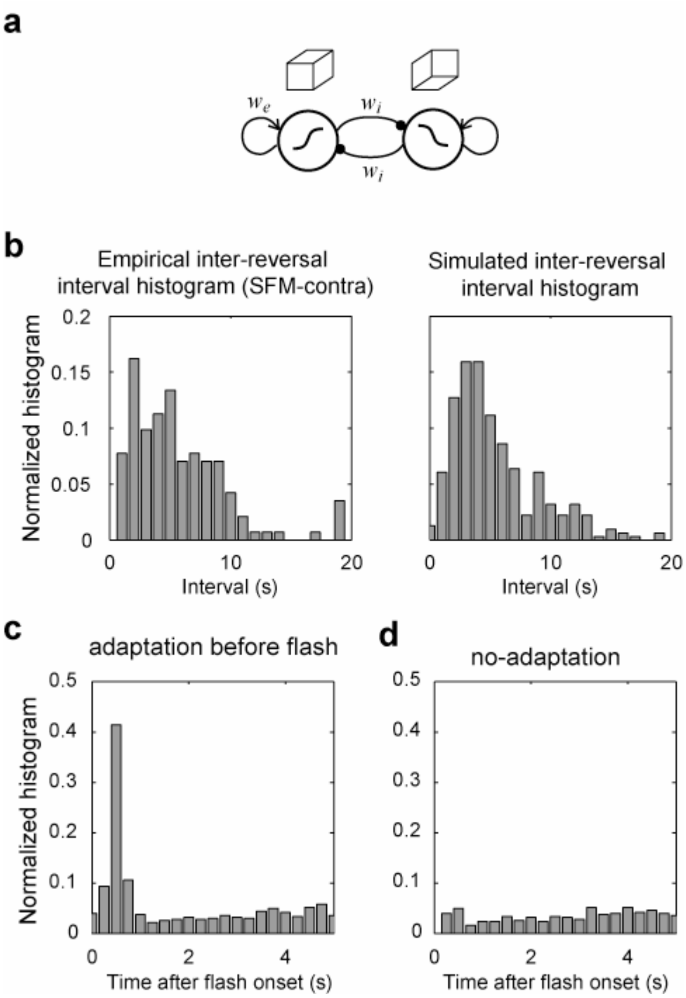

**Figure 18.** Implementation and simulation.

(a) Bistability model: two opponent neurons inhibit each other.

(b) Histogram of the intervals between perceptual reversals for experimental data (3.1.2, SFM-contra) vs. simulation.

(c) Simulated effect of the flash. Flash onset was 5 sec after onset of each simulated trial.

(d) Flash by itself does not result in any effect in the model. Flash occurs at the onset of simulated trial, thus the neurons are not adapted at the time of the flash. Figures are based on 500 simulated trials with a time-step of 10ms.

The output of each Ising neuron at each time-step is modeled as follows (Hinton and Sejnowski 1986):

$$\text{output} = \begin{cases} 1 & \text{with probability } \dfrac{1}{1+e^{-2(ax-b)}}, \\ -1 & \text{otherwise,} \end{cases}$$

where $x$ is the total input given $w_e = -w_i = 1$, $a = 2.5$ is the slope, and $b$ reflects the change in threshold following adaptation:

$$\tau \frac{db}{dt} = \begin{cases} 2-b & \text{if output} = 1, \\ -b & \text{otherwise,} \end{cases} \qquad \tau = 1\,\text{s},$$

Figure 18b compares the distribution of intervals between perceptual reversals in experiment 3 (SFM-contra, actual data) and simulation data. This rudimentary model seems to at least qualitatively capture the stochastic nature of spontaneous perceptual alternations.

The effect of transient was modeled by a transient decrease in the slope as follows:

$$a(t) = a - k\left(e^{-\frac{t-t_0}{\tau_2}} - e^{-\frac{t-t_0}{\tau_1}}\right), \qquad t > t_0,$$

where $\tau_1 = 150$ ms, $\tau_2 = 300$ ms, $k = 3$, and $t_0$ reflects the onset of the transient plus 150 ms visual processing delay. Figure 18c demonstrates that such reduction in the slope can induce reversals comparable to the empirical data in figure 12a (reaction time is not included in the simulation). We also verified that if the transient slope change occurs before enough adaptation, it fails to induce any alternation (figure 18d).

Thus, this model can explain the time-locked nature, and the requirement of adaptation in IPA. In this model, the effect of a transient is a brief loss of neural sensitivity. Previously, we have shown that modeling the effect of a transient in a similar fashion can explain the perceptual disappearance induced by visual transients (2.2). Thus, our simple model covers both the perceptual alternation and disappearance phenomena

### 3.2.2 Underlying neural mechanism

Findings described in 3.1.5 suggest that IPA results from a combination of two components: adaptation to a dominant percept and the effect of a transient. What are the neural foundations underlying these components? The adaptation process is specific for the stimulus and is likely to occur in early visual areas where visual inputs are still retinotopically organized. For example, it is known that adaptation to a Necker cube is specific to the location at which the stimulus is presented. Alternation rates of Necker cube usually increase during continuous viewing. However, the accelerated alternation rate due to adaptation restores to the original level when the cube is moved elsewhere in the visual field (Babich and Standing 1981). Recently, Blake, Sobel and Gilroy (2003) have shown that bistable stimuli (BR and SFM) that are moving continuously in the visual field manifest slower alternation rates. This indicates also the involvement of location specific (retinotopic) adaptation.

On the other hand, the neural circuitry responsible for the effect of a flash is somewhat elusive. The increase in gain and the smoothing of the energy landscape in our proposed model could be achieved biophysically at the single neuron level via nonspecific shunting inhibition (Torre and Poggio 1978). Whether this is mediated through local interactions or attentional mechanisms via top-down feedback remains unclear. Nonetheless, we are tempted to attribute this effect of visual transients to attentional mechanisms mediated by the parietal attention system. First, attentional shift is suggested to induce perceptual alternations in ambiguous figures (Georgiades and Harris 1997; Tsal and Kolbet 1985). Also the alternation slows down when observers are engaged in a secondary task (Reisberg 1983). While we emphasized that the effective range of transients is spatially confined, this does not necessarily mean that the interactions should occur within the retinotopically organized visual areas. In particular in the parietal cortex, many cells have spatially confined receptive fields and they are involved in attentional control (Colby and Goldberg 1999). The involvement of the parietal system in both the perceptual disappearance and perceptual alternation has been suggested before. Bonneh et al. (2001) compared motion-induced blindness to the extinction of salient stimuli experienced by patients with parietal lesions. Parietal patients often fail to perceive a salient object presented contralateral to the damage cortical hemisphere (Driver and Vuilleumier 2001; Rees *et al.* 2000). Moreover, their perceptual disappearance is facilitated (Mennemeier *et al.* 1994; Wolpert, Goodbody and Husain 1998).

Previous studies on bistable perception concern internally induced alternations (i.e., spontaneous alternations during the view of a constant stimulus) or voluntary (top-down) control of dominant percept (Leopold and Logothetis 1999; Lumer *et al.* 1998; Pelton and Solley 1968; Reisberg 1983). In these cases, endogenous shifts of attention have been suggested to play a causal role in perceptual alternations. On the other hand, our method of presenting a transient stimulus is closely related to exogenously triggered attention (Hikosaka, Miyauchi and Shimojo 1993; Posner and Cohen 1984; Theeuwes *et al.* 1999). In this view, the IPA may be regarded as the exogenous counterpart of attentional shifts in bistable perception. And the parietal area involved in orienting spatial attention (LIP in particular (Colby and Goldberg 1999)) is a likely candidate for producing perceptual alternations in response to transient inputs.

Our experiment 2b showed that the spatial specificity of IPA is not strictly confined to the location of the target stimulus. This mild form of spatial specificity is also observed in perceptual disappearance induced by transient stimuli. This extended spatial specificity is in contrast with sensory adaptation that typically requires strict stimulus overlap.

The finding that a flash sometimes influences the percept in an object-based manner (3.1.4), also seems to suggest the involvement of a slightly higher mechanism rather than nonselective effects in the lower sensory areas. In 3.1.4, a flash presented on a coaxial SFM cylinder sometimes induced an alternation in the other cylinder, which was presumably perceptually grouped. This implies that the effect of a flash can be transferred to a distant, but grouped object. Previously, a similar effect has been reported in perceptual disappearance (Kanai and Kamitani 2003). When a long bar is presented in a periphery, presenting a flash at one end of the bar was sometimes sufficient to induce a fading of the entire bar. This also suggests an object-based effect of visual transients.

These comparisons suggest that there is a connection between perceptual fading and frontoparietal functions. Moreover, recent evidence indicates the involvement of top-down feedback in the perception of bistable stimuli. For example, the right frontoparietal cortex is involved in the disambiguation of bistable stimuli such as the Necker cube (Bisiach *et al.* 1999; Inui *et al.* 2000; Sengpiel 2000). Also, frontoparietal areas associated with selective visual attention are considered to be involved in initiating perceptual alternation (Kleinschmidt *et al.* 1998; Leopold and Logothetis 1999; Lumer *et al.* 1998; Miller *et al.* 2000; Pettigrew and Carter 2002; Sterzer *et al.* 2002). So the current evidence shows that frontoparietal areas play a critical role both in perceptual fading and alternation. This makes it tempting to suggest that these alternation-related areas may be the source of the inhibition by a flash, and causing IPA.

### 3.2.3 Concluding remark

In the field of the perception of bistable stimuli, there has been an extensive debate as to the mechanisms underlying perceptual alternations. The first explanation involves adaptation of the currently dominant stimulus interpretation (Blake *et al.* 2003; Köhler and Wallach 1944; Long *et al.* 1992). Proponents of the second explanation assume that attention-related processes actively trigger perceptual alternations (Kleinschmidt *et al.* 1998; Leopold and Logothetis 1999; Lumer *et al.* 1998; Miller *et al.* 2000; Pettigrew and Carter 2002; Sterzer *et al.* 2002). However, these explanations are not necessarily mutually exclusive and bistable perception seems to be mediated at a multitude of processing levels in the visual system (Blake and Logothetis 2002). Our model combines adaptation at lower sensory level and transient gain change via feedback. Finally, it is the first model that provides an account for both perceptual alternations and disappearances in a single scheme.

# 4 THE FATE OF INVISIBLE STIMULI

Retinal input that is suppressed from visual awareness can nevertheless produce measurable aftereffects, revealing neural processes that do not directly result in a conscious percept. We here report that the face identity-specific aftereffect requires a visible face; it is effectively cancelled by binocular suppression or by inattentional blindness of the inducing face. Conversely, the same suppression does not interfere with the orientation-specific aftereffect. Thus, the competition between incompatible or interfering visual inputs to reach awareness is resolved before those aspects of information that are exploited in face identification are processed. We also found that the face aftereffect remained intact when the visual distracters in the inattention experiment were replaced with auditory distracters. Thus, cross-modal or cognitive interference that does not affect the visibility of the face does not interfere with the face aftereffect. We conclude that adaptation to face identity depends on seeing the face[4].

## 4.1 Face adaptation depends on seeing the face

Psychologists have perfected a number of techniques that render retinal inputs invisible yet that still result in visible aftereffects and other measurable phenomena, including orientation-specific adaptation (Blake and Fox 1974; He and MacLeod 2001; Montaser-Kouhsari et al. 2004; Rajimehr 2004; Young et al. 1996), motion aftereffect (Lehmkuhle and Fox 1975; O'Shea and Crassini 1981), and orientation-contingent color aftereffect (White *et al.* 1978). This reveals the existence of stages in the visual processing hierarchy that precede

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[4] This chapter has been published in Neuron (Moradi, F., C. Koch, and S. Shimojo (2005). Face adaptation depends on seeing the face. *Neuron* **45**, 169-175.).

regions that are necessary and sufficient for visual awareness; an inference Bela Julesz called *psycho-anatomy* (Julesz 1971). The fact that some low-level aftereffects do not require awareness of the inducing stimulus raises the general question to what extent more complex aftereffects such as those for object identity that are mediated by neurons in the upper echelons of the ventral pathway, require visual awareness. Imaging (Moutoussis and Zeki 2002; Pasley, Mayes and Schultz 2004; Williams *et al.* 2004) and priming (Paller *et al.* 2003) experiments suggest that selected aspects of face processing can occur without conscious perception of the face. We therefore set out to test the dependency of the recently discovered face aftereffect on conscious perception (i.e., subjective visibility) of the inducing face.

The retinal input can be rendered perceptually invisible by presenting an incompatible image to the other eye. Binocular rivalry occurs when the visual system fails to establish correspondence between the two images. Each image then undergoes exclusive periods of visibility (dominance) and invisibility (suppression). Yet this perceptual suppression has little effect on the build-up of orientation-selective adaptation (Blake and Fox 1974) and the linear-motion aftereffect (Lehmkuhle and Fox 1975). How does binocular suppression affect face adaptation? In the first set of experiments we study adaptation to realistic face images (Leopold *et al.* 2001) under dichoptic viewing condition (that is, the two eyes receive different inputs). Identification of a specific face is selectively facilitated after a few seconds of adaptation to a face that has opposite global features (corresponding “antiface”), whereas adaptation to an unrelated face slightly impairs identification (Leopold *et al.* 2001). If suppressed input reaches face selective neurons, then adaptation to such input might affect identification of subsequent faces. For comparison, we investigate the orientation-dependent aftereffect using the same setup.

Selective attention and task-relevance also affect conscious registration of visual inputs (Mack and Rock 1998; Simons and Chabris 1999). Attention is suggested to be involved in binocular suppression and other disappearance phenomena (Bonneh *et al.* 2001; Mitchell, Stoner and Reynolds 2004; Ooi and He 1999). Whether inattention and binocular suppression influence the formation of aftereffects in the same manner is not known; for example, inattention (Chaudhuri 1990)—but not binocular suppression (Lehmkuhle and Fox 1975)—reduces the magnitude of the linear motion aftereffect. In contrast, binocular suppression (Wiesenfelder and Blake 1990)—but not lack of attention (Aghdaee 2005)—eliminates the spiral motion aftereffect. Thus, an aftereffect may or may not correlate with awareness, depending on the method used for suppressing visibility.

Inattention might affect adaptation in ways other than suppressing visibility. Attention can increase neural responses to the attended stimuli, improve selectivity, or enhance adaptability (Boynton 2004). Consequently, aftereffects may be weaker (although still present) when the stimulus is not or only weakly attended during adaptation.

In a second set of experiments, we measured face adaptation while observers were engaged in an attentional demanding working memory task. Will the face aftereffect be reduced, revealing a residual effect that requires little attention, or even be eliminated under this condition? If face adaptation correlates with awareness regardless of the paradigm used for suppression, then it is likely that visual awareness is required for the face-specific aftereffects.

### 4.1.1 Methods

Healthy, paid volunteers with normal visual acuity were recruited from the campus student population. Participants were naïve to the purpose of the experiment, and were trained to identify four target faces in a 4-AFC task. Auditory feedback was given after each misidentification. Training blocks of 100 trials were repeated until observers performed better than 95% accuracy in training level 1 (identity strengths = 0.3, 0.4), 84% in level 2 (strengths = 0.2, 0.3, 0.4), and 75% in level 3 (strengths = 0.15, 0.25, 0.4). Participants were trained using this protocol at the beginning of each session. We observed that overtraining reduces the face-aftereffect, so for experiment 4 and 5 observers only completed levels 1 and 2.

Face stimuli were identical to a previous study (Leopold *et al.* 2001), except that the contrast of the antifaces were reduced by dividing pixel intensities by two. Our pilot experiments showed that this reduction had little effect on the magnitude of the aftereffect, but it considerably reduced the predominance periods of antifaces during rivalry.

Stimuli were presented using Matlab Psychophysics toolbox on a PC computer. Participants heads were stabilized using a chinrest located 80 cm away from the 19” CRT display (resolution = 1027x768, 100 Hz refresh rate). In experiment 1 we used a mirror haploscope to present images separately to each eye. No feedback on face identification was given in the experimental blocks. Auditory feedback was given in experiment 3 on the memory task. Visual feedback on the memory task was given after each trial in experiment 4. We used a loose exclusion criterion based on observers’ performance in the working-memory task (detecting more than half of the repetitions). One participant was excluded each experiment. The orientation-selective adaptation control was carried on seven naïve observers using the same setup as in experiment 3.

For experiment 5, participants were trained to associate names to antifaces. Each trial started with a name followed by a face and observers were asked to report if they match. Incorrect responses were followed by auditory feedback. In the imagery practice session, observers were instructed to imagine the face whose name was displayed briefly for 3-4s and report the vividness of their imagery before the face-to-match was displayed. Participants performed 200-300 practice trials. The experimental session was similar to the practice session, except observers had to identify the target faces after imagining the antiface.

### 4.1.2 Results

Participants were trained to identify four individual, colored faces. Experimental sessions started after observers reached a fixed performance level on a four alternative forced-choice (4-AFC) face identification task (see methods). The average face (defined as the three-dimensional morph—or mean—of a sample of 200 faces of young adults (Blanz and Vetter 1999)), was presented in the right visual field, and replaced subsequently by the antiface of one of the original faces (adaptor). After adaptation, a second face (target) briefly appeared in the left visual field, and observers were asked to identify it. Since the adaptor and target did not overlap, the effect of local adaptation is minimized.

Original faces were morphed with the average to create targets with different *identity strengths*. The original faces have identity strengths of one, and the average face has identity strength of zero. For each individual face, identity strengths between zero and one were obtained by linear interpolation between the original and the average face (Leopold *et al.* 2001). The antiface can be thought of as having negative identity strength relative to its associated, matching face (Leopold *et al.* 2001).

In experiment 1 (figure 19a), the antiface was always presented to one eye for 4 s. The adapting eye was determined by asking the observer to point a finger to a distant target. The eye that was not aligned with the finger was used for adapting. In half of the trials, a pattern of moving random dots was presented to the other eye and observers were asked to monitor the visibility of the adaptor and press and hold a key whenever it disappeared. In a considerable number of trials the moving pattern completely erased percept of the antiface, making it invisible (figure 19b). After the 4 s presentation interval, the target face was flashed for 200 ms to both eyes followed by a mask (figure 19a).

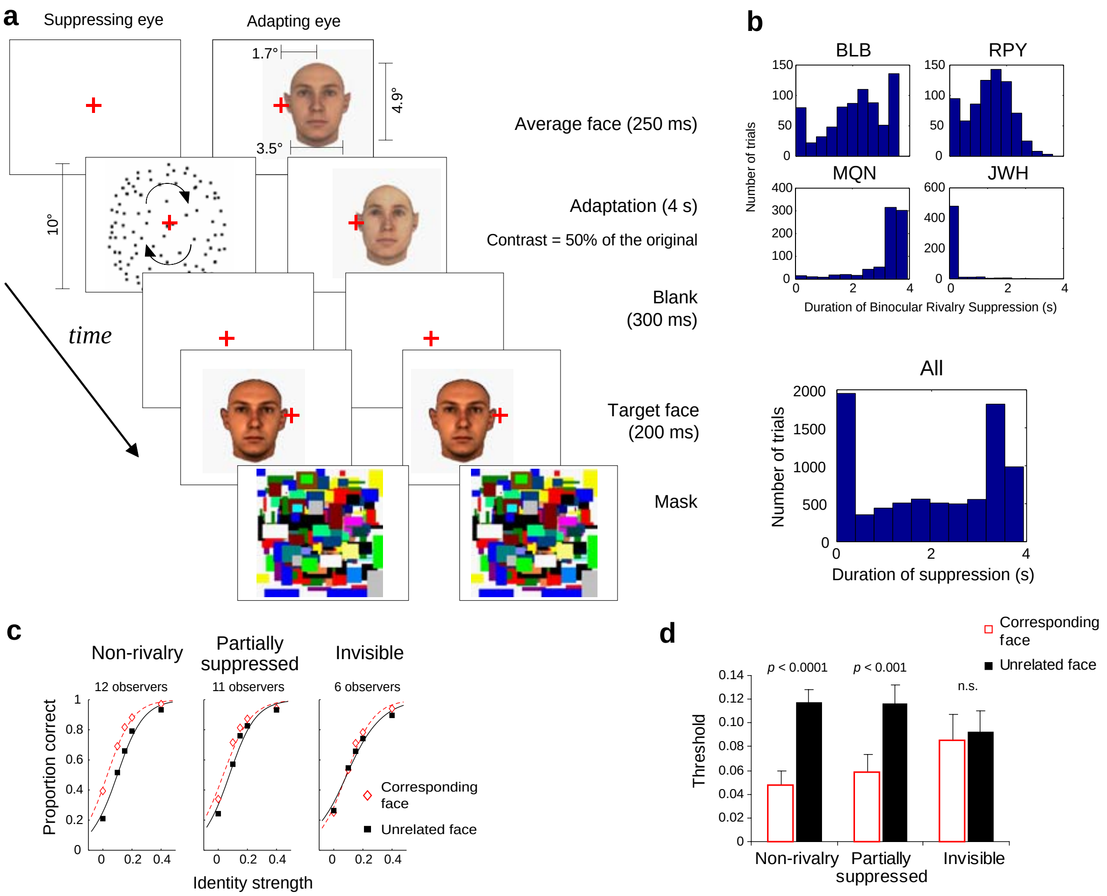

**Figure 19.** Face adaptation under dichoptic viewing.

(a) Twelve observers were exposed to a specific antiface for four seconds in the adapting eye, while viewing a rotating sphere of random dots in the other eye. Participants were instructed to continuously monitor and report the visibility of the face. After adaptation, they were asked to identify the subsequent face. In the nonrivalry condition (not shown), the other image was blank.

(b) Histograms of total duration of suppression of the face stimuli for four representing observers (top four histograms), and all twelve pooled observers.

(c) Psychometric face identification curves after adaptation. The difference between the dashed and solid curves reflects an antiface specific aftereffect.

(d) Adaptation to an antiface decreased the detection threshold of the corresponding face compared to the threshold for unrelated faces in non-rivalry condition, but not when the face was suppressed and invisible for more than 3 s. Partial suppression indicates trials where the antiface was visible for more than 1 second.

In control experiments, we confirmed that during the suppression periods, faces could not be identified, and verified that face aftereffect transfers between the eyes (i.e., the aftereffect does not depend on which eye the adaptor and the target are presented to).

Figure 19c depicts identification accuracy as a function of identity strength, with chance performance corresponding to 1 in 4 (0.25). In all conditions, identification of the target improved as identity strength increased. The difference between dashed and solid curves reflects the identity-selective aftereffect of the adapting antiface. The left plot depicts adaptation in the non-rivalry condition, with a horizontal shift of 0.07±0.01 ($p<0.0001$) between dashed and solid curves. When the antiface adaptor was clearly visible (non-rivalry trials), the corresponding face was identified more frequently compared to non-matching faces. This difference virtually disappears when the adaptor is suppressed by rivalry for more than 3 s (right plot in figure 19c, labeled “Invisible”, shift = 0.01±0.01, n.s.). The middle plot (partially suppressed) includes all other trials during binocular rivalry (i.e., when the antiface was suppressed for 0 to 3 s). The two curves are separated by 0.06±0.01 unit identity strength ($p<0.001$). Thus, mere presentation of a second stimulus does not seem to affect face adaptation.

Identity thresholds, defined here as the facial identity strength that was correctly identified in half of the trials (figure 19d), were estimated by fitting a sigmoid curve to the data for each condition. The threshold for the corresponding face was significantly lower than unrelated face in non-rivalry trials as well as when adaptor was only partially invisible (<3 s). Only six observers that had more than 160 trials with >3 s suppression were included in the invisible condition. The threshold for the corresponding face was the same as the threshold for unrelated faces in the invisible trials. The magnitude of the aftereffect in the non-rivalry and partially invisible trials for these six observers were similar to the rest of the subjects that did not experience suppression in most of the trials ($p>0.4$).

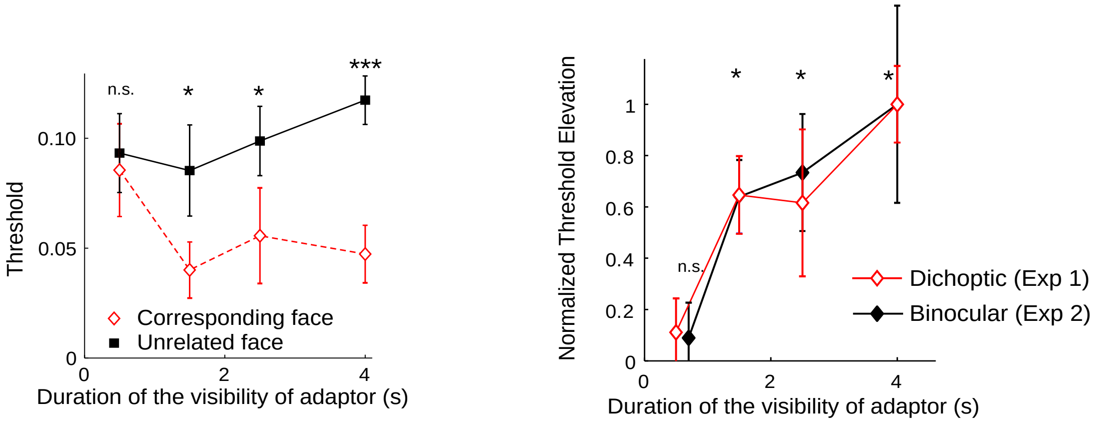

**Figure 20.** The face aftereffect depends on the duration of predominance of the antiface.

(a) We pooled the data of all twelve observers in experiment 1. A significant aftereffect occurs when the antiface is visible for more than 1 s. Error bars correspond to S.E.M.

(b) The time dependence of the face-aftereffect is parallel to the effect of the duration of physical exposure in the binocular setup where the antiface is always visible (experiment 2, 5 observers). The threshold change is normalized relative to the group mean of threshold change after 4 s visibility in each experiment. (* $p < 0.05$, *** $p < 0.001$, one-tailed paired t-test).

The difference in threshold increased as a function of the cumulative duration of visibility (figure 20a). In experiment 2, we measured the face aftereffect as a function of adaptation time for fully visible adaptors (figure 20b). As expected, the magnitude of the aftereffect depends on the adaptation time, matching the effect of the visibility in experiment 1.

It could be argued that our particular setup or the choice of rival stimuli blocks any retinal input from reaching the visual cortex. Therefore, we verified that orientation-selective adaptation is fully retained under our conditions of perceptual invisibility by using the same setup as experiment 1 except that the adaptor consisted of slowly drifting sinusoidal gratings rather than a face. We measured contrast detection threshold of a subsequent Gabor patch with the same spatial frequency of either the same or the orthogonal orientation (figure 21a).

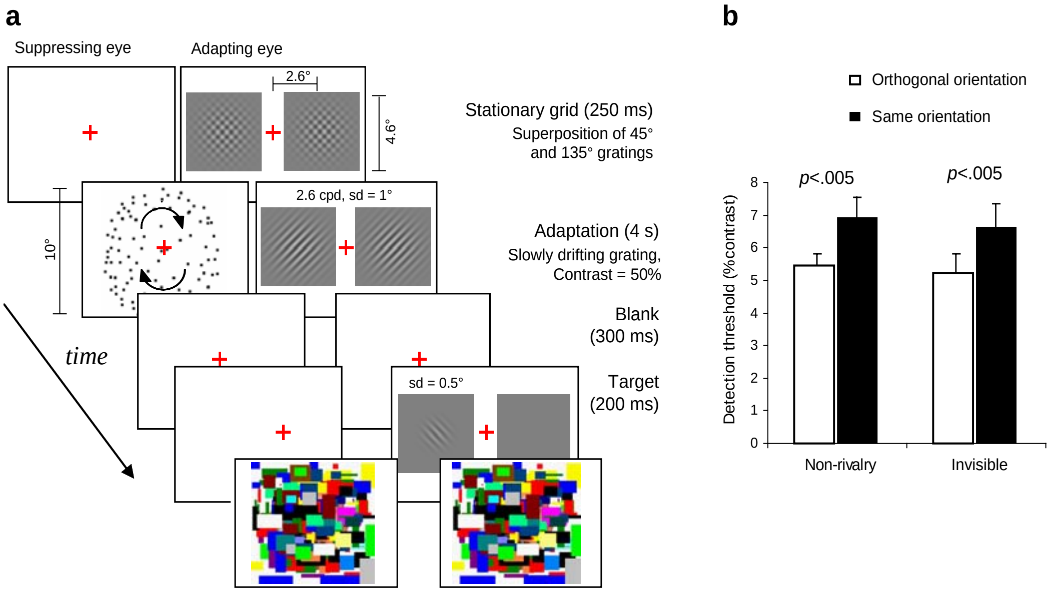

**Figure 21.** Orientation-selective adaptation is not affected by binocular suppression. (a) Seven observers were first exposed to a grid for 250 ms, followed by two slowly-drifting gratings for four seconds in the adapting eye, while viewing a rotating sphere of random dots (rivalry condition) or blank screen (non-rivalry condition) in the other eye. Participants were instructed to continuously monitor and report the visibility of the grating. After adaptation, they were asked if the subsequent low contrast grating was in the left or right visual field.

(b) Adaptation to a particular orientation increased detection threshold for the same orientation compared to the threshold for orthogonal orientation in both non-rivalry and invisible (suppressed > 3 sec) trials. In agreement with previous findings, the orientation of the stimulus can be suppressed from awareness (“Invisible”), without causing a reduction in the orientation-dependent aftereffect relative to control (“non-rivalry”).

Thresholds were significantly elevated for the same orientation compared to the orthogonal orientation after adaptation to both visible (non-rivalry) and perceptually-invisible (suppressed > 3 s) gratings (27±5% vs. 28±7%, n.s. between conditions. figure 21b). Although suppression—as measured by key press—was even stronger than for faces, binocular suppression did not have any effect on the orientation-selective adaptation.

Thus we established that the face aftereffect depends on the perceptual visibility of the antiface, rather than on the duration of the stimulus. In contrast, more low-level aftereffects such as orientation-selective adaptation depend on the physical stimulus rather than the percept (Blake and Fox 1974).

Experiments 3 and 4 addressed the question whether within, or between modalities competition for attentional resources can suppress identity-specific face processing, including the face aftereffect. When attention is distracted and engaged in a highly demanding task, task-irrelevant stimuli can be suppressed from awareness (inattentional blindness) (Simons and Chabris 1999). The antiface was presented binocularly for 4 s, and observers were required to either passively view the antiface, or actively attend to a stream of distracters and perform a 2-back memory task (figure 22a). In experiment 3 visual distracters (digits) were presented at fixation. In experiment 4, distracters were either sinusoidal tones or a recorded voice speaking the digits. Both tasks require attention to nonface stimuli and engage working memory to the same extent. However, memorizing an auditory stream does not necessitate visual competition (Duncan, Martens and Ward 1997).

Figure 22b depicts the psychometric curves after exposure to the relevant or irrelevant antiface (experiment 3). It is not necessary to actively attend to the adapting face to experience the aftereffect (both passive viewing condition and auditory memory task). However, attending to a competing stream of nonface visual distracters presented at the fixation practically eliminated the face-aftereffect. The residual aftereffect is only marginally significant ($p$=0.07, one-tailed t-test).

The results are compared with experiment 1 in figure 22c. Performing the same task with an auditory stream of inputs did not reduce the aftereffect.

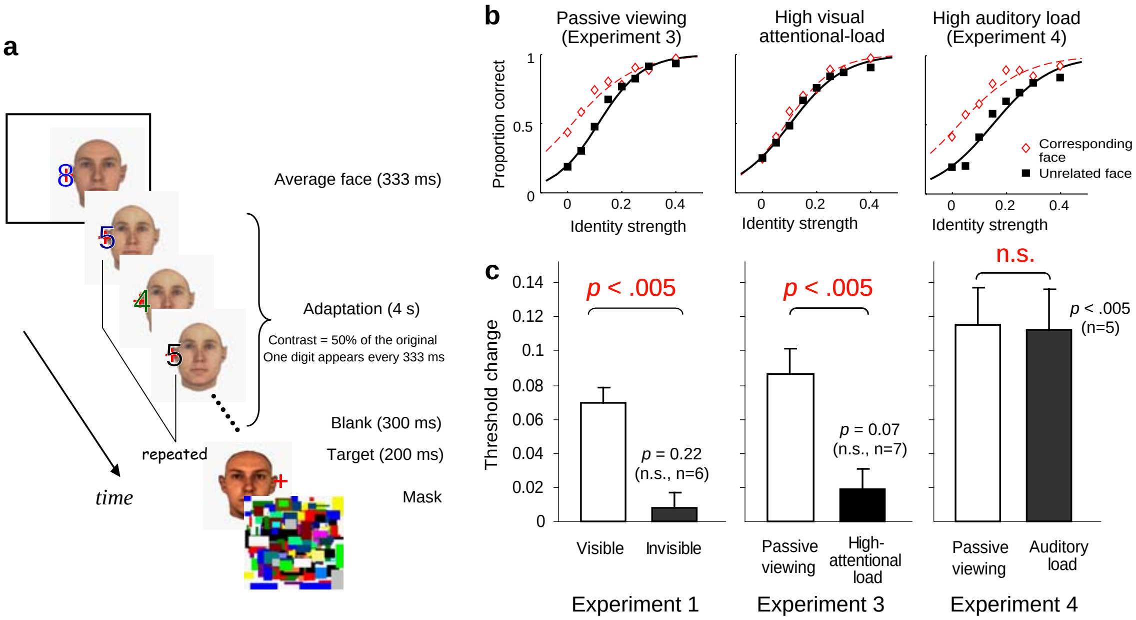

**Figure 22.** The face aftereffect is reduced under high-attentional load.

(a) Observers were asked to perform a 2-back memory task during 4 s of adaptation (high-attentional load condition, experiment 3). A stream of digits appeared at fixation. Observers were required to perform two tasks: the 2-back task during adaptation and the target detection task when the target face appeared.

(b) Identification curves following adaptation to the corresponding antiface (dashed) vs. an unrelated face (solid). The two curves are almost identical when observers are engaged in a highly-attentional demanding visual (experiment 3, 7 naïve observers)—but not the auditory task (experiment 4, 5 naïve observers). In the “passive viewing” trials observers were not required to carry out any interfering task during the adaptation.

(c) Summary data comparing the reduction of the face-aftereffect by binocular suppression and within- and crossmodal attentional load.

Although auditory distracters and cognitive load are known to affect the performance of some visual tasks, cross-modal inattention does not actually suppress visibility (Arnell and Larson 2002; Duncan *et al.* 1997). The above findings indicate that subjective visibility (awareness) and adaptation for faces are closely related. In contrast, we observed a significant orientation-specific aftereffect following adaptation to inattended drifting gratings (19±5%, *p*=0.01). The magnitude of the orientation-selective aftereffect was comparable to the passive viewing condition (11±5%, *p*=0.03, n.s. between conditions). Remarkably, the absolute thresholds were higher in the inattended condition compared to the control (*p*=0.015, two-tailed t-test) demonstrating that the 2-back memory task interfered with the conscious registration of the subsequent grating.

Adaptation to face identity is presumably driven by bottom-up visual input. To investigate cognitive, top-down contributions to face-adaptation, experiment 5 measured the effect of mental imagery on identification of subsequent physical faces. Six naïve observers were familiarized with antifaces and practiced imagining them. In the experimental sessions, observers imagined a particular antiface for a few seconds before a target was briefly presented which they had to identify. Six observers were instructed to imagine these faces as vividly as possible and report the vividness of their mental picture in each trial. Face imagery has been shown to activate the same brain areas and neurons that are activated by the physical stimulus (Kreiman, Koch and Fried 2000b; O'Craven and Kanwisher 2000). Yet, imagining an antiface did not affect the identity threshold for its corresponding vs. unrelated faces (threshold change = 0.007±0.01, *p*=0.28), regardless of the clarity of the mental image or the duration of the imagery. Therefore, it is unlikely that the suppression of the face aftereffect in experiments 1 and 3 can be attributed to a cognitive component.

## 4.2 Discussion

Binocular suppression virtually eliminated the face aftereffect whereas it had no effect on orientation-selective adaptation. Other studies provide evidence of aftereffects that do not depend on consciously seeing the adaptor (Blake and Fox 1974; Lehmkuhle and Fox 1975; O'Shea and Crassini 1981; White *et al.* 1978). These findings indicate that binocular rivalry is resolved after features such as orientation, color, and linear morion, but before complex stimuli such as faces are represented in the ventral pathway. So far, no other aftereffect originating in the ventral stream has been shown to require visibility.

Like face adaptation, the magnitude of the spiral motion aftereffect is a function of the duration of the dominance period of the adaptor in binocular rivalry (Wiesenfelder and Blake 1990). This dependence indicates that spiral motion is processed in the visual system beyond binocular interactions. Yet under different circumstances, spiral motion can result in an aftereffect without reaching awareness (Aghdaee 2005). In this study, the direction of a spiral was made subjectively invisible by crowding, that is, surrounding it with similar spiral flankers. Although the observers failed to resolve and discriminate the direction of the adapting spiral in the crowded condition and reported it at chance level, the aftereffect (measured by presenting an ambiguous spiral afterwards) was preserved (Aghdaee 2005). The crowding effect occurs when the distance between stimuli are smaller than the resolution of attention, that is, crowding can be considered as a form of inattention. Therefore, the spiral motion aftereffect is preserved under inattentional blindness.

The suppression of face-adaptation under a high attentional load favors a relatively early site for attentional competition within the ventral stream: competition for attentional resources is resolved before face identity-specific processes in FFA. Our results are compatible with the notion that observers' failure to notice unexpected and irrelevant stimuli in inattentional blindness (Mack and Rock 1998; Simons and Chabris 1999) reflects a genuine suppression of such stimuli, rather than a retrospective failure to recall them. Presumably, elimination of the aftereffect is due to the suppression of visual input from reaching face-selective neurons, and not because face processing requires attention. Interestingly, spatial, selective attention is not necessary for face gender or identity categorization (Reddy, Wilken and Koch 2004). Likewise, our results indicate that face adaptation can be obtained under passive conditions. This indicates a dissociation between spatial visual attention and visual awareness. Indeed, we have demonstrated that the magnitude of BOLD response to peripheral faces does not decrease when observers are engaged in an attentional-demanding central task, as long as observers are aware of the faces (Reddy, Moradi and Koch 2004).

Our findings are seemingly at odds with reports showing implicit priming (Mack and Rock 1998) and increased activity in face and scene selective occipitotemporal areas in human observers in the absence of awareness (Marois, Yi and Chun 2004; Moutoussis and Zeki 2002). Increased BOLD activity in those studies may reflect an incomplete suppression of stimuli from awareness in those paradigms. Alternatively, it is plausible that priming and an increased BOLD signal in the absence of awareness reflect insufficient neural activity—or different neural populations—to mediate adaptation and conscious registration of the input. FMRI is not necessarily more sensitive than psychophysically measured adaptation to uncover implicit activations: Rees, Frith, and Lavie (1997) reported strong suppression of fMRI activity in the human V5/MT complex but only a modest 23% reduction in the duration of the motion aftereffect under high attentional load. Thus, although inattended motion did not produce any measurable BOLD activity in their experiment, it still invoked a measurable aftereffect. Further studies and better control for awareness are necessary to resolve the discrepancy between fMRI studies and adaptation results.

It is possible, that the neural substrate that underlies both conscious face recognition and the identity-specific aftereffect is distinct from the substrate that underlies implicit face recognition or other aspects of face perception. Face perception is mediated by a distributed neural system that may involve multiple regions or pathways (Haxby *et al.* 2001). The amygdala, for example, has been implicated in perception of emotion in facial expression (Young *et al.* 1996). Interestingly, two recent imaging studies showed activation in amygdala in response to binocularly suppressed images of facial expression (Pasley *et al.* 2004;

Williams *et al.* 2004). Sporadic residual activation in such a distributed system may explain implicit face recognition in prosopagnosia (de Gelder *et al.* 2000; De Haan, Bauer and Greve 1992). Nonetheless, our results indicate that adaptation to face identity is specific to the pathways that are affected by inter-ocular suppression and inattention, and shares the same underlying neural substrate with conscious face identification. If configural adaptation to facial expressions involves the same pathway, then it should also depend on visibility. Alternatively, it is possible that adaptation to the emotional expression of a face is preserved for invisible faces.

In summary, our findings establish a close relationship between configural face adaptation (Leopold *et al.* 2001) and visual awareness. If you do not see a face, you will not adapt to its identity, even though you may adapt to other aspects of the face such as orientation or color. It appears paradoxical that some aftereffects such as negative afterimage or orientation-dependent aftereffect do not require seeing the inducing stimulus. Contrariwise, the result reported here for the identity aftereffect is more in line with common expectation. Together, these findings provide insight into brain organization and the neural correlates of conscious perception.

# 5 ATTENTIONAL EFFECTS IN THE BRAIN: STIMULUS-INDEPENDENT EFFECT

We studied the correlation between perception and hemodynamic activity in visual cortex in a change detection task. Whenever the observer perceived the location of a change, rightly or wrongly, the blood oxygenation-level dependent (BOLD) signal increased in primary visual cortex and nearby extrastriate areas above baseline activity caused by the visual stimulation. This nonsensory evoked activity was localized and corresponded to the perceived location of the change. When a change was missed, or when observers attended to a different task, the change failed to evoke such a response. The latency of the nonsensory component increased linearly with subjects' reaction time, with a slope of one, and its amplitude was independent of contrast. Control experiments are compatible with the hypothesis that the nonsensory hemodynamic signal is mediated by top-down spatial attention, linked to (but separate from) awareness of the change[5].

## 5.1 Activity in Visual Cortex is Modulated by Top-Down Attention Locked to Reaction Time

A central question in sensory neuroscience is the search for neuronal populations that directly contribute to phenomenal experience (Crick and Koch 1995; Koch 2004). Within this

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[5] This chapter will be published in Journal of Cognitive Neuroscience (Moradi, F., C. Hipp, and C. Koch (2007). Activity in visual cortex is modulated by top-down attention locked to reaction time. *Journal of Cognitive Neuroscience* **19**.). The idea of the experiments was conceived by FM, CH, and CK. Experiments were conducted by CH and FM and the results were analyzed by FM.

context, the extent to which early visual cortex correlates with conscious perception, with selective visual attention, a combination of both, or with something else and whether this requires feedback from higher regions has been vigorously pursued (Chen *et al.* 1998; Kamitani and Tong 2005; Lee and Blake 2002; Polonsky *et al.* 2000; Ress, Backus and Heeger 2000; Ress and Heeger 2003; Tong and Engel 2001).

Thus, the seminal experiments (Polonsky *et al.* 2000; Ress and Heeger 2003; Tong and Engel 2001) stress a connection to conscious perception and awareness on the basis of binocular rivalry or a pattern detection task. This suggests that the amplitude of V1 activity determines which stimuli reach phenomenal awareness. It is also possible, though, that the operations that underlie awareness occur at higher processing stages, such as the frontal lobes, which then feed back signals to the occipital lobe (Dehaene and Changeux 2005; Lamme and Roelfsema 2000). In addition, it is well documented that selective visual attention—directed by an explicit external cue—can modulate activity in early visual cortex in a topographic manner (Brefczynski and DeYoe 1999; Ress et al. 2000; Tootell, Hadjikhani, Hall et al. 1998), and enhances visual processing (Liu, Pestilli and Carrasco 2005; Ress *et al.* 2000). Nonetheless, it is not clear whether top-down attentional feedback is intrinsically deployed when a stimulus reaches awareness.

To investigate the nature of the correlation between activity in early cortex and subject's behavior further, we designed a novel change-detection/blindness display that allows us to manipulate stimulus parameters as well as the attentional state of the subject. In particular, our task is characterized by long and variable reaction times and therefore ideally suited to dissociate purely stimulus-driven from response-related modulations of the BOLD signal. We find that BOLD activity in striate and extrastriate regions can be decomposed into a large sensory and a small nonsensory component, and that the second component can be activated by spatial, top-down attention. The timing of the peak of this response correlates strongly with the subject's reaction times. Control experiments indicate that the nonsensory fMRI component originates outside visual cortex and expresses an attentional, spatially specific, signal.

### 5.1.1 Methods

Two investigators (FM and CH) and twenty paid and naïve volunteers from the Caltech campus, aged 20–32 with normal or corrected vision, participated in one or more experiments. All experiments were conducted according to the guidelines of the institute's committee for protection of human subjects. The stimuli were generated on a PC using the Psychophysics Toolbox (Brainard 1997) and presented to the subject via optical goggles (Resonance Technology, Northridge, CA, VisuaStim XGA. 800×600 resolution at 60 Hz. Visual field = 30×24 deg$^2$. Maximum contrast ratio = 18:1). Responses were collected using a five-button right hand keypad. Reaction times were measured from the onset of the change until the subject released the button. In the two subjects for whom we also recorded the onset of each response, subjects released the key on average 200–300 ms after pressing it.

#### Visual stimuli

The display comprised seven concentric ring segments (arcs), as illustrated in figure 23A. To compensate for the cortical magnification the width of each arc was systematically increased from center (1.4 deg) to the periphery (6.1 deg). Each arc contained alternating black and white stripes (gratings) with random widths (between 0.1 and 1 deg) that were tilted 45 deg left or right, and were separated from other arcs by a thin grey area. Every 400 ms, the stripes were replaced with a new, randomly generated set of stripes, thus the whole display appeared as flickering at 2.5 Hz. The new stripes had the same orientation as the old one, except every 4-8 s, in one of the arcs the orientation of the stripes flipped by 90 deg. Thus the change in orientation and local phase/spatial frequency occurred at the same time.

To avoid subjective grouping effects, we made sure that at any time during the experiment no more than two consecutive arcs have the same orientation.

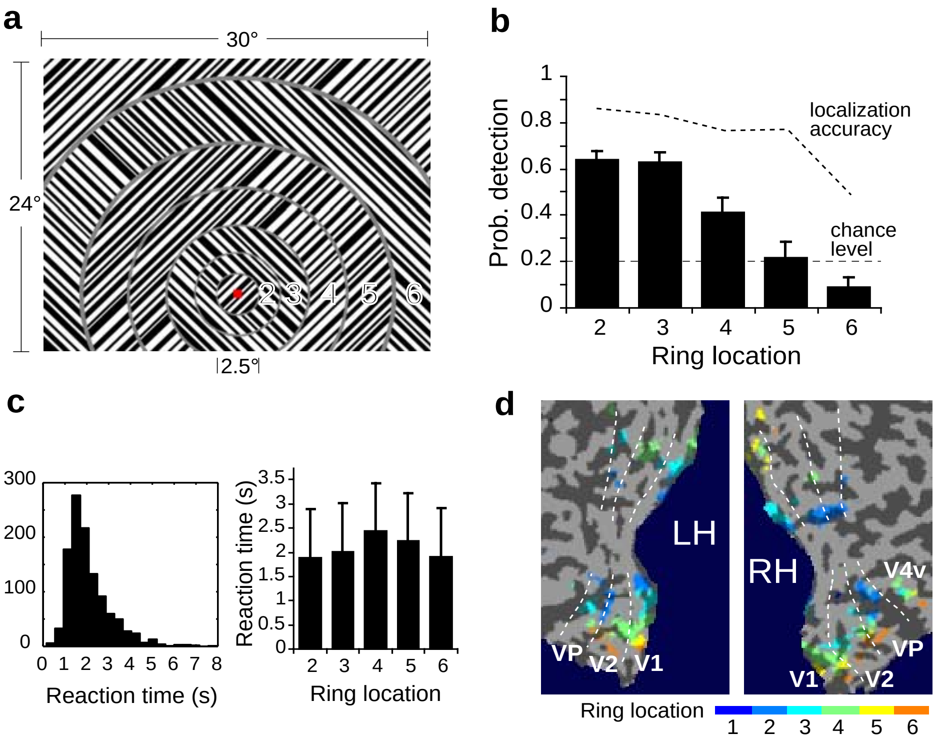

**Figure 23.** Stimulus and behavioral results.

(a) A schematic of the display used in the main experiment. Observers monitored arcs 2–6 while fixating the central red square, and indicated if there was any change in the orientation by pressing one of the five keys. Every 0.4 s, each strip within the grating was varied randomly in width (range=0.1-1 deg). Every 4–8 s, the orientation of one of the gratings changed by 90 deg. Observers did not know when to expect the change (non-cued design). The orientation in each arc flipped every 30–50 s in random order.

(b) Probability of the detection of the change as a function of the location (eccentricity) of the arc across observers. Dotted line depicts localization accuracy (Hit/(Hit + False alarm) for the location of the change). Error bars indicate S.E.M.

(c) Reaction-time histogram and reaction-times as a function of the arc (mean±S.D. across trials).

(d) Voxels corresponding to each arc (based on localizer scans) are represented on the flattened cortex for one observer.

A red fixation mark was continuously displayed at the center of the rings, 6 deg below the center of the display. Observers were instructed and trained to monitor arcs 2–6 and ignore the innermost and outermost ones.

### Change detection experiments

Nine subjects performed 8–11 change-detection runs. Behavioral responses were recorded inside the scanner. Before the session, subjects were trained outside the scanner with a similar task. To familiarize observers with the task, an easy version of the experiment was used outside the scanner for training. In the main experiment, the transient associated with the change was masked by the synchronous changes in local phase and spatial frequency of other gratings. Seven participants underwent additional sessions, similar to the main experiment, but using a low-contrast (20% of the maximum contrast) display. In all other experiments, the high-contrast (100% of the maximum) gratings were used.

Additionally, each observer conducted 3 localizer runs, in which arcs were sequentially presented for 5 s, followed by a 5 s blank period (repeated 6 times). In another 2–3 runs, we mapped a 30 deg rotating wedge (9 deg/s) of a flickering checkerboard pattern, and used the polar component of the resulting retinotopic map to identify V1–V2 borders (Engel, Glover and Wandell 1997; Sereno *et al.* 1995).

In a subset of participants we made sure that horizontal eye movements (measured outside the scanner during training) were confined to 1 deg from the fixation. Additionally, two observers performed the experiment while we tracked their eye movements inside the scanner (Resonance Technology, Northridge, CA, MREye eyetracking system).

*Data acquisition:* T2* weighted Echo-planar images (TR=2 s, TE=30 ms, FA=90 deg, FOV=210 mm, 31 3-mm interleaved axial slices) were acquired in the Caltech 3.0 Tesla Trio whole body scanner (Siemens) using the whole-head coil and an in-line motion correction sequence (Thesen *et al.* 2000). The slices were positioned to cover the occipital lobe. Each functional run comprised 152 volumes (304 s); the first seven volumes were discarded. After the initial 14 s a fixation point was presented on a homogenous grey screen for 20 s, followed by the dynamic gratings whose width changed every 400 ms (2.5 Hz). Another 20 s of grey screen appeared at the end of the run. A 12-minute high-resolution (1×1×1 $\text{mm}^3$) T1-weighted MPRAGE sequence (T1=1.5 s, TI=0.8 s, TE=3.05 ms, 160 sagital slices) was acquired for cortical flattening.

### Distracted attention control

We presented a stream of digits at fovea (every 1.6 s) and asked observers to perform a two-back task and ignore the peripheral change. Subjects had to quickly press a single button whenever of the last three digits seen, the first and third one were identical. The display and data acquisition was the same as for the high-contrast change detection experiment.

### Top-down attention controls

Transient and sustained endogenous attention controls were conducted on naïve subjects who did not participate in the main experiment. In the transient endogenous attention control, a semantic cue (a digit between 2 and 6) was displayed every 3–9 s (uniformly distributed) at fixation and observers had to report the orientation of the grating inside the corresponding arc by pressing one of the two buttons. The orientation of the grating in the cued arc was not changed for at least 2 seconds after the cue. In the sustained attention control, a target arc was displayed in isolation at the beginning of each scan. In the subsequent five minutes, observers had to report orientation changes in the target arc (high-contrast display identical to the main experiment) by pressing a single key as fast as they could while ignoring changes in other arcs.

*Data acquisition:* T2* weighted Echo-planar images (FOV=192 mm, 30 × 3 mm interleaved axial slices) were acquired using a phase-array surface coil. The flickering display was presented for 5 minutes after the 4 s initial scans were discarded. Other acquisition parameters were the same as for the rest of the experiment.

**Analysis:** Linear and low-frequency ($<0.01$ Hz) temporal drift was removed for each slice in the Fourier space. Student's t-maps for each localizer and retinotopic-mapping run were computed separately. For each subject, images were coregistered between runs using a Linear Image Registration Tool (FLIRT) (Jenkinson *et al.* 2002). Retinotopic maps were projected onto flattened cortical surface maps created in *BrainVoyager* QX (Brain Innovation B.V., Maastricht), and the V1/V2 boundaries were identified following a well-established method (Engel *et al.* 1997; Sereno *et al.* 1995). These boundaries were used in conjunction with the localizer data to define the regions of interest (ROI) for each arc. Statistical t-maps for each arc were thresholded at $t<3$ ($p<.006$, uncorrected), and voxels that were significantly activated by more than one arc were excluded. Figure 23D illustrates ROIs for one observer depicted on the flattened cortex. Our analysis is robust with respect to the exact value of the threshold for defining regions of interest and we replicated all findings using a lower threshold ($t<2.5$) as well.

The time-course of the BOLD signal was calculated by summing all voxels inside each ROI after slice-timing correction and resampling at 1 Hz using cubic-spline interpolation, normalized to the sum of all voxels in the ROI for the first volume in each run. Evoked responses were averaged with respect to the onset of the change (figure 24–figure 26) or the response (figure 28). The average BOLD signal 10 s before the onset was subtracted from each trial to correct for shifts in the baseline. Trials in the first and last 30 s were excluded. The amplitude of BOLD signal for each condition for each participant was calculated by averaging the responses 6 s after the change occurred. Averages comprising less than 16 trials were excluded from further analysis. Statistical significance was determined by Student's t-test (or ANOVA when appropriate) on the average amplitude. The latency of the peak (trough) was calculated after binning trials based on reaction time for the average response of each bin: the response was resampled at 10 Hz (cubic-spline) and the maximum value between 2 and 10 s (4 and 16 s) after change onset was identified as the peak (trough). The sensory component (response to the gratings themselves) was calculated by subtracting average activation 10 s before the onset and 10–20 s after the offset of the gratings (baseline) from the average BOLD signal 10–20 s after the onset and 0–10 s before the offset (stimulation) for each run.

### 5.1.2 Results

The stimulus display (figure 23a) consists of seven concentric arcs of gratings whose width changed every 400 ms (that is, phase and spatial frequency changed locally), giving the entire display a flickering appearance. In addition, and much less frequently (every 4–8 s), the orientation of a single grating making up an arc flipped by 90 deg. The change in orientation was synchronous with the changes in phase and spatial frequency in other gratings. Observers had to report the location of the grating that had changed orientation in arcs 2 to 6 and ignore everything else (figure 23a).

Subjects easily see the orientation of any of these dynamic gratings when shown in isolation. They can also discern the orientation of gratings inside a particular arc throughout the entire display if the location is cued. However, because of crowding (He *et al.* 1996), it is not possible to consciously and simultaneously register the orientation of all arcs. More importantly, the visual transients associated with phase and spatial frequency changes effectively masks the transient associated with the synchronous orientation change (change-blindness; Rensink 2002; Rensink, ORegan and Clark 1997). Consequently, in 60±3% of trials, subjects failed to notice the change in orientation (all values indicate mean±S.E.M across observers, unless otherwise stated). Changes in the peripheral arcs were missed more frequently than in the more central ones (figure 23b).

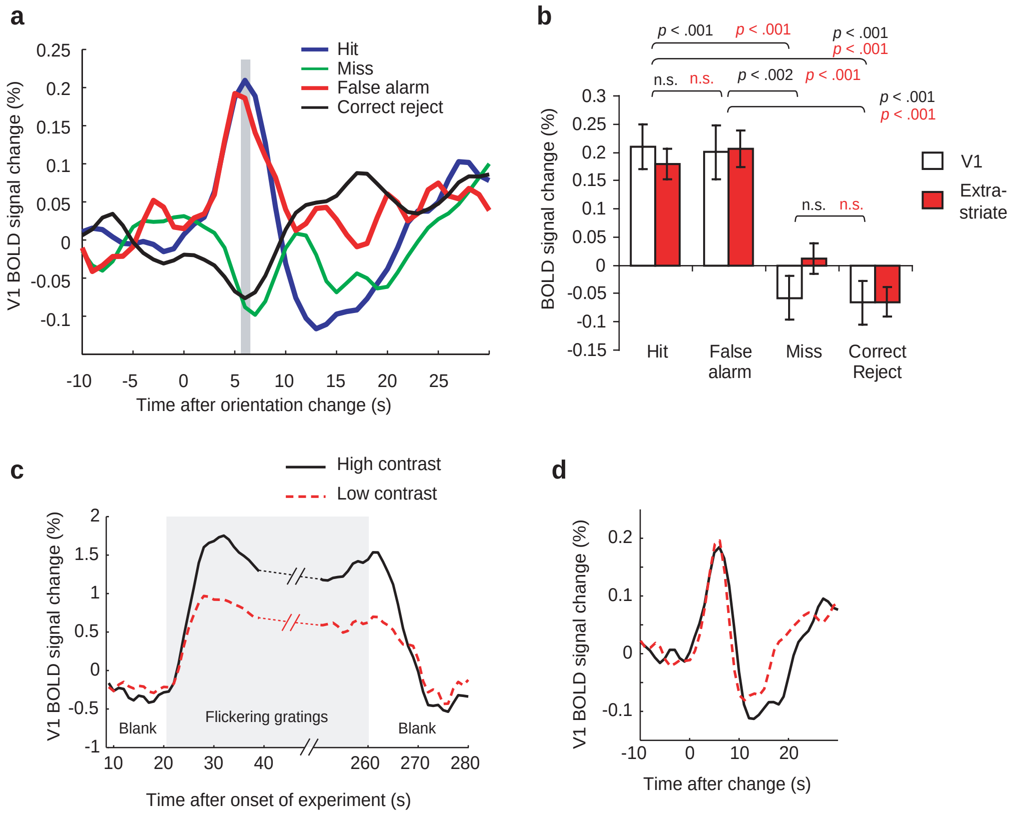

**Figure 24.** The evoked response depends on perception.

(a) Average BOLD response in V1 in correctly detected (Hit), missed (Miss), falsely localized (False alarm), and correctly rejected trials for the high-contrast display (averaged across nine observers. See analysis in the methods section for details). The response to the ongoing change in width (every 0.4 s) of the gratings was discounted by subtracting the average signal in a 10 s window before the onset of the change. Hit and False alarm traces are based on the activity in the voxels corresponding to the reported location. The Miss trace corresponds to the location of the change and the Correct reject trace to the average of voxels for arcs 2–6. In Correct reject trials, either the first or last arc flipped, but observers were instructed not to report changes in these two locations.

(b) Amplitude of the BOLD signal 6 s after change in orientation (gray bar in a) in the four different types of trials in A. White: V1 activation, Red: V2 and VP activation. Error bars depict S.E.M across observers. The same pattern of results was observed for all arcs.

(c) V1 sensory component was higher in the high-contrast display compared with the low-contrast display.

(d) The nonsensory component was similar in both the high- and low-contrast displays. Note that the hemodynamic response evoked by the change in orientation adds to the much larger response evoked by the gratings whose width changed every 400 ms. Panels c and d both depict average signal across observers.

When a change was noticed, the reported location was usually correct (80±3%, chance level is 20%). The average reaction time was 2.13±0.12 s (figure 23c, see 5.1.1), consistent with spontaneous, serial deployment of attention.

The visual areas in the occipital lobe corresponding to each arc and the borders between these retinotopic areas were identified in separate scans (figure 23d). In the main change blindness experiment, the BOLD signal comprised two components: a large, sustained increase (relative to the homogenous gray background) in response to the visual transients, and a much smaller transient component that followed the flip in orientation. Notably, this transient response occurred only when the change was detected by the observer ($F(3,29)=13.9$, $p<.00001$, Tukey-Kramer post hoc test: Hit vs. Correct reject: $p<.001$, Miss vs. Correct reject: not significant. figure 24a,b). A similar increase in the BOLD signal in False alarm trials suggests that the transient activity in V1 and nearby extrastriate areas (V2: visual area 2, VP: ventral posterior area) correlates with the subjective percept rather than with the physical change in the display. When the change in the orientation was not perceived, it did not evoke this transient response. In two observers, we tracked eye position inside the scanner and verified that the correlation between BOLD signal and observers' response are not caused by eye movements. Hereafter (and for reasons that shall soon be clear), the sustained response to the changing gratings and the transient response to the perception of the change will be referred to as the *sensory* and *nonsensory components*, respectively. In a small subset of trials, observers falsely reported a change at a location that was not an immediate neighbor of the arc that changed. In these trials, the evoked BOLD signal was larger in the reported location than in the actual location of the change (paired $t_8$=2.69, $p$<.05).

In a variant of the main experiment, participants viewed a similar display, but the contrast of the gratings was lowered five fold to 20%, resulting in a substantially smaller sensory-evoked component (0.94% vs. 1.73%, $t_6$ = 11.6, $p$<.0001; figure 24c). Despite the reduced contrast, behavioral performance was similar to the high-contrast session (42% vs. 40% correct, low vs. high contrast, respectively, n.s.). If the peak in figure 24a reflected modulation of V1 responses by the visual input alone (for example, by changing the gain of LGN or layer 4 neurons), lowering the contrast should have reduced both components. Contrariwise, reducing the contrast had little effect on the magnitude of the nonsensory BOLD signal (0.23% vs. 0.22%, low vs. high contrast; $t_6$=0.31, $p$=0.77; figure 24d), and the spatial and temporal pattern of the nonsensory component was quite similar to the non-sensory component of the high-contrast stimulus. Average contrast modulation (ratio between low- and high-contrast conditions per subject) were 1 and 0.52 for nonsensory and sensory components of the BOLD signal, respectively ($t_{12}$ = 3.08, $p$<.01). Thus, the evoked V1 non-sensory component appears to be additive, not modulatory or multiplicative. A similar trend was observed in V2 (sensory component, low vs. high contrast: 0.93% vs. 1.45%, $p$<.001; nonsensory component: 0.16 vs. 0.22, $p$=0.18) and VP (sensory component: 1.06% vs. 1.56%, $p$<0.001; nonsensory component: 0.16% vs. 0.19%, $p$=0.53).

Remarkably, the latency of the peak nonsensory BOLD activity in striate and extrastriate areas increased with the reaction time (figure 25a): that is, the longer the subject took to report a change, the later the peak in the BOLD signal. Sensory activation will be time-locked to the change, although it might be modulated by attention. In contrast, components of activation in the visual areas that are induced by top-down feedback will be more closely related to the response. A highly significant linear relationship with a slope of one (1.03±0.4) exists between reaction-time and the time the BOLD response peaked. We did not find any consistent effect of subject, arc location, correctness of the response, or binning parameters on the slope. The evoked BOLD activity shifts with the reaction time without any major change in the shape of the hemodynamic response function (figure 25b,c).

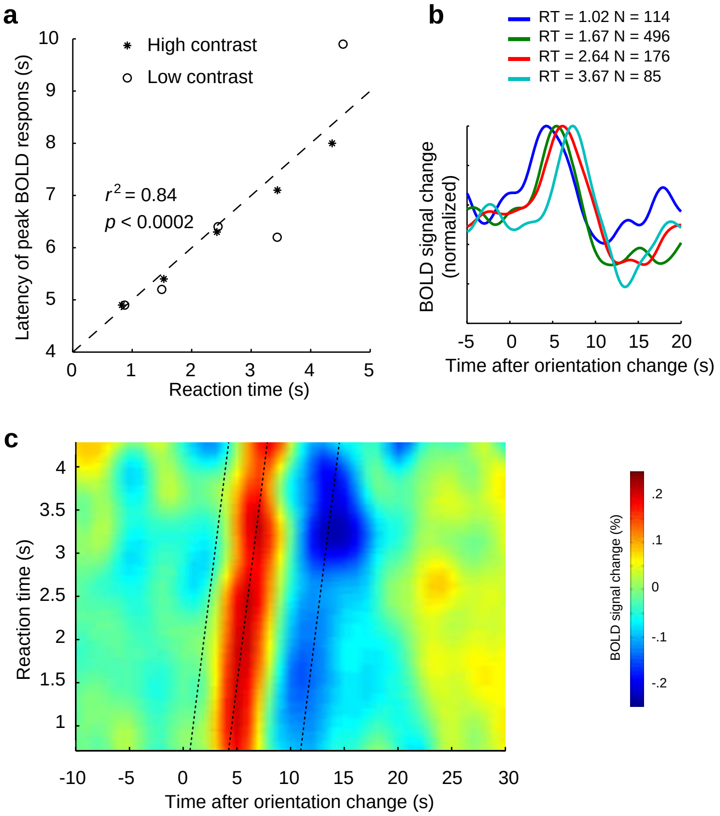

**Figure 25.** The latency of the V1 nonsensory component increases with reaction time.

(a) Time of peak BOLD response with respect to the stimulus onset as a function of observers' reaction times (data pooled within 1 s bins). Abscissa: average reaction time of trials in each bin; ordinate: time of peak of the average BOLD response.

(b) Average V1 hemodynamic response as a function of reaction time. Responses were normalized by dividing by the peak.

(c) Moving average of the BOLD activity (Gaussian window, FWHM = 0.6 s) sorted by reaction time. Note the significant dip following the sharp increase. Dashed lines with a slope of one illustrate reaction time, the positive peak, and the negative peak of response, respectively.

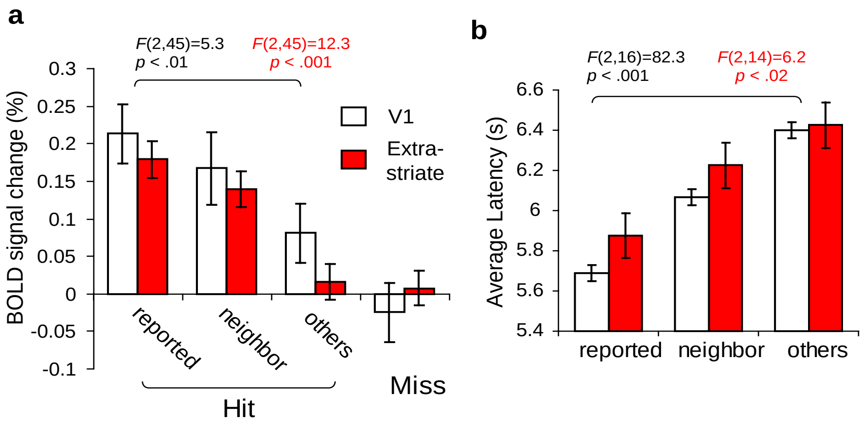

**Figure 26.** Location-specificity of the evoked BOLD response.

(a) The nonsensory BOLD signal increased mainly in the region of visual cortex that corresponded to the perceived location of the change (and its immediate neighboring arcs). Pooled high- and low-contrast data. The amplitude of the BOLD signal 6 s after change in orientation (Hit) is compared between the reported location, its immediate neighbors, and other (distant) arcs. The activity in Miss trials is shown for comparison. Error bars indicate S.E.M. across sessions (seven observers carried out both high and low contrast sessions. Two individuals carried out the high contrast session only).

(b) Time of the peak nonsensory BOLD signal following the change (pooled data across all observers. Latencies were estimated based on bins of 100 trials sorted by reaction time). Error bars depict standard error estimates (Tukey-Kramer post hoc test), respectively.

Absence of a nonsensory BOLD component in missed trials, and the linear dependence of the latency of the activity on the reaction time of the observer indicate that the increased BOLD signal is not driven by the change in the image. Further analysis of the average V1 BOLD signal relative to the time of the button press demonstrates that the increase in signal 4–5 s after reporting the change is followed by a significant (but more variable) decrease for Hit and False alarm trials (average trough 8 s after the response. Hit: -0.12±0.02%, $p<0.01$, False alarm: -0.11±0.04%, $p<0.05$), time-locked to the response ($r^2 = 0.8$, $p < 0.001$). There was no indication of such a trough for Miss trials.

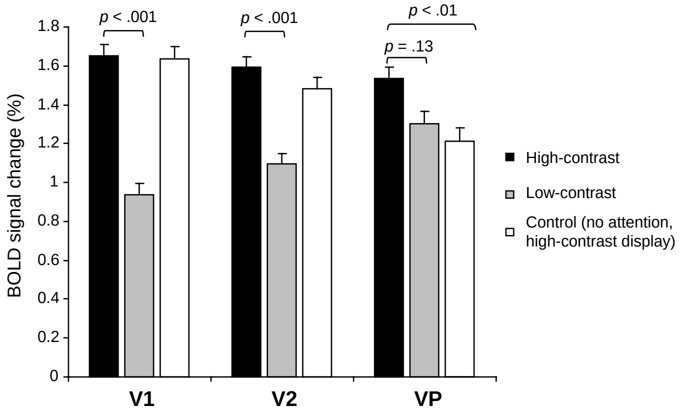

**Figure 27.** Modulation of sensory component by reducing contrast vs. withdrawing top-down, spatial attention.

The activation depicts the average BOLD signal increase compared with a blank screen (sensory component) in voxels of visual cortex that correspond to arcs 2–6. In both high- and low-contrast change detection conditions, observers attended to the arcs. In all visual areas, activation increased with contrast, but the effect was stronger in V1 than in VP. In the distracted attention control, high contrast gratings were used, but observers were instructed to attend to a stream of digits appearing at the fovea and to carry out a two-back memory task. The difference between the high-contrast and distracted attention control, which reflects modulation by top-down and spatial attention, is significant in VP and virtually nonexistent in V1 (pooled data from four observers who participated in all three conditions, $F(8, 1243) = 19.32$, $p < 0.0001$). Error bars indicate S.E.M. across observers. * The difference reaches significance if all 7 observers who participated in high and low contrast experiments are included (data given in the text).

In both change detection experiments, the nonsensory response in the correctly detected trials was spatially localized: the amplitude of the signal was highest and the latency of the peak BOLD signal in V1 was shortest at voxels that corresponded to the region of the reported arc (figure 26). Similar results were observed in adjacent extrastriate areas V2 and VP. The amplitude of the nonsensory response was comparable, although V1 activation was slightly stronger than extrastriate activation (pooled data: 0.22% vs. 0.18%, $p < 0.03$).

A first control experiment, referred to as *distracted attention*, was conducted on five observers to address if the visual activity correlates with the task or the motor response. Participants were asked to ignore the gratings, and instead to attend and respond to a foveal stimulus. The display consisted of the same high-contrast gratings as in the main experiment, except that a stream of digits (at 0.625 Hz) was superimposed onto the display at fixation. Observers had to perform a cognitively engaging two-back memory task (see methods).

Engaging in this attentionally demanding task at the fovea had little effect on the V1 and V2 sensory responses (figure 27). Yet the nonsensory BOLD signal disappeared: We averaged the BOLD activity based on the time of the change and regardless of the response or reaction time. The amplitude of the unsorted average (6 s after the change) in the distracted attention condition was significantly smaller than the same unsorted average in the main experiment (-0.01% vs. 0.09% BOLD increase, $t_8=3.62$, $p<.01$). Thus, neither the visual input nor the motor response per se can explain the nonsensory signal following Hit and False alarm trials in the main experiment. Taken together with previous findings, the results demonstrate a double dissociation of sensory and nonsensory components in early visual areas: the sensory component depends on the contrast of the display but is task independent, while the nonsensory component is contrast independent but task dependent. This binary distinction into sensory and nonsensory components broke down in area VP. Attending to the foveal distracters and engaging in the memory task significantly reduced the BOLD response to the gratings in VP (figure 27).

It is possible that the nonsensory BOLD component is mediated entirely by spatial attention. Ress, Backus, and Heeger (2000) reported localized, stimulus-independent activity in early visual cortices following an attentional cue. In our change blindness experiments, there is no explicit cue, and deployment of attention is spontaneous. Following the hypothesis that the nonsensory component is due to shifting spatial attention, we predict that if the location of the change is cued (either by increasing the saliency of the change or with a high-level cue), a nonsensory component should occur. We thus conducted control experiments to investigate the effect of top-down attention. Furthermore, if the nonsensory component is solely due to attentional feedback, then perceiving the change at an already attended location should not result in an additional increase in the BOLD signal. In contrast, if perception of the change evokes a localized nonsensory BOLD component at an already attended location, then mechanisms other than spatial attention need to be invoked.

In a second control experiment, the *transient endogenous attention control,* we transiently shifted spatial attention to a distinct location. A cue (arc number) presented at fixation instructed subjects where to attend; observers had to immediately report the orientation (binary choice) of the gratings inside the corresponding arc. In this experiment, changes in orientation were completely irrelevant to the task and they did not coincide with the cues at fixation. Since the cue is a high-level one, any localized signal increase would be due to the top-down shift of spatial attention. Four naïve participants judged the orientation at 91.6±1.5% correct and all showed significant increases of the amplitude of the BOLD signal at the attended location (average increase 0.4±0.08%, $t_3 = 4.9$, $p < 0.02$). As expected, this attentional BOLD signal was localized (paired $t_3 = 9.8$, $p < 0.01$ target vs. distant arcs); its amplitude was almost double the nonsensory component in the main experiment.

We further studied the nature of the nonsensory hemodynamic component to orientation changes in a final *sustained endogenous attention control*. Subjects had to continuously monitor orientation changes at a single, pre-specified location during the entire experiment and press a button every time a change occurred. This control is complementary to the transient endogenous attention control, as the location of spatial attention remains at one location; consequently, any observed signal changes will be related to the task-relevant changes rather than shifts of spatial attention.

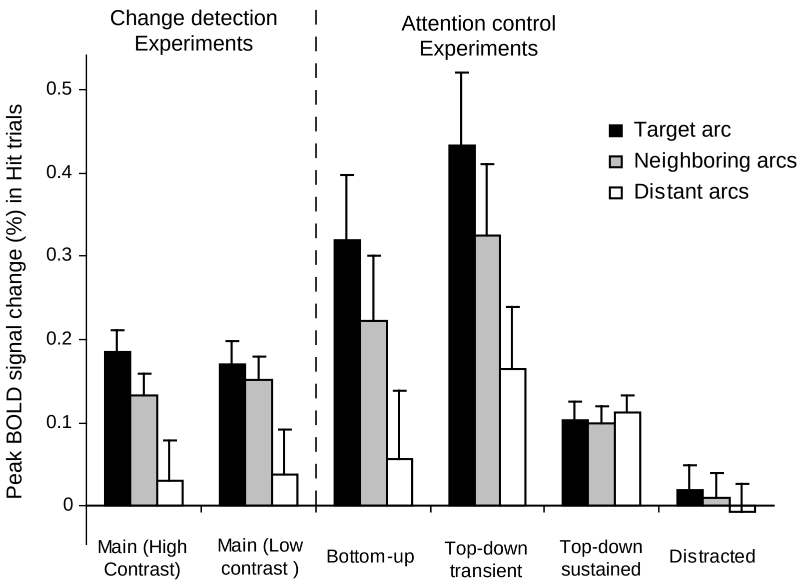

**Figure 28.** Comparing visual activity following hit events in change detection experiments vs. attentional controls.

Bars depict the peak of the average BOLD signal increase following the response in the target arc, its immediate neighbors, and distant (nonneighboring) arcs. Error bars depict S.E.M across observers. The peaks of the transient BOLD signal in transient condition were larger than the nonsensory component in the main experiments with high and low contrast gratings, although they all show similar location specificity. In comparison, in the sustained attention condition, the hemodynamic signal time-locked to the response is weak and not spatially localized. This transient nonspecific BOLD response cannot account for the localized non-sensory component in the main experiment. For the distracted attention condition, hit refers to correct responses in the memory task, and target refers to the arc that changed at the same time as the target digit appeared at fovea.

Five participants performed at 90.5±3.3% correct (indicating that they successfully attended the target). The amplitude of the BOLD signal increased following the change in Hit (0.11±0.02%, $t_4$=6.4, *p*<.001. figure 28), but not in Miss trials (0±0.03%, *p*=0.94). However, the amplitude of the increase in hit trials was about half of the amplitude of the nonsensory component in the main experiment. Furthermore, unlike in the change detection experiment or the transient endogenous attention control, this signal was not spatially localized. That is, when observers already attended to a particular location there was no further localized response to a reported change.

In a variant of the sustained endogenous attention control, every 4–14 s a high-level cue at fixation indicated the location of the subsequent change. After a variable interval (2–13.6 s), the orientation of that arc flipped. Four observers correctly reported 87.6±1.9% of the changes. The V1 BOLD signal increased significantly following the cue (0.3±.013%, $p<.001$). The effect of top-down attention was spatially localized ($F(2,9)=25.9$, $p<.001$), and remained high until the change occurred. Therefore, the absence of a localized transient BOLD signal cannot be interpreted as an absence of attentional effects in V1 in the sustained attention control. A similar sustained increase occurred in Miss trials (0.32±.09%, $p<.05$). Comparing Hit and Miss trials did not reveal any BOLD response to the perception of the change, confirming the hypothesis that the transient nonsensory component in the change detection experiment is caused by a shift of spatial attention to a previously unattended location.

## 5.2 Discussion

Our findings can be summarized as follows: in the main experiment, perception of the change correlated with a small but highly significant and localized increase in hemodynamic activity in early visual cortex. This nonsensory signal component was independent of the contrast of the display and was time-locked to subjects' response. When the change was not perceived, it did not evoke any measurable hemodynamic signal. The distracted attention control demonstrated that neither the motor response per se nor the same stimulus coupled to a different task that forced subjects to attend to the center of the display induced a similar transient BOLD signal increase in visual cortex. Top-down attentional cues induced a localized transient increase. However, when observers already attended to a task-relevant location (sustained endogenous attention control), the increase in the hemodynamic signal following the perception of the change was small and not spatially localized. This suggests that shifts of visuo-spatial attention—and not the awareness of the change at a particular location—underlie the nonsensory component in the change blindness experiment. This component is dissociable from the stimulus-driven activity in early—but not late—visual areas. Its amplitude (~0.22%) is only a fraction of the response to the dynamic gratings (~1.7% for high-contrast display), and small compared with baseline fluctuations or the effect of contrast. Given its small size, it may be overlooked in studies that focus primarily on the sensory component.

It is conceivable that the long reaction times in our main experiment are due to the physical change in the orientation of the arc not being perceived until random fluctuations of the geniculate input or of intrinsic activity in V1 (Kenet et al. 2003) temporarily increase the neuronal signal in visual cortex, thereby enhancing the chance that this larger signal is detected in higher regions and made accessible to conscious perception and motor control. This feed-forward account is compatible with the observed linear relationship between the timing of the peak BOLD activity and reaction time. It does, however, also predict that the same response (on average) should follow the change regardless of the task, while no nonsensory response occurred in our distracted attention control. This finding is unlike that reported by Muckli et al. (2005) studying V1 activity without stimulation of the corresponding retinal location in apparent motion. Their signal was not reduced when attention was distracted. Thus, Muckli et al. did not rule out that such activity is driven by the sensory input (via horizontal connections from stimulated V1 neurons) and is not directly and immediately linked to the percept. Similarly, Beck and Kastner (2005) recently reported a pop-out effect in early visual cortex that did not require top-down attention. In contrast, absence of the nonsensory signal in our distracted attention control indicates that sensory input by itself is insufficient to drive this component.

This nonsensory component could be akin to the attentional increase in visual activity in the absence of an image (Kastner *et al.* 1999), or unrelated to the visual stimulus (Ress *et al.* 2000)—except that in our experiments the activity does not follow an explicit external cue. Thus, the same top-down signal in V1 is observed whether the input has high, low or even zero contrast (Kastner *et al.* 1999), and whether or not an explicit attentional cue is present (main vs. transient endogenous attention experiments). Our results extend these studies by demonstrating a link between nonsensory attentional component and perception that is not mediated by external cues.

Ress and Heeger (2003) used near threshold stimuli and found V1 activation following the stimulus when the stimulus was seen, and no activation when it was missed. Their result at the surface appears to be the same as our correlation between V1 activity and change detection. However, their paradigm was designed to engage attention continuously and to minimize attentional shifts; that is, it was designed to insure sustained attention. Under those conditions, the activation for seen targets was retinotopically localized (Ress and Heeger 2003). In our sustained attention control, the transient signal increase was not localized. Therefore, in contrast to Ress and Heeger (2003), we interpret our control experiments as indicating that the localized nonsensory activity in V1 and V2 is mediated by top-down attentional mechanisms. Remarkably, the nonsensory component in the change detection experiment correlates with perception of a change that could precede deployment of attention by a few seconds. Therefore, the link between perception and V1 activity cannot be attributed to a facilitation of the response to the change in Hit trials due to the trial-to-trial variability in the deployment of attention.

In the transient endogenous attention control, the nonsensory signal that followed the cue was robust and localized, indicating that top-down activation can evoke a BOLD response similar to the one in the main experiments. Indeed, it was about twice the size. The nonsensory component in the main experiment could be smaller because a change may occur at an already attended location, with no need for a shift of spatial attention. Top-down feedback, linked to spatial attention and possibly originating in parietal or frontal sites, is the most parsimonious account explaining the correlation between reporting the change and the nonsensory response in all conditions that we examined, including the reaction times data.

Our change-detection task reveals concurrent and independent sensory and nonsensory signals in early visual cortex. The dominant, sensory component depends on contrast and is largely unaffected by attention, while the nonsensory, attentional component is smaller, independent of contrast, depends on the task, and reflects whether the orientation change is reported. The nonsensory BOLD component could mediate different, nonexclusive functions. It could act as a "read-out" signal (Kamitani and Tong 2005) permitting conscious access to the neural information in V1 (Ress *et al.* 2000). Or, it may relate to the precise localization of the change or it may be necessary to initiate long-term plasticity and perceptual learning.

Previous studies of visual change blindness have revealed a network of parietofrontal regions associated with visual attention (Beck *et al.* 2005; Beck *et al.* 2001; Huettel, Guzeldere and McCarthy 2001; Pessoa and Ungerleider 2004), correlated with detection of the change. Those findings provide indirect evidence of involvement of attention in change-detection. None of the above studies carried out a detailed analysis of attentional enhancement of early visual activity as we have done here. Thus, our results directly demonstrate for the first time that shift and deployment of attention in V1 and nearby visual areas is tightly linked to perceiving and reporting the change among several items.

The linear relationship between the timing of the fMRI peak activity and reaction time suggests that attention shifts around the time that the subjects committed to a response. If attention to the change itself determined how fast a change was registered, then we would have expected a correlation between the amplitude of the BOLD activity—rather than its latency—with reaction time (i.e., a weaker BOLD activity for longer RT than for shorter ones). Alternatively, the activity in V1 could have increased from the time of the change and saturated until the time that the observer responded. This was the case in one of the attention controls, but not in the change-detection experiment. Another possibility is that trials with short reaction time correlate with the activity in visual areas, but as time passes, this correlation disappears due to the involvement of other areas and processes. Other studies have reported a correlation between timing of brain activity and perception in parietal and frontal, but not in primary sensory areas (Formisano *et al.* 2002; Menon, Luknowsky and Gati 1998). Such a lack of a meaningful relationship between the timing of peak V1 BOLD activity and reaction time could have suggested that change is represented entirely outside the primary visual cortex.

The nature of our display insures considerable variability in reaction times, with subjects reporting a change occasionally 3 or more seconds after it occurred. Our interpretation of the nonsensory BOLD component as reflecting top-down attention rather than change awareness per se leaves open the fundamental question of the causal relationship between attention and awareness, and the interesting possibility that the change is perceived much sooner but is not reported until later, due to a variety of confounding factors (attention, sensory-motor mapping, visual memory, etc.). That is, the nonsensory BOLD component represents an attentional feedback after subjects have perceived the change. If true, it would provide further evidence in favor of a dissociation between visual attention and visual awareness (Dehaene and Changeux 2005; Lamme 2003; Tsuchiya and Koch 2005).

# 6 ATTENTIONAL EFFECTS IN THE BRAIN: GAIN ENHANCEMENT

Selective attention evokes fMRI responses even in the absence of retinal input. Yet it remains unclear whether attention solely increases baseline activity or also enhances stimulus-dependent activation. We dissociated stimulus-dependent effects from changes in baseline BOLD response by cueing attention either before or after a peripheral grating was displayed. When attention was deployed prior to target presentation, the attentional enhancement of BOLD activity increased from V1 to V4. Although post-stimulus cueing led to stronger BOLD activity in V1 than pre-cuing, this enhancement did not increase along the visual hierarchy. These results support a model in which attention increases baseline activity as well as enhancing feedforward processing by increasing neural gain. Consequently, stimulus-driven activity is amplified in successive stages of visual processing in a cascaded manner.

## 6.1 Differential attentional effects in human visual cortex are consistent with a feedforward gain cascade

Directing attention improves our ability in discerning an item at the attended location (Posner, Snyder and Davidson 1980), or recalling an item previously displayed there (Averbach and Coriell 1961). At the neural level, spiking activity evoked by an attended stimulus is enhanced throughout the monkey visual system (Ito and Gilbert 1999; Martinez *et al.* 1999; McAdams and Maunsell 1999; Moran and Desimone 1985; Motter 1993; Reynolds, Pasternak and Desimone 2000; Roelfsema and Spekreijse 2001). A stimulus appearing inside the receptive field of a V4 neuron drives it more strongly if the monkey attends to the location of the stimulus (McAdams and Maunsell 1999; Reynolds *et al.* 2000).

Human functional brain imaging studies likewise demonstrate topographically specific increases in hemodynamic responses in striate and extrastriate visual areas following covert attention to a particular location of the visual field (Brefczynski and DeYoe 1999; O'Connor et al. 2002; Tootell, Hadjikhani, Hall et al. 1998). However, there are discrepancies between neuronal and hemodynamic effects of attention: First, electrophysiological studies show that attention increases the neural gain (McAdams and Maunsell 1999; Reynolds *et al.* 2000), with only small effects on the baseline firing rate. On the other hand, fMRI studies demonstrate only that attention increases the baseline activity (Chawla, Rees and Friston 1999; Kastner *et al.* 1999; Ress *et al.* 2000), while there is no convincing evidence for an increase in gain. Second, whereas recordings from single neurons in monkeys (Ito and Gilbert 1999; Marcus and Van Essen 2002; McAdams and Reid 2005; Roelfsema and Spekreijse 2001) and human visual event related potentials (Martinez *et al.* 1999) show tenuous facilitation of the initial feedforward processing in V1, attentional effects in humans measured by fMRI occur as early as lateral geniculate nucleus (O'Connor *et al.* 2002), and are invariably observed in V1.

These discrepancies can be explained by assuming that attentional effects are dissociable into stimulus-dependent (via gain modulation) and stimulus-independent (via a change in the baseline activity) components, and that fMRI is more sensitive to the stimulus-independent component than single cell recordings. We examined the possibility that there is a stimulus-dependent component in fMRI by manipulating the timing of attention (figure 29). Attention might increase the gain of stimulus driven feedforward activity only if it is cued before the stimulus appears. However, attentional effects that are independent of the input might be observed regardless of whether the cue comes before or after the stimulus. The difference between the two cue conditions can be used to measure stimulus-dependent effects and dissociate them from baseline shifts.

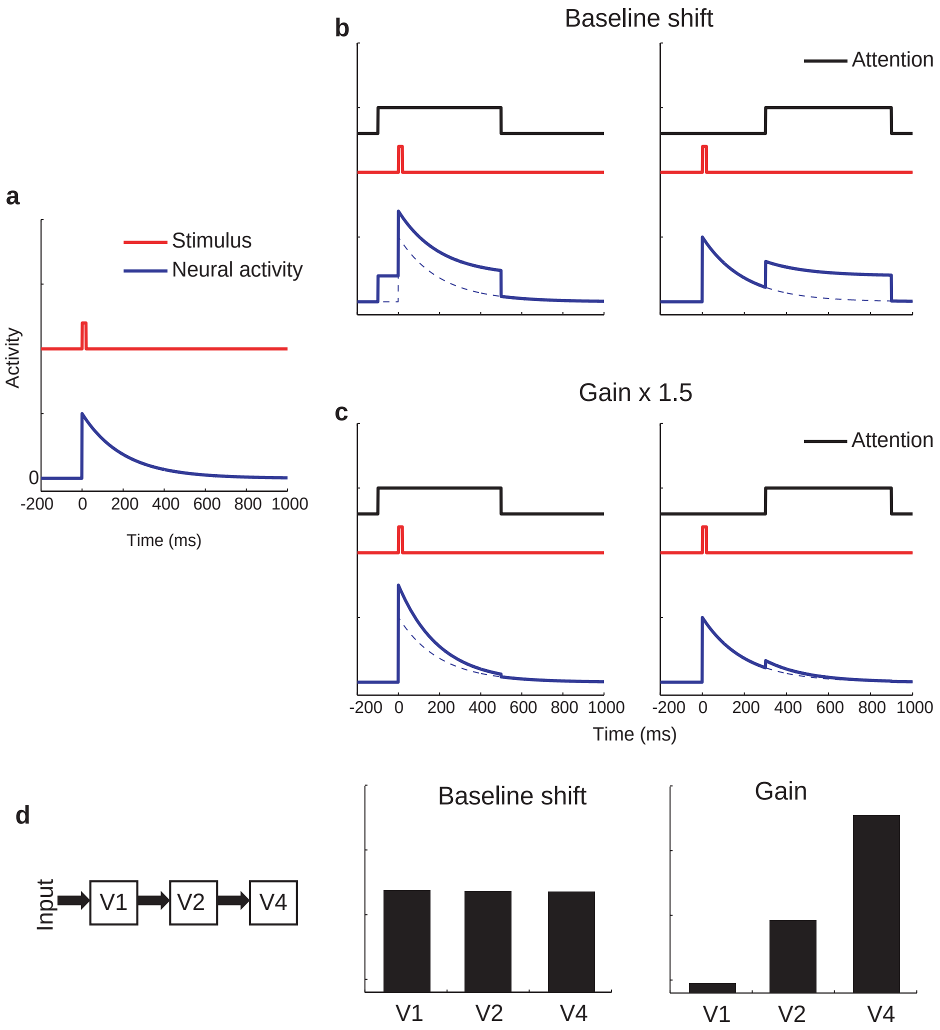

**Figure 29.** Attentional modulation of baseline and gain and timing of attention.

(a) Hypothetical illustration of the time-course of neural activity evoked by external visual stimulation.

(b) If attention increases the baseline activity then the increase in the signal does not depend whether stimulation and stimulation temporally coincide.

(c) If attention enhances the neuronal gain then a significant increase is observed only if stimulation and attention temporally overlap. Deployment of attention per se is not enough for enhancing the neural response.

(d) Schematic illustration of the pattern of attentional activity in different visual areas. Increasing the neural response gain should result in a cascaded amplification of the stimulus-driven activity along the visual processing pathways.

### 6.1.1 Methods

Seven naïve observers from the campus community with normal or corrected to normal vision participated in the experiment. Stimuli were presented using a back projecting system viewed through a mirror mounted to the occipital coil. The display comprised a small fixation mark (0.2×0.2 $\text{deg}^2$, 3.13 deg below the center of the screen), a parafoveal cue (0.5 deg from fixation), and two peripheral square wave gratings (1.5 cpd) with a Gaussian envelope (sigma = 1 deg, min/max luminance = 58/273 $\text{cd/m}^2$ centered in upper quadrants 10 deg from fixation) on a homogenous gray background (152 $\text{cd/m}^2$, 25×20 $\text{deg}^2$). The gratings were displayed for 175 ms (polarity flipped once at 62 ms). In all except the precue condition, four digits appeared 0.36 deg from fixation for 125 ms, followed by masks (50 ms). The digits were not displayed in the precue condition to minimize any distraction from deployment of attention to the target location (figure 30).

The cue was presented either 400 ms before, or 250 ms after the onset of the gratings and digits for 50 ms. A green cue instructed observers to report the orientation of the peripheral gratings in the same quadrant as the cue by pressing the left button for counterclockwise and the right button for clockwise rotation (binary choice). A red cue instructed observers to attend to the digits and report which one was the highest number by pressing one of four buttons. In the precue central condition, attention was directed to the fovea prior to displaying the digits and peripheral gratings. Therefore, this condition measures the response to the peripheral gratings in the absence of attention. In postcue central and central-task only conditions, the red cue was displayed following either central digits and peripheral gratings, or central digits alone, respectively. The two to one ratio of central/peripheral task was intended to discourage observers from splitting attention between the central and peripheral stimuli.

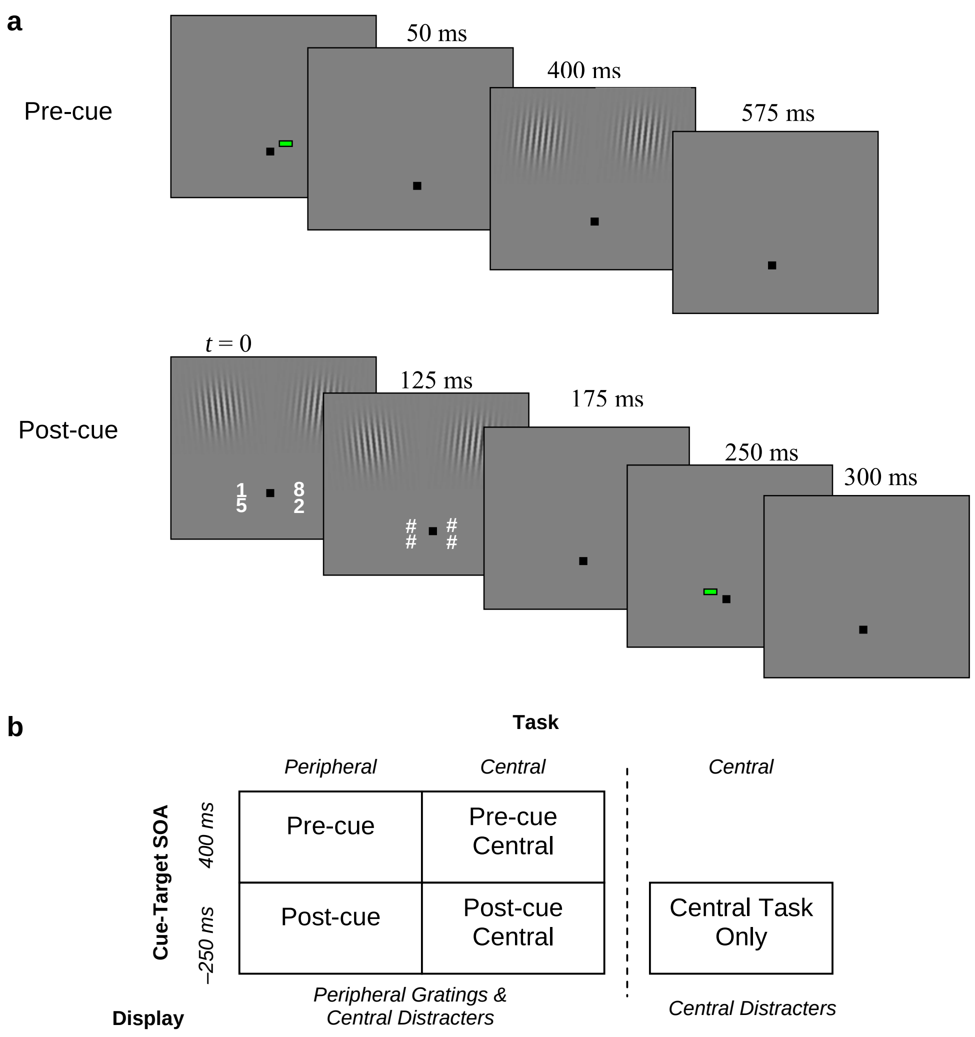

**Figure 30.** Experimental design.

(a) Schematic illustration of pre- and postcue trials. Gratings, digits, and the green cue appeared 10 deg, 0.36 deg, and 0.5 deg from fixation, respectively. Subjects had to indicate whether the cued peripheral grating was tilted to the left or to the right. A red cue color was used to prompt the central task (reporting which digit is the highest).

(b) A 2x2 design was used to study the effect of task (central vs. periphery) and timing of attention (cue before or after target stimulus). A fifth condition (central task only) was added to control the effect of cuing per se and to discourage observers from splitting attention to the peripheral locations.

Observers held a response box in each hand and were instructed to use the box on the same side as the target pattern/digit. Feedback was given if the wrong button was pressed. A three-way analysis of variance was used to test effects of attention, tilt, observer, and their interactions on performance (probability of reporting correct orientation given that the location of the grating was correctly reported).

T2* weighted echo-planar images were acquired (TE=35 ms, TR=2 s, FA=80 deg, FOV=192 mm, 30 slices of 3 mm isotropic voxels) in the Caltech 3.0 Tesla Trio whole body scanner (Siemens) using a phased array occipital coil (Nova Medical). Observers were instructed to fixate a black marker for the duration of the experiment and avoid making eye movements or excessive blinks. Eye position was recorded (Applied Science Laboratories, model R-LRO6) in 6 observers during imaging. Each functional run comprised 184 volumes during which observers performed 70 trials, spaced every 2–7 s. The first six volumes of each run were discarded. Six participants completed 9 and one finished 10 runs.

Linear and low-frequency (<0.01 Hz) temporal drift was removed for each slice in Fourier space. For each subject, images were co-registered between runs using a linear image registration tool (FLIRT) (Jenkinson *et al.* 2002). Retinotopic (50 deg wedge rotating at 40 s per cycle) and two localizer scans were conducted in a separate session. Generalized linear model (GLM) maps for localizer and retinotopy runs were used to define regions of interest. Retinotopic maps were projected onto inflated cortical surface maps created in BrainVoyager QX (Brain Innovation B.V., Maastricht), and the boundaries between visual areas were identified. following a well-established method (Engel *et al.* 1997; Sereno *et al.* 1995). These boundaries were used in conjunction with the localizer data to define the regions of interest (ROI) for the two peripheral locations. The t-maps from the localizer runs were thresholded at $p<0.001$. Three regions were manually identified in each hemisphere: V1, V2/VP (ventroposterior), and V4.

The timecourse of the BOLD signal was calculated by summing all voxels inside each ROI after slice-timing correction and resampling at 1 Hz using cubic-spine interpolation, normalized to the sum of all voxels in the ROI for the first volume in each run. Evoked hemodynamic responses for correct trials were estimated using a GLM by fitting the following basis functions per subject/area/orientation (Friston *et al.* 1998):

$$H_1(x) = \mathrm{gampdf}(x, 6) - \mathrm{gampdf}(x, 16)/6,$$

$$H_2(x) = dH_1(t) / dt,$$

$$H_3(x) = \mathrm{gampdf}(x, 10),$$

where gampdf($t$, $a$) returns the gamma probability density function with shape and scale parameters $a$ and 1, respectively. To account for systematic deviations from fitted models, residuals were averaged with respect to the onset of the trial and were added to the model response. Compared to the standard deconvolution, this method introduces fewer free parameters and therefore requires fewer trials per condition. The activation for each condition was then calculated by measuring the area under the response curve 2–8 s after the onset of the trial. Similar results are obtained if the peak of the BOLD response is used in the analysis or if responses were calculated based on the onset of the target stimuli (except for the difference between pre- and postcue central task conditions which became significant in the later analysis). Significance was tested using mixed ANOVA models with observer and orientation (where applicable) as random effects. The dependence of attentional effects on cortical level was tested by including their interactions.

Eye tracking data showed that subjects maintained fixation well (standard deviation <1 deg) in all experimental conditions. Trials with saccades larger than 1 deg, blinks longer than 70 ms, and incorrect trials were discounted. All statistical significances reported in the manuscript also hold if only the six subjects with eye-tracking data are included.

An additional scan was conducted on five participants to localize parietal regions involved in visual processing or deployment of attention. The activation paradigm consisted of epochs of attention interleaved with blank intervals (10 s attention to right, 2 s blank, 10 s attention to left, 13 s blank, repeated 10 times). During epochs, observers reported small letters (1.25 deg) in the attended hemifield without making eye movements. Target letters were displayed sequentially at random locations 3–10 deg from the vertical, and -1–8 deg above the horizontal meridian. Distracting letters were displayed at mirror symmetric locations in the opposite visual hemifield. GLM maps were thresholded at $p < 0.001$ (uncorrected) and ROIs in the left and right superior parietal lobules (SPL) were manually defined. SPL activity is implicated in covert shifts of attention (Yantis *et al.* 2002). Although based on our localizer we cannot rule out a response to visual stimulation, lack of lateralization and a significant activation in trials that only the central digits were displayed suggest involvement of these regions in deployment of selective attention.

### 6.1.2 Results

A brief green cue near fixation directed subjects' attention to one of two peripheral gratings in the left and right upper visual quadrants. The cue was displayed either 400 ms before (precue condition), or 250 ms after (postcue condition) the gratings appeared (figure 30). Observers pressed one of four buttons to indicate location (left/right) and orientation (tilted clockwise/counterclockwise) of the target grating.

We assessed the performance as a function of the orientation of the target gratings (figure 31). Seven observers made fewer errors in pre- than in postcued trials. The effects of pre- vs. postcuing ($F(1,18)=9.8$, $p<0.05$), orientation ($F(3,18)=10.7$, $p<0.05$), and the interaction between them ($F(3,18)=12.59$, $p<0.001$) were significant, demonstrating that precuing

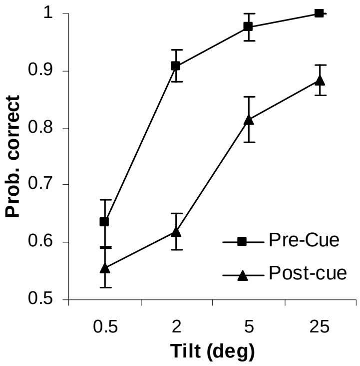

**Figure 31.** Precueing improves performance. Discrimination of the peripheral target depends on whether the green cue appears 400 ms before or 250 ms after stimulus onset. Note that the test gratings were removed 75 ms before the postcue appeared. Chance level is 0.5. Error bars indicate S.E.M.

lowers the orientation discrimination threshold (Lee, Koch and Braun 1997). Thresholds were estimated from the averaged behavioral data by fitting a Weibull function. The tilt threshold in the post cue condition was 3.9 times the threshold in the precue condition (see Lee et al. 1997).

Blood oxygenation level-dependent (BOLD) activities in the two cue conditions were compared with each other and also to the responses evoked by the gratings in trials in which a red cue instructed observers to perform an attention-demanding task near fixation (central task). The central task was to attend to the four digits presented near fixation and report which of them is the highest number (4-AFC). This red cue could similarly appear 400 ms before (precue central condition) or 250 ms after (postcue central condition) the onset of the stimuli (figure 30b). Regions of visual cortices corresponding to the gratings were identified in separate scans (see 6.1.1). BOLD responses reported hereafter correspond to the peripheral activity in those regions of interest.

Pre-cuing enhanced fMRI activity in voxels corresponding to the peripheral locations (figure 32a,b). A mixed ANOVA model (attention×area×observer) was used to evaluate the results. Contralateral BOLD activity in the precue condition was significantly enhanced compared to BOLD activity in the precue central condition ($F(1,30)= 100$, $p<0.0001$). In the precue condition itself, activity contralateral to the target was significantly higher than ipsilateral activity ($F(1,30)=18.5$, $p<0.001$). In both comparisons, the interaction between attention and visual area was significant ($F(2,30)=13.4$, $p<.0001$ and $F(2,30)=4.1$, $p<0.05$, respectively). The effect of precueing was small in V1 (paired Student t-test, $t_6=1.9$, n.s.) and highly significant in V2/VP (ventroposterior) and V4 ($t_6>6.4$, $p<0.001$).

Post-cuing to the peripheral target enhanced BOLD activity compared to activity in the postcue central condition ($F(1,30)= 33.4$, $p<0.0001$), and compared to the ipsilateral activity ($F(1,30)=12.2$, $p<0.01$). Attentional effects slightly increased from V1 to V4, although in contrast to the precue condition, the interaction between area and attention was not significant ($F(2,30)=0.88$, $p=0.42$, and $F(2,30)=1.2$, $p=0.31$, respectively). In both pre- and postcue conditions, the enhancement of activity indicates deployment of selective focal attention to the cued location.

BOLD responses to the peripheral gratings were comparable in pre- and postcue central conditions ($F(1,30)=2.6$, $p=0.07$), even though the activity with respect to the onset of the gratings (as opposed to the onset of the trial) was slightly but significantly larger in the postcue condition ($F(1,30)=5.2$, $p=0.03$). The difference did not interact with area ($F(2,30)=0.21$, $p=0.81$). The central stimuli alone did not evoke a significant positive or negative response in the periphery in any of the visual areas.

We next compared BOLD activity in pre- vs. postcue conditions to evaluate the stimulus-dependent component of attention. Both conditions match in terms of stimulus, task, and selective attention to the periphery. The critical difference between pre- vs. postcue condition is the temporal overlap between stimulation and attention. If attention enhances visual processing in the initial 250 ms after the stimulus onset in a certain cortical region, then we expect a larger BOLD signal there in the precue than in the postcue condition.

Contrary to this prediction, in V1 post-cuing induced a stronger signal than pre-cuing ($t_6=2.94$, $p<0.05$, figure 32c,d), contradicting the hypothesis that attention enhances subsequent sensory processing in V1. The difference vanished in V2/VP, and an opposite effect was observed in V4: BOLD activity in the precue condition was stronger than in the postcue condition. These results demonstrate a stimulus-dependent attentional component that increases along the visual stream. The effects of visual area and orientation (which determines task difficulty) on pre- vs. postcue activity were evaluated using a mixed ANOVA model. Since hemodynamic activity might not be directly comparable across different areas, as a precaution, responses were normalized to the mean of pre- and postcue response for each area and each observer prior to the analysis. The effect of cortical area (V1, V2/VP, V4) was highly significant ($F(2,66)=15$, $p<0.01$, figure 32C; $F(2,66)=23$, $p<0.01$, without normalization), and did not interact with orientation ($F(6,66)=0.25$, $p=0.96$. $F=0.21$, $p=0.97$ without normalization). Similar results were obtained if activity in corresponding central task conditions were subtracted before the comparison (effect of area: $F(2,66)=9.6$, $p<0.05$; interaction with orientation: $F(6,66)=0.2$, $p=0.97$).

Figure 32d shows the profile of activity as it travels through the visual hierarchy. In the absence of attention (pre- and post cue central conditions), the response to the peripheral pattern decays from V1 to V4, whereas in the precue condition, the response increases. In the postcue condition, attention is deployed after the initial feedforward activity has subsided. Therefore, the stimulus independent component dominates the activity in all visual areas.

There are a couple of confounds that may contribute to the differences between pre- and postcue condition but nonetheless cannot explain our results. First, it is likely that the duration of attention is not the same in all conditions. A difference in the duration of attention between pre- and postcue condition would cause differences in measured BOLD activity that is proportional to the amount of feedback that each area receives. Thus, if V1 activity in the postcue condition is higher than the precue condition, then we expect the postcue V4

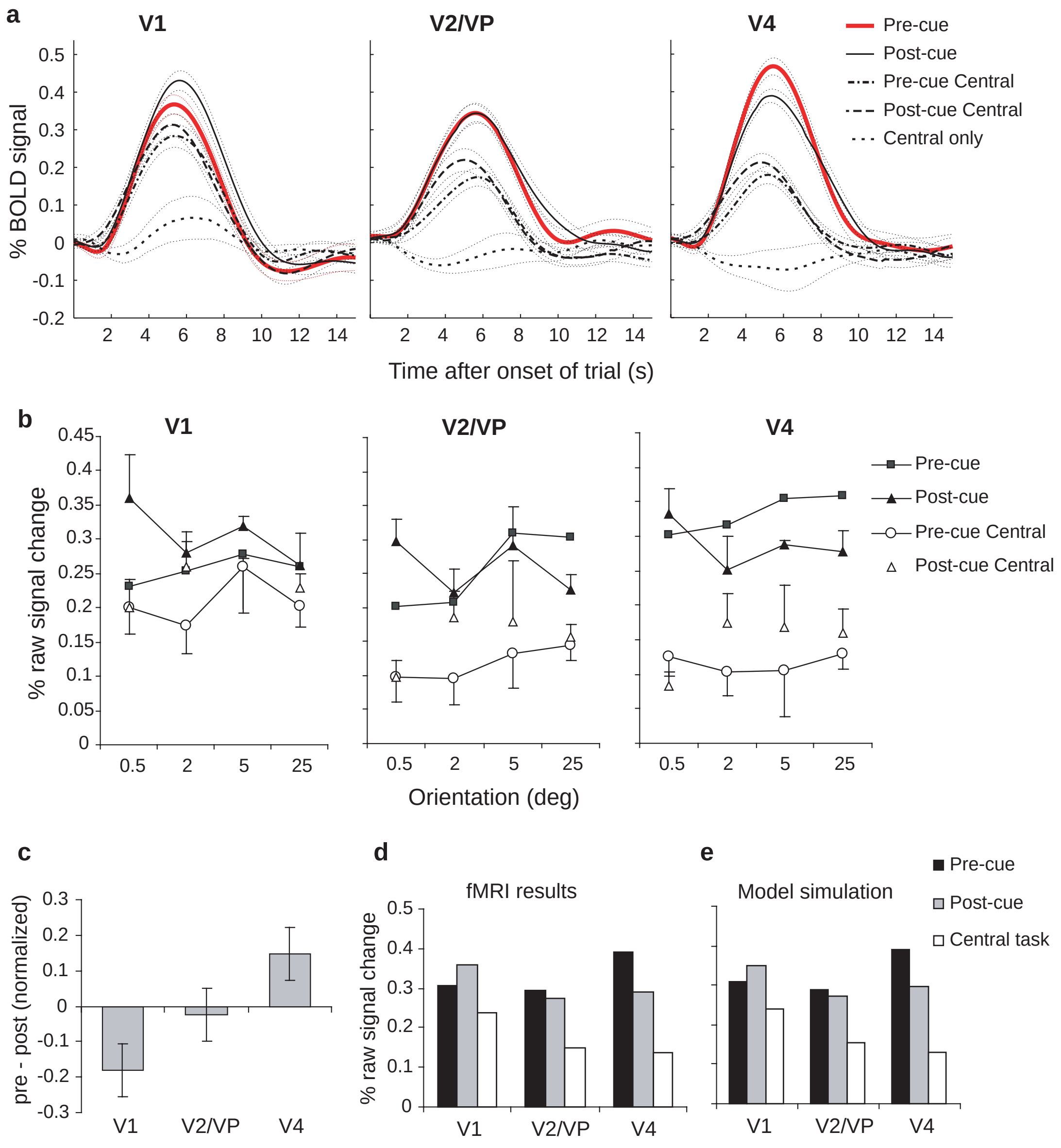

**Figure 32.** Effect of stimulus on BOLD signal in regions of interest.

(a) Estimated BOLD time-courses in different conditions (averaged over orientation).

(b) Differential effects of a cue presented before (precue) or after (postcue) the target on fMRI activity (area under the response curve in A) in striate and extrastriate cortices. Error bars illustrate estimated standard errors.

(c) Effect of SOA on BOLD modulation (difference between pre- and postcue conditions normalized to the average of the two conditions) varies systematically along the visual hierarchy.

(d) Comparison of fMRI signal change in different conditions (averaged over all orientations).

(e) A model that assumes homogenous modulation of gain and baseline activity explains the data.

activity to be even higher than precue activity. In contrast, it was 15% lower. Assuming that the attentional feedback is excitatory and the BOLD activity increases monotonically with attention, differential effects with opposite sign in different regions are very difficult to explain.

Second, cognitive factors such as task difficulty may modulate top-down attention (Pinsk, Doniger and Kastner 2004) and may therefore confound our results. As task difficulty varies substantially with the orientation of the target (figure 31), we evaluated the effect of orientation using a mixed ANOVA model (orientation×area×observer). In the precue condition, the difference between peripheral and central task did not vary with orientation of the target grating ($F(3,66)=1.6$, $p=0.28$), consistent with the hypothesis that deployment of attention in the precue condition is not modulated with subsequent information about the target. Postcue modulation varied with orientation ($F(3,66)=33.9$, $p<0.001$), thus co-varying with task difficulty. The effect, however, did not interact with visual area ($F(6,66)=0.28$, $p = 0.94$). Post hoc analysis showed a significant differences between 0.5 deg and 2 deg ($p < 0.001$), even though the performance was comparable for those conditions (55.6% vs. 61.9% correct), but only a negligible effect across other orientations, despite a greater range of performances. Thus, task difficulty either does not have any effect on the top-down enhancement of the BOLD activity, or if there is such an effect, it equally affects all three regions for our task (in contrast to Pinsk *et al.* 2004) and as such cannot explain the opposite patterns found in V1 and V4.

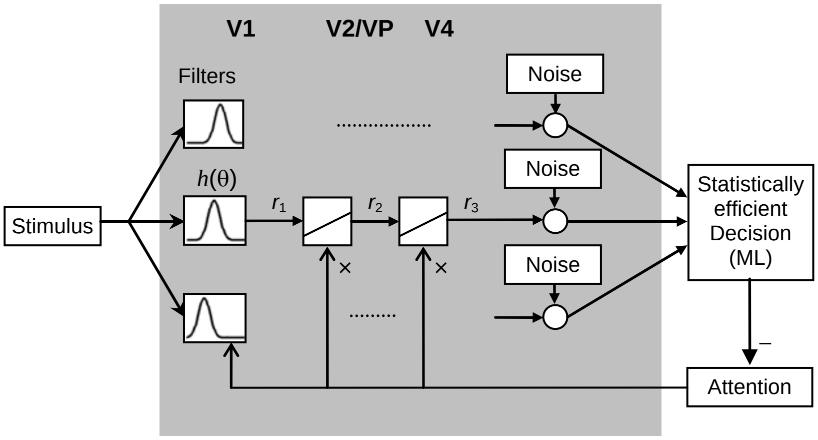

**Figure 33.** Schematic illustration of the cascade model.

## 6.2 A gain cascade model

We postulate a simple cascade model of attentional amplification (figure 33) to quantitatively explain the fMRI results (figure 32e). The model is consistent with general feedforward schemes of object recognition that are based on physiological evidence (Riesenhuber and Poggio 2000; VanRullen and Thorpe 2002). The input stage comprises orientated channels whose outputs can be expressed as:

$$h(\theta) = e^{-\frac{(\theta_s-\theta)^2}{2\sigma^2}},$$

where $\theta_s$, $\sigma$, and $h(\theta)$ denote the orientation of the stimulus, the tuning width, and the response of the first stage (V1) neurons at time zero. In the postcue condition, the cue appears 75 ms after the offset of the stimulus. Thus we assume that neurons retain some memory of the input as the residual activity:

$$r_1(t,\theta) = e^{-t/\tau}\, h(\theta),$$

where $t$ denotes time after stimulus onset, and $\tau$ denotes the time-constant of the decay of activation. To simplify the model, it is assumed that the activity propagates to V2 and V4 without going though further computations. Responses of the units in the second (V2/VP) and third (V4) stages are given by

$$r_2(t,\theta) = a(t) \cdot r_1(t,\theta),$$

$$r_3(t,\theta) = a(t) \cdot r_2(t,\theta).$$

We assume that both stages have the same attentional gain *a*. While subjects attend to the location of the target, *a* is grater than one. If attention is directed to the central task, the gain in periphery becomes smaller than one and the initial response gradually fades out as it moves up the visual hierarchy.

Previous fMRI studies have reported that in the absence of stimulation, spatial attention increases BOLD response in visual cortices (Kastner *et al.* 1999). This observation dictates a stimulus-independent attentional component in the model and we need to consider how it would be affected by the gain cascade. In one scenario, attention increases the background firing activity in orientation-tuned neurons; thus the cascade model predicts that the stimulus-independent effect would increase from V1 to V4. However, this is unlikely on empirical grounds because there is little attentional modulation of background firing activity in V1 (Luck *et al.* 1997; Marcus and Van Essen 2002), and because the stimulus-independent BOLD activity does not increase from V1 to V3 (Ress *et al.* 2000). In a second scenario, the stimulus-independent effect does not amplify along the visual hierarchy. This is the case if, for example, the stimulus-independent component reflects increases in synaptic activity without directly affecting the firing rate (McAdams and Reid 2005), if it reflects equal increases in excitation and inhibition, or if it affects neurons that do not project to the next cortical stage. Given previous studies, the second scenario (no amplification of stimulus-independent effects from V1 to V4) is the more likely one, and it is adopted by modeling the stimulus-independent component as a separate additive term outside of the gain cascade. Thus, the response of each area is the sum of responses of all units, plus a stimulus-independent attentional term $b(t)$ which does not undergo amplification by the gain cascade. This additional term accounts for the attentional shift in the BOLD signal in the absence of a stimulus:

$$R_i(t) = b(t) + \sum_\theta r_i(t,\theta) .$$

Without loss of generality, we assume that $b(t)$ is zero when attention is directed outside the region of interest. We also assume that $b(t)$ is the same for all three areas.

The hemodynamic activity of each area is given by convolving $R_1$, $R_2$, and $R_3$ with the hemodynamic response functions for each area. We assume that the shape of the hemodynamic response is the same everywhere, but that each area has its own scaling factor.

The remaining parameters specify the onset and duration of attention. The onset of attention is controlled by the onset of the cue. We assumed that attention launches at $t_0$ = 200 ms after onset of the cue (the model exhibited a very similar behavior for other values such as 150 or 250 ms after the cue, or even if $t_0$=300 ms for precue and $t_0$=100 ms for postcue condition). The duration of attention not only affects the predicted BOLD activity, but also determines how much information reaches the decision making stage, linking BOLD activity and performance. Assuming stationary, uncorrelated, independent neuronal noise, we show (6.2.1) that the variance of the statistically optimal estimate is proportional to

$$e^{2t_0/\tau} \frac{(t_1 - t_0)}{\left(1 - e^{-(t_1 - t_0)/\tau}\right)^2} ,$$

where $t_1$ denote the offset of the attentional integration window ($\tau$ is the time constant of the decay). If the underlying representation of orientation is homogenous, the variance does not depend on the orientation of the input. The bottom right panel in figure 34 demonstrates how the error in estimation of the orientation of the input changes as a function of the onset and duration of attention.

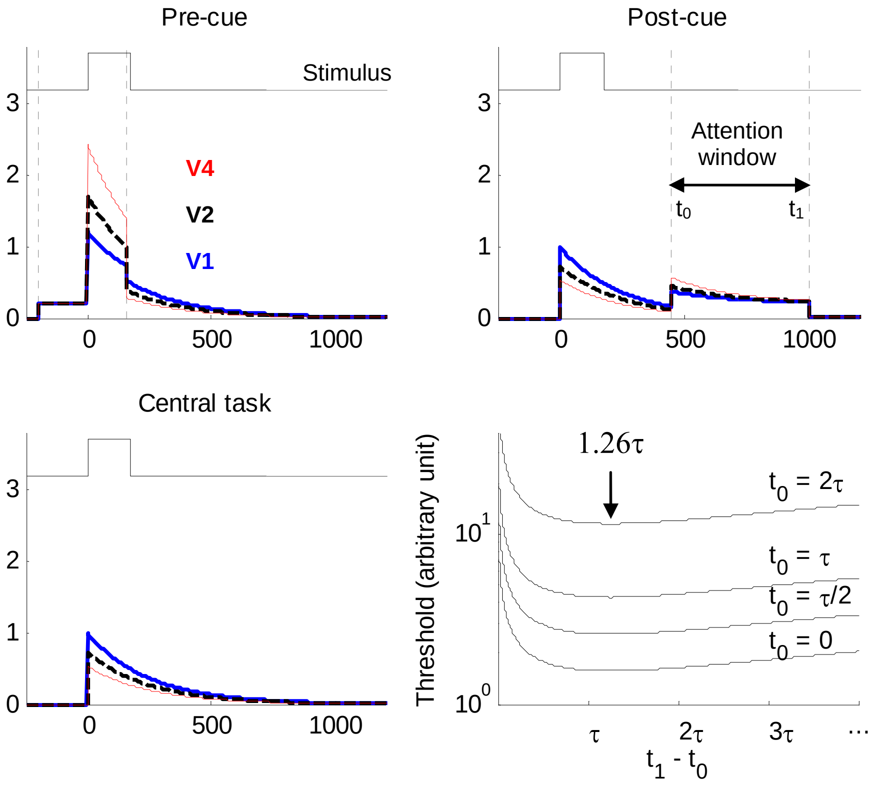

**Figure 34.** Simulation of responses in stage 1–3 of the model.

V1: thick curve, V2/VP: dashed curve, V4: thin curve. The square wave on the top of each panel illustrates stimulus presentation. Vertical dotted lines indicate the integration window. Abscissa: time (ms), Ordinate: activity (arbitrary unit). Simulation parameters were obtained by fitting the model to the empirical BOLD data and behavioral performance (figure 32). The bottom right panel illustrates how estimation error (variance of maximum likelihood estimate) changes as a function of $t_0$ and $t_1$ (integration window onset and offset, respectively). The square root of the variance of the estimate is essentially the same as the discrimination threshold.

The cascade model was fitted to the BOLD data by minimization of the mean square error. Eight free parameters ($a$, $b$, $\tau$, $t_1$ for pre- and for postcue conditions, and one scaling factor per area) were estimated using a Nelder-Mead simplex method (*fminsearch* function in Matlab). The model was further constrained by minimizing the difference between the measured and modeled increase in tilt threshold. Simulation results for the best fit model to one behavioral and nine BOLD values are depicted in figure 32e and figure 34: Attention modulated the gain *a* by a factor of 2.04. Other parameters are: $\tau = 247.7$ ms, $b(t) = 0.21$ for $t_0 < t < t_1$, and zero otherwise. Integration windows are -200 to 159 ms in the precue, and 450 to 1000 ms in the postcue conditions, respectively. These values are biologically plausible, demonstrating that the model conceptually explains the experimental results. The root mean square error of the fit for measured BOLD values was 5.4% of the average activity and the increase in the threshold in the postcue condition was 4.05 fold (against the empirical increase of 3.9). The fitted model was moderately robust: isolated changes up to ±5% for gain and scaling factors and ±12% or more for other parameters resulted in only a fit error of 10%. The cascade model was not able to fit surrogate data obtained by shuffling the BOLD values (fit errors were 60% or higher).

### 6.2.1 Dependence of decision making on the attentional integration window

During the attentional integration window, $[t_0, t_1]$, information (output of V4 units) reaches the decision process. The input to the decision process is

$$\int_{t_0}^{t_1} r_3(t,\theta)\,dt + \xi = h(\theta)\cdot \int_{t_0}^{t_1} a^2\, e^{-t/\tau}\, dt + \xi$$

where *a* is the attentional gain, $\tau$ denotes the time-constant of the decay of activation, and $\xi$ denotes the neural noise. We assume that the noise is Gaussian, stationary, uncorrelated, and independent across units. Thus, the variance of the noise accumulated during integration can be expressed as $\sigma^2 = \varepsilon(t_1 - t_0)$. It can be verified that the signal-to-noise is proportional to

$$\frac{\left(e^{-t_0/\tau} - e^{-t_1/\tau}\right)^2}{\varepsilon(t_1 - t_0)}.$$

With a large number of units, the maximum likelihood estimate is statistically optimal (Lee *et al.* 1999; Paradiso 1988; Pouget *et al.* 1998; Seung and Sompolinsky 1993). The variance of the estimate is equal to the Cramér-Rao bound

$$E\left[\left(\hat{\theta}_{ML} - \theta_s\right)^2\right] = \frac{1}{I},$$

$$I = E\left[-\frac{\partial^2}{\partial\theta_s^2}\log P\left(X \mid \theta_s\right)\right],$$

where $\hat{\theta}_{ML}$ is the estimated orientation, $\theta_s$ is actual the orientation of the stimulus, and $X = (x_1, \ldots, x_N)$ are the $N$ inputs to the decision making stage. $I$ is the Fisher information of the input to the decision process. Because noise is independent among units,

$$I = \sum_{i=1}^{N} E\left[-\frac{\partial^2}{\partial\theta_s^2}\log P\left(x_i \mid \theta_s\right)\right].$$

Given the normal distribution of noise,

$$\frac{\partial^2}{\partial\theta_s^2}\log P\left(x_i \middle| \theta_s\right) = \frac{\partial^2}{\partial\theta_s^2}\left(x_i - f_i\left(\theta_s\right)\right)^2 / 2\sigma^2 = \frac{-f_i'\left(\theta_s\right)^2 - \left(f_i\left(\theta_s\right) - x_i\right)f_i''}{\sigma^2},$$

where $f_i\left(\theta_s\right) = a^2\tau\left(e^{-t_0/\tau} - e^{-t_1/\tau}\right)h\left(\theta_i\right)$ is the expected value of the $i$th input ($h$ is the tuning function of the filters in the first layer). The expected value of $f_i\left(\theta_s\right) - x_i$ is zero. Thus,

$$I = \sum_{i=1}^{N}\frac{f'\left(\theta_s\right)^2}{\sigma^2} = \frac{\tau^2\left(e^{-t_0/\tau} - e^{-t_1/\tau}\right)^2 a^4}{\varepsilon\left(t_1 - t_0\right)}\sum\nolimits_{\theta} h'(\theta)^2 .$$

Assuming a homogenous representation of orientation, the sum on the right hand term is independent of the orientation of the input. Thus, the variance of the optimal estimate is inversely proportional to the signal-to-noise ratio.

## 6.3 Discussion

Our results demonstrate two different and dissociable top-down effects in early visual cortices: the enhancement (difference in peripheral BOLD activity between peripheral and central tasks) evoked by post-cuing (in which top-down attention and sensory stimulation did not temporally overlap) is similar in visual areas V1, V2/VP and V4. In contrast, the enhancement in the precue condition (in which top-down attention and stimulation temporally overlapped) increases significantly along the visual hierarchy. Both effects are topographically selective and appear to be independent of the task difficulty over a wide range of subjective performances (63.4%–100% and 61.9%–88.3% correct, respectively).

The differential enhancement in the pre- vs. postcue conditions can be explained by amplification of the processing of an attended stimulus along the visual hierarchy in a cascaded manner. Alternatively, these results could be due to the involvement of two different top-down processes depending on the relative timing of the cue and target. The second account is less parsimonious and requires additional mechanisms to control which area receives feedback depending on the timing of the cue, even though observers perform the same task. Separate feedback mechanisms consistent with this account have not been reported in electrophysiological and anatomical studies of the visual system. The site of attention depends on target attributes (Hopf *et al.* 2006), and since the target attributes in pre- and postcue conditions are identical, it is likely that the same representation and consequently the same feedback mechanisms are involved in both conditions. In particular, our postcue results do not indicate that the site of visual memory resides in V1, as comparable enhancement of activities is observed in V2/VP and V4.

A quantitative feedforward model based on the assumption that attentional feedback enhances both gain and baseline activity does explain the results. The model makes testable predictions about the duration of attention and the performance difference between pre- and postcue conditions. The cascade model predicts that in postcue trials, observers—on average—attended longer to the location of the target compared to precue condition: in the presence of neural noise, making decisions requires temporal integration of information. The duration of the integration window in postcue condition needs to be longer compared to the precue condition to compensate for the decay of stimulus-induced activity before attention is deployed. If activation of the frontoparietal attention network would increase linearly with the duration of attention, the cascade model predicts a pre- to postcue activity ratio of 0.65. We measured parietal activity in five observers and found a ratio of 0.62±0.05 (vs. 1: $t_4=7.5$, $p<.01$) consistent with the predicted value. Since the order of trials is randomized, this scheme implies that the attentional window is set dynamically for each trial depending on the timing of the cue and target (Ghose and Maunsell 2002). Despite longer integration time, the model accounts for the four fold increase in tilt threshold in post- vs. precue condition (see 6.2.1).

Previous fMRI studies have generally examined only the stimulus-independent attentional component (Kastner *et al.* 1999; Ress *et al.* 2000). Some find that attentional effects increase along the visual hierarchy (Kastner et al. 1999; O'Connor et al. 2002) without examining gain enhancement. Chawla et al. (1999) reported that attentional effects are larger when the stimulus is present than when absent, but they did not rule out that such an effect may be due to a hemodynamic nonlinearity or may merely reflected stronger (or longer) attention when the stimulus is present. Our experiment controls for these confounds, thus enabling us to isolate a stimulus-dependent component that is enhanced along the visual hierarchy by attention.

Our model explains the stimulus-independent effects for near-threshold stimuli reported by Ress et al. (2000). The output of the filters in the first stage (V1) is a function of the image contrast. At low contrast, the signal evoked by the stimulus is weak, presumably requiring long integration times. Because a near-threshold stimulus evokes a small response, changes in the baseline are likely to dominate the overall hemodynamic activity. As a result, the hemodynamic response does not seem to depend on the presence or absence of the stimulus and is strong in either case in all visual cortices. In contrast, when the expected contrast of the stimulus is high, integration is short and attentional effects are small. That is, the hemodynamic response is high when the stimulus is present and low when it is absent. By choosing appropriate values for activation and integration window for each contrast level, the cascade model can replicate the results of Ress et al. (2000, Figures 6,7).

Another testable prediction of the cascade model is that if the duration of attention is variable between trials, then the BOLD signal and behavior will correlate with each other. As illustrated in figure 34, up to a critical duration, the signal-to-noise level at the decision making stage (or equivalently, performance measured by $d'$) increases with the duration of the attentional window ($t_1 - t_0$). Increasing the duration of attentional window also increases BOLD responses in visual areas (because the baseline shift is integrated during the attentional window). Thus, if the duration of the integration window is variable, then the attentional BOLD response and performance will covary. Figure 35 illustrates the relationship between trial-to-trial fMRI amplitude (relative to mean) and $d'$ for two different probability distributions of integration windows ($t_1 - t_0$), and assuming fixed Gaussian noise in the BOLD measurement ($\sigma = 0.5$). For this simulation, trials are sorted into eight bins based on the fMRI amplitude and $d'$ is calculated by averaging signal-to-noise for all trials in each bin (Ress et al. 2000, Figure 2). Overall, these results demonstrate that the gain cascade model not only explains our results, but can also be applied to other studies of attention and BOLD activity.

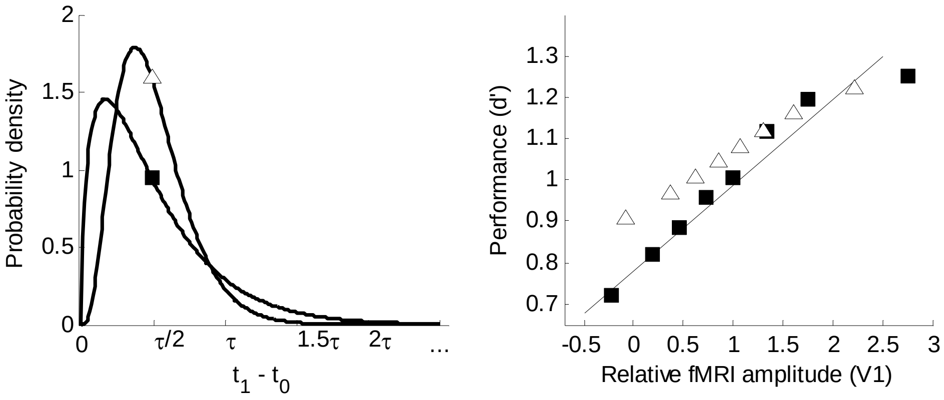

**Figure 35.** Performance and BOLD signal covary with the duration of attention. The model predicts that variability in the duration of integration window (left panel, two different distributions with the same mean of τ/2) manifests itself as a monotonic and near-linear relationship between BOLD activity and performance (right). fMRI amplitudes are normalized to the mean. Solid line in the right panel illustrates the linear fit to empirical data (from Ress et al. 2000 Figure 2). Maximum *d'* is assumed to be 1.3 in both simulations. Solid and empty symbols depict the results for the corresponding distributions.

The notion of gain in our experiment is related to the effect of attention on the neuronal contrast-response function (Reynolds *et al.* 2000). However, studying contrast gain with fMRI is not trivial. First, the BOLD response is largely determined by nonsensory effects, and it is more susceptible to modulation of attention with contrast compared to the firing rate. Such modulation makes it rather difficult to dissociate shifts in baseline activity from changes in gain (Hillyard, Vogel and Luck 1998). Second, the response of higher stages of visual hierarchy shows some degree of invariance to contrast (Avidan, Harel et al. 2002). The mechanisms that underlie such invariance depend on attention (Murray and He 2006), which further complicates interpretation of the effect of attention on the stimulus-response curve. We avoid these issues by using a single contrast level and focusing on how attention gates processing along the visual hierarchy by modulating the gain—regardless of whether this modulation is via shifting the contrast-response function or via other mechanisms (Williford and Maunsell 2006).

In the absence of attention, the gain cascade model predicts that the stimulus-driven activity decreases from V1 to V4. The decay of activity along the visual hierarchy in the pre- and postcue central conditions is consistent with studies demonstrating a larger decrease of the BOLD response to task-irrelevant stimuli in V4 than in V1 as attentional load increases (Pinsk *et al.* 2004; Schwartz *et al.* 2005). Presumably, both the probability of attending to task-irrelevant stimuli and the duration of attention to them would decrease as the attentional demands of the main task increases. Under these assumptions, our model predicts that the visual BOLD activity decreases with increasing attentional load and that the decrease of BOLD activity is larger in V4 than in V1. Thus, the model is consistent with previous findings and provides a simple account for them. On the other hand, it is unlikely that the differential effects of cognitive load in V1 and V4 (de Fockert *et al.* 2001; Rees *et al.* 1997) confound our interpretation: First, we found no interaction between task difficulty and cortical area. That is, the effect of difficulty was similar in V1 and V4 in our paradigm. Second, the response to the ignored gratings in the precue central condition is comparable to the response in the postcue central condition, suggesting that the cognitive load in the postcue condition is not larger than in the precue condition.

In summary, we demonstrate that the profile of activity along the visual hierarchy depends on the timing of attention and stimulation. Our data reveals a differential pattern of pre- vs. post-stimulus cue-influence along the early visual processing hierarchy, a pattern that can be simply explained as the cascaded effect of attentional gain. Such a model is in agreement with human EEG (Martinez *et al.* 1999) and monkey single cell studies (Ghose and Maunsell 2002; McAdams and Maunsell 1999; Moran and Desimone 1985; Reynolds *et al.* 2000), reconciles them with fMRI studies (Brefczynski and DeYoe 1999; Chawla et al. 1999;

Kastner et al. 1999; O'Connor et al. 2002; Ress et al. 2000; Tootell, Hadjikhani, Hall et al. 1998), and explains the improved discrimination performance with attention.

# 7 POSITION-INVARIANT HIGH-LEVEL REPRESENTATIONS

High level representations exhibit spatial constancy: whenever we make a saccade, our brain integrates inputs from different retinal locations to attain a coherent percept. We examined whether such a representation can be probed for face identity, and whether it resides within the face selective region in the fusiform cortex. After adaptation to a stimulus for a few seconds, we examined its effects on a subsequent stimulus at the same, or at a different position. Psychophysical adaptation virtually completely transferred across retina with eye movements. Adaptation of fusiform fMRI activity transferred from fovea to periphery and from contralateral to ipsilateral visual field but not from periphery to fovea or from ipsilateral to contralateral, nor was it preserved across large saccades. These findings are compatible with an intermediate representation of faces in the human fusiform cortex and show that the fusiform face area is not the site of the face identity specific aftereffect.

## 7.1 Representation of faces at intermediate levels in human visual cortex

Faces are among the most ecologically significant stimuli, and the neural mechanisms underlying face processing have been extensively studied in humans and other primates. Face processing in humans is thought to involve a specialized region in the fusiform gyrus, often referred to as the fusiform face area or FFA (Grill-Spector *et al.* 2004; Kanwisher *et al.* 1997; McCarthy *et al.* 1997), located outside and anterior to the retinotopic visual areas (Halgren *et al.* 1999). We set to address whether or not such a category specific region is the site of the representation of face identity (Vuilleumier *et al.* 2003) by using a paradigm that incorporates two different phenomena: selective sensory adaptation and spatial constancy.

Selective adaptation is often used to probe neural representations of sensory information and to isolate perceptual and neuronal mechanisms. Visual aftereffects reflect selective adaptation of neurons (Barlow and Hill 1963) and are used to study specific sensory processes psychophysically (Frisby 1979). FMRI adaptation (Avidan, Hasson et al. 2002; Grill-Spector and Malach 2001) is similarly linked to neural adaptation (Sawamura, Orban and Vogels 2006), and can be used as an effective tool for examining the invariant properties of neurons.

Spatial constancy was used to probe the level of face adaptation. During normal vision, as the position of the retina changes due to movements of the eye, the input to the early retinotopic visual cortices drastically changes (Gur and Snodderly 1997; Nakamura and Colby 2002). Spatial constancy refers to the integration of the pre- and post-saccade inputs in a nonretinotopic frame of reference which is necessary for recognition and interaction with objects (Carlson-Radvansky 1999; Khayat, Spekreijse and Roelfsema 2004; Ross and Ma-Wyatt 2004). Gain modulation of neurons in parietal cortex (Andersen, Essick and Siegel 1985; Andersen and Mountcastle 1983) is suggested as a basis for visuo-motor coordination (Andersen and Zipser 1988; Xing and Andersen 2000). Spatial constancy in the ventral stream can just as well be attributed to translation invariance in higher areas (Salinas and Abbott 1997; Tovee, Rolls and Azzopardi 1994).

We measured the transfer of the psychophysical face aftereffect (Leopold *et al.* 2001) and fMRI adaptation (Grill-Spector and Malach 2001) across space with and without eye movement in order to examine if fMRI and psychophysical adaptation involve identical or similar mechanisms. This paradigm also enables us to examine whether there is a coordinate transformation from eye-based to head-based (or body- or world-based) in the object recognition hierarchy, and whether position-invariance is achieved at the level of FFA.

While a number of psychophysical aftereffects modulate with gaze (Mayhew 1973; Melcher 2005; Nieman *et al.* 2005; Nishida *et al.* 2003), transfer of the face aftereffect is particularly interesting. First, neuroanatomical evidence places face processing at the top of the visual processing hierarchy. Face selective neurons are abundant in monkey inferior temporal cortex (Gross 1992; Tsao *et al.* 2006) but virtually nonexistent in early retinotopic visual areas. Second, the face identity aftereffect is closely linked to conscious perception (Moradi et al. 2005; chapter 4). Unlike aftereffects of simple features such as contrast or orientation which do not require subjective awareness (He *et al.* 1996; Lehmkuhle and Fox 1975; White *et al.* 1978), psychophysical adaptation to face identity occurs after the levels of binocular suppression and attentional selection (Moradi *et al.* 2005). Third, face aftereffect persists much longer than the duration of typical saccades (Leopold *et al.* 2005), so it is easy to measure its transfer with eye movements (Leopold *et al.* 2001; Melcher 2005).

It is already known that there is little reduction of the face aftereffect with eye movements within the face (Leopold *et al.* 2001), and the transfer of face aftereffect from fovea to periphery is modulated with the gaze (Melcher 2005). Nonetheless, previous studies have neither examined the extent of the transformation of face identity information to a nonretinotopic representation, nor have they determined at what stage of the cortical processing hierarchy this transformation occurs.

If both FFA adaptation and psychophysical aftereffect are invariant to position, or if they both modulate with eye movements or retinal position, then the results are compatible with the hypothesis that the site of the face aftereffect is located at the FFA and adaptation of face identity selective neurons in FFA is thus reflected in both psychophysical and fMRI aftereffects. In contrast, if one exhibits spatial constancy while the other does not, then we should conclude that the neural substrate of psychophysical adaptation to face identity is different from the neural substrate of fMRI adaptation in FFA.

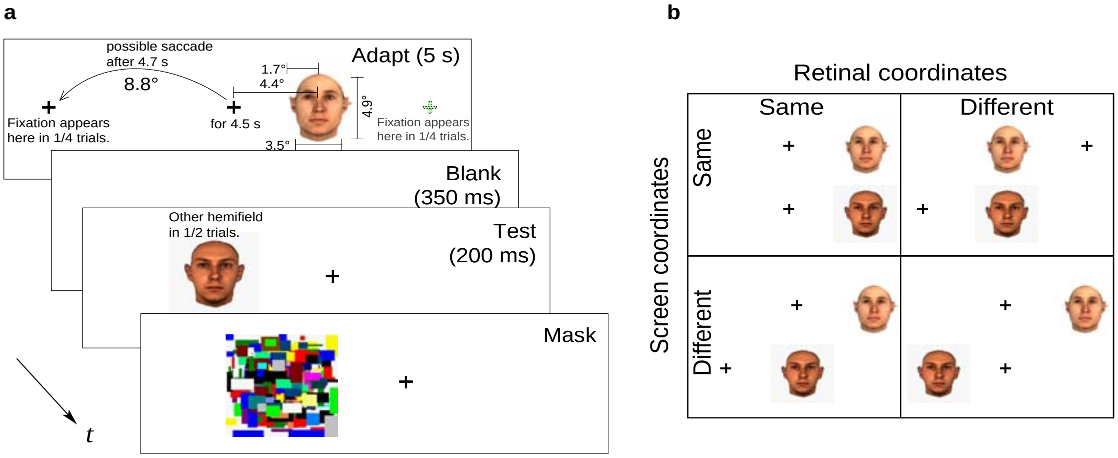

**Figure 36.** Psychophysical face adaptation paradigm.

(a) Sequence of events in each trial.

(b) Design of the experiment 1.

### 7.1.1 Methods

Healthy, paid volunteers with normal visual acuity were recruited from the campus student population. Participants were naïve to the purpose of the experiment. Experiments were conducted according to the guidelines of the institute's committee for protection of human subjects.

#### Psychophysical experiments

Participants were trained to identify four target faces in a 4-AFC task in a separate session. Auditory feedback was given on error trials. Subjects were then familiarized with the adaptation paradigm, and performed a few training blocks in the same task. The data from this initial session were not included in the analysis.

Experimental sessions were conducted on separate days, and participants were retrained on the identification task at the beginning of each session and between each experimental run.

Eye movements were recorded during the experimental blocks. Ten observers participated in experiment 1 (four completed 3 sessions, four completed 2) and five (four from experiment 1) participated in experiment 2 (one completed 1, three completed 2, and one completed 3 sessions).

**Stimuli and setup:** Stimuli were presented on a 19" CRT display (1027x768 resolution at 100 Hz refresh rate subtending $28.8\times21.6$ $deg^2$ of visual angle) using MATLAB Psychophysics toolbox (Brainard 1997) on a PC computer. A chinrest located 75 cm from the screen was used to minimize head movements.

Face stimuli comprised colored images of morphed faces (identity strengths from 0 to 0.4) and antifaces (strength = -0.4) identical to previous studies (Leopold *et al.* 2001; Leopold *et al.* 2005; Moradi *et al.* 2005) except for the scale and eccentricity. Identification threshold for the morphed face corresponding to the adapting antiface and for unrelated identities were estimated for each condition by fitting a sigmoid to the psychometric curves. Stimuli were presented on a black background. Experiments were conducted in a dimly lit room but the frame of the monitor was easily visible.

**Experiment 1:** Faces subtended $3.5\times4.7$ $deg^2$ and were centered 4.4 deg from fixation. Each started with a green fixation crosshair at the center of the screen. The adapting face (the antiface of one of the four faces that observers were trained with) was presented either on the right or the left side of the fixation (figure 36a). After 4.5 s fixation was briefly removed for 0.2 s before either appearing at the same position or moving to the periphery. The adapting face was displayed for a total of 5 s. After a 0.35 s blank interval (during which the fixation was displayed), a second face was briefly displayed for 0.2 s and was masked with a Mondrian pattern.

There were four different conditions (figure 36b). In the “same” and “different” conditions, the fixation reappeared at the center (no eye movement was made). Thus, spatial and retinal coordinates are equivalent. In the "same" condition, both the first (adaptor) and second face (target) were presented to the same side of the fixation. In the "different" condition, adaptor and target were presented in opposite halves of the screen.

In the other two conditions, the fixation moved to a peripheral position, and participants made a saccade during the blank interval. Fixation always appeared 8.8 deg to the left or to the right of its original position. In the "same (different retinal)" condition, both adaptor and target stimuli were displayed in the same screen position, but because of the eye movement, the target is projected to the opposite retinal hemifield. In the "different (same retinal)" condition, adaptor and target were presented in opposite halves of the screen but because of the eye movement, they project on the same retinal area. In sum, in the first two conditions retinal and screen coordinates are congruent, where as in the last two conditions retinal and screen coordinates are anti-correlated. Each session comprised of eight 60 trial-blocks in a randomized order.

**Experiment 2:** Faces subtended 6 deg × 8 deg and were centered 6.9 deg from fixation. Fixation remained at the center of the screen for the first 4.5 s of adaptation, and was removed for 200 ms, and appeared in the periphery 13.8 deg from the center of the screen. Observers made a saccade to the new position of the fixation. A target face appeared 6.9 deg from fixation between it and the center of the screen. Depending on the direction of eye movement and the position of the adaptor, the target face was either at the same screen position but the opposite retinal hemifield, or it was at the same retinal position, but the opposite half of the screen. Observers performed seven blocks of 64 trials per session.

### Eye tracking

An infrared (IR) eye tracking system (ISCAN, inc.) was used to record subjects' eye position at 120 Hz. A beam of low-intensity (1 mW/cm$^2$) invisible infra-red light (850 nm) illuminated the eye from below. Positions and diameter of the pupil, and corneal reflection were extracted from a close-up image of the eye. Each block started and finished with a seven point calibration sequence along the horizontal meridian. The vector difference of the center of the pupil and of the corneal reflection was used as a measure of eye position that is independent of head position. A trial was excluded if observers blinked during the blank or test phase, if the onset of the eye movement was before the offset of the adaptor or after the onset of the target, or if the position of the eye during the test phase deviated more than 15% away from the fixation.

### FMRI adaptation

Twenty-seven volunteers participated in one or more fMRI experiments (8 in experiment 3, 15 in experiment 4, 10 in experiment 5, 5 in experiment 6). For each experiment each observer completed 3–9 runs. Before the experiment participants were familiarized with the task outside the magnet.

Images consisted of 134 faces (75 male/59 female), 103 scenes (houses, indoor scenes, outdoor and city landscapes). Faces images (including hair and upper torso on a homogenous white background) subtended $9.6\times11.3$ deg$^2$ (the face on the average was $5.7\times8.2$ deg$^2$). Scene images subtended approximately $11.3\times9.0$ deg$^2$.

**Experimental methods**: Each run started with an eight second blank interval followed by 40 trials (64 in experiment 4), and a final 16–20 s blank interval. Each trial started with 800 ms initial fixation. Afterwards, the adapting image was displayed on a homogenous gray background for 4 s, followed by 800 ms blank. A black rectangular frame ($11.8\times12.6$ deg$^2$) surrounded the image. A test image (either the same as the adaptor or a different image of the same category) were displayed for 800 ms. In one third of the trials, the second image was absent. Observers had to indicate whether the second image was the same as the adaptor, a different image, or is missed by pressing one of the three keys. If observers did not respond within 300 ms after the offset of the test image (or 1900 ms after the offset of the adaptor when test image was absent) or if they pressed the wrong key, a text feedback was displayed at fixation. After a random inter-trial interval (3–6.5 s in experiment 4, 4–10.5 s otherwise) the next trial started. Each image was used only in one trial. After each run, we presented 20 images, half of which were displayed during the run, and tested their memory using a yes/no forced choice paradigm with feedback. Both tasks were intended to motivate observers to attend to both adaptor and test stimuli, which is important for adaptation (Moradi *et al.* 2005; Murray and Wojciulik 2004; Yi *et al.* 2006).

In experiments 3–5 observers fixated at the center of the screen. A fixation crosshair at the center was displayed during blank intervals to assist fixation. In experiment 3, images of faces and scenes were always presented at the center of the screen. In experiment 4, the stimuli were displayed 6.9 deg from the central fixation and at the same horizontal plane (either on the same side, or on the opposite sides). In experiment 5, adapting and test stimuli were displayed both at the fovea (similar to experiment 3), both in the same peripheral position 6.9 deg from the central fixation, or one at the fovea and the other in the periphery.

In experiment 6, adapting and test stimuli were presented at the center of the screen, but the fixation mark was displayed 6.9 deg from the center, and after adaptation in each trial moved to the opposite side. Subjects were instructed to follow the fixation mark by making a saccade during the 800 ms blank interval.

**Data acquisition and analysis:** T2* weighted Echo-planar images were acquired (TE=30 ms, TR=2 s, FA=80°, FOV=192 mm, 30 slices of 3 mm isotropic voxels, 50% phase over-sampling) in the Caltech 3.0 Tesla Trio whole body scanner (Siemens) using a phase-array surface coil and an in-line motion correction sequence (Thesen *et al.* 2000). Each functional run comprised 170-180 volumes. Linear and low-frequency (< 0.01 Hz) temporal drift was removed for each slice in Fourier space. For each subject, images were co-registered between runs using a Linear Image Registration Tool (FLIRT) (Jenkinson *et al.* 2002). Regions of interest were defined based on statistical maps contrasting face vs. scene for the adapting stimuli. A simplified generalized linear model (GLM) was used to generate these maps (adaptation was not modeled). Maps for all runs in the same experiment were collapsed together. A potential problem in defining the region of interests is that foveal and peripheral stimuli may activate different voxels. Both FFA and PPA are reported to show an eccentricity bias in their activity (Hasson *et al.* 2002; Levy *et al.* 2001). In a subset of thirteen participants that had been exposed to both foveal and peripheral stimuli we could verified that the regions of interest for foveal and peripheral stimuli overlap. Time course of each activity in each region of interest was extracted after slice-timing correction and was resampled at 1 Hz.

The results for both cortical hemispheres were similar and therefore we pooled them in the analysis. Average of each region (sum of all voxels inside the region of interest normalized to the sum for the first volume) was used as a single data point in the statistics. Lateralization and foveal bias were assessed using a Student's *t*-test at each time point. The significant intervals are reported in the results section. It should be noted that because of the serial correlation, these statistical tests for consecutive time points are not independent.

The effect of fMRI adaptation was estimated using a GLM. Predictors were defined by convolving events with the canonical hemodynamic response function. One predictor was defined for each unique combination of the category of the stimulus (face/scene), its position (ipsilateral/contralateral/central), and order (adaptor/test). Additional predictors were defined to reflect hemodynamic adaptation during the adaptation phase of the trial, and for each repeated condition for the consistent category (position of the adaptor×position of the test). That is, 16, 24, and 12 predictors were defined for experiment 4–6, respectively. Predictors for repeated conditions were orthogonalized to other predictors. The negative of beta values corresponding to repeated conditions are depicted in figure 39–figure 41. A two way analysis of variance (condition × participant) and Tukey-Kramer post hoc test was used to establish significance differences. Significant of adaptation in each condition was determined using a t-test across participants.

Adaptation maps were calculated in experiments 3 and 6 using FEAT (fMRI Expert Analysis Tool), Version 5.63 (http://www.fmrib.ox.ac.uk/fsl). Higher level analyses (per subject and consequently group averages) were carried out using local analysis of mixed effects (FLAME stage 1) (Beckmann, Jenkinson and Smith 2003; Woolrich *et al.* 2004). Z statistics images were thresholded using clusters determined by $Z>2.3$ and a corrected significance threshold of $p = 0.05$ (Worsley *et al.* 1992). Six explanatory variables (adaptor, repeat test, and novel test face/scene regardless of the position) were used for the first stage of the analysis. Individual brains were co-registered to the MNI152 template and the overlap between the ROIs and adaptation contrast maps (novel test > repeat test) were visualized in Matlab.

### 7.1.2 Results

#### Psychophysical experiments

In experiments 1 and 2 we examined the transfer of adaptation to realistic face images across visual hemifields with and without eye movements. In a training session, participants learned to identify four individual, colored faces. After reaching a stable performance level, participants were familiarized with the adaptation paradigm.

Each adaptation trial comprised three phases: adaptation, blank, and test. During adaptation, the “antiface” of one of the four learned identities was displayed in the periphery for five seconds. Identification of a specific face is selectively facilitated after adaptation to a face that has opposite global features (hence the name “antiface”), whereas identification of other faces are generally impaired (Leopold *et al.* 2001; Moradi *et al.* 2005). Observers fixated at a crosshair at the center of the screen (figure 36). After 4.5 s (500 ms before the adapting face was removed), the fixation crosshair disappeared, and 200 ms later it reappeared either at the same position, or in the periphery at twice the eccentricity of the face (figure 36a). Observers were instructed to follow the fixation by making a saccade as fast as they could. Eye movement recordings showed that saccades were generally executed during the blank interval (a few trials in which the saccade started during adaptation were excluded from analysis). Cueing the eye movement before adaptation ends nonetheless enabled us to minimize the duration of the blank interval between adaptation and test phase, minimizing the decay of the aftereffect before it is measured (Leopold *et al.* 2005). In the test phase, one of the learned identities was presented briefly and was masked. Observers were instructed to report the identity of the second face (target) by pressing one of the four keys. The identity strength of the target image was varied by morphing it to the average face. Identification thresholds for the face corresponding to the adapting antiface and for unrelated identities were estimated for each condition by fitting a sigmoid to the psychometric curves. The difference between the two thresholds determines the size of the aftereffect (Leopold et al. 2001; Moradi et al. 2005; See Methods for details).

In experiment 1, the target could be displayed either at the same screen position as the adaptor, or at the opposite side of the screen. By manipulating the gaze and the location of the target we varied screen and retinal position independently. The retinal eccentricity of the target always remained the same. This paradigm enables us to isolate the retinotopic and nonretinotopic components (figure 36b).

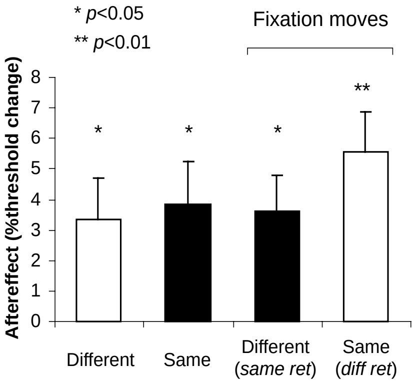

**Figure 37.** Face aftereffect transfers to the other hemifield.

The magnitude of the aftereffect is about the same whether or not the target appears at the adapted retinal or screen location. Error bars depict S.E.M. across 10 observers.

The magnitude of the aftereffect in each condition is plotted in figure 37. Adaptation in all four conditions resulted in a significant aftereffect ($t_9>2.49$ for all conditions, $p<0.05$), and there was no significant difference between the conditions ($F(3,36)=0.62$, $p=0.61$). These results indicate that face aftereffect is not yoked to the retinal position of the adaptor. Even without eye movement, adaptation in one hemifield transfers to the other one.

Nonetheless, the results of experiment 1 did not have enough statistical power to resolve potential differences between conditions. In the next experiment we examined a subset of conditions in experiment 1 but in each condition observers performed twice as many trials, so the thresholds were estimated more accurately.

Experiment 2 quantified the contribution of a retinotopic component by comparing the aftereffect at the same retinal but different screen position vs. different retinal but same screen position. Faces subtended 6×8 $\text{deg}^2$ and were centered 6.9 deg from fixation. The results essentially confirmed that face aftereffect has little or no retinal component: in four out of five observers, the aftereffect was stronger at a different retinal position than the same position (same screen vs. same retinal position in all observers: 6.6% vs. 4.2%, $t_4=1.45$, $p=0.22$). The 95% confidence interval for the aftereffect transfer index (magnitude of the aftereffect at a different retinal position divided by the average aftereffect) was 0.95-1.95.

Thus, the retinal component ought to be smaller than 5%, establishing that adaptation to face identity is primarily mediated by mechanisms that are invariant to the retinal position of the face.

### FMRI adaptation

Are the mechanisms underlying nonretinotopic face identity aftereffect located within the known neural systems involved in face identity processing (Haxby, Hoffman and Gobbini 2000)? To examine this question, we adopted an fMRI paradigm similar to the psychophysical adaptation in experiments 1 and 2. Therefore, it is possible to make a direct comparison between the psychophysical and fMRI results. Face stimuli comprised frontal grayscale photographs of male and female faces with natural expression from the AR face database (Martinez and Benavente 1998). We tried to maximize identity specific adaptation by using a wide range of identities (including both genders, this also minimizes cross-adaptation between trials) and contrasting adaptation between identical vs. unrelated face pairs. Images were scaled to the same size as faces in experiment 2. Face adaptation trials were intermixed with scene adaptation trials (photographs of indoor and outdoor scenes and landscapes). The adapting image was presented for 4 s, and after a 0.8 s blank interval, either the same, or a different image was presented. If the second image (test image) is identical to the first one, because neurons selective for that stimulus are already adapted, they fire less strongly than if the adapting stimulus had activated a different population of neurons. Consequently, the fMRI response to the repeated image will be attenuated compared to a novel image (Avidan, Hasson et al. 2002; Grill-Spector and Malach 2001). To avoid local adaptation in early areas, the second image was displaced by 0.4 deg.

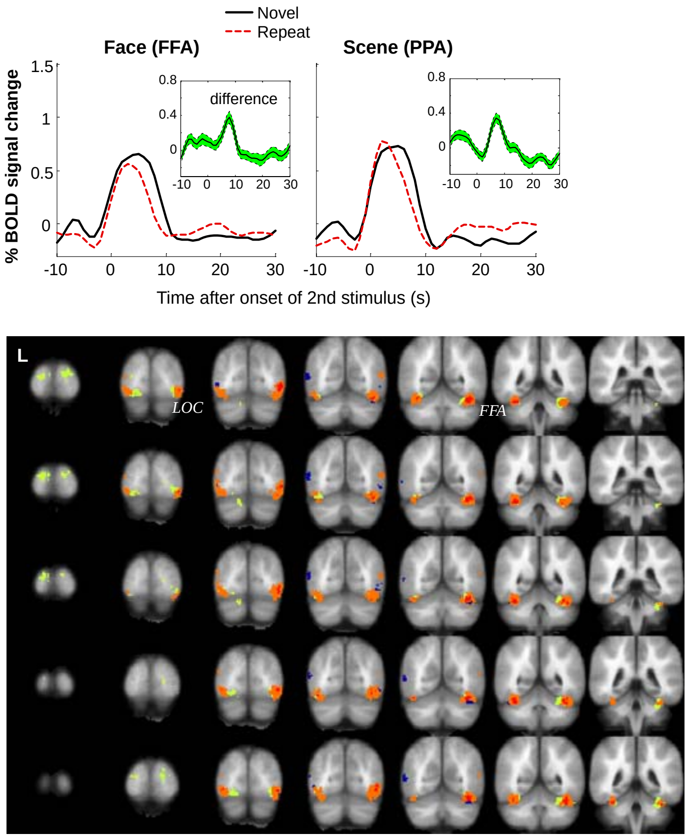

**Figure 38.** Face adaptation in fMRI.

Top: Hemodynamic adaptation to faces and scenes in the FFA and PPA, respectively. Inset shows the difference between novel vs. repeated second stimulus (the shaded area depicts the standard error).

Bottom: There is a substantial overlap (orange, red) between brain areas that respond more to the novel face compared to the repeated face (yellow) and those areas that respond to faces more than scenes (FFA and LOC, dark blue).

The reasons we used both scenes and faces for testing fMRI are twofold. First, scenes activate FFA to a much lesser extent than faces; therefore we used scene adaptation trials as spacers between face adaptation trials to minimize the overlap of the slowly changing hemodynamic response to faces between trials, while keeping the participant engaged in the same task. Second, both FFA and parahippocampal place area (PPA) (Epstein and Kanwisher

1998) are considered as the highest stages of purely visual processing. The FFA responds strongly to faces whereas PPA responds strongly to scenes. Thus, comparing FFA adaptation to faces with PPA adaptation to scenes reveals to what extent our results can be generalized beyond face proceeding. However, the PPA results are not the focus of the present study since we do not have a suitable psychophysical scene adaptation paradigm for comparison.

In the first fMRI adaptation experiment (experiment 3), we presented both adapting and test stimuli at the center of the screen (Foveal presentation). Figure 38 depicts the average hemodynamic responses in FFA and PPA in face and scenes adaptation trials, respectively (8 observers). Both areas respond robustly to foveal stimuli of the consistent category (faces for FFA, scenes for PPA). The response to the adaptor (the first component of the response) was the same for both repeated and novel conditions (repeated and novel refer to the second image in each trial). However, a novel image elicited a stronger response peaking 6 s after its onset (significant at $t_7>2.4$, $p<0.05$, 5–8 s after the onset of the second image for face adaptation in FFA, 6–8 s for scene adaptation in PPA). Results thus establish that psychophysical paradigm can be adopted to study adaptation in the brain using fMRI.

In addition to FFA, we found clusters of voxels in the lateral occipital cortex (LO) that responded selectively to faces and underwent adaptation, albeit to a lesser extent than FFA (figure 38, bottom panel). Therefore, areas other than FFA might also be involved in adaptation to faces.

In experiment 4, we measured the transfer of fMRI adaptation between visual hemifields in the absence of eye movements. Experiment 1 shows that adapting to a peripheral face can result in a measurable aftereffect in both visual hemifields. Therefore, we expect bilateral

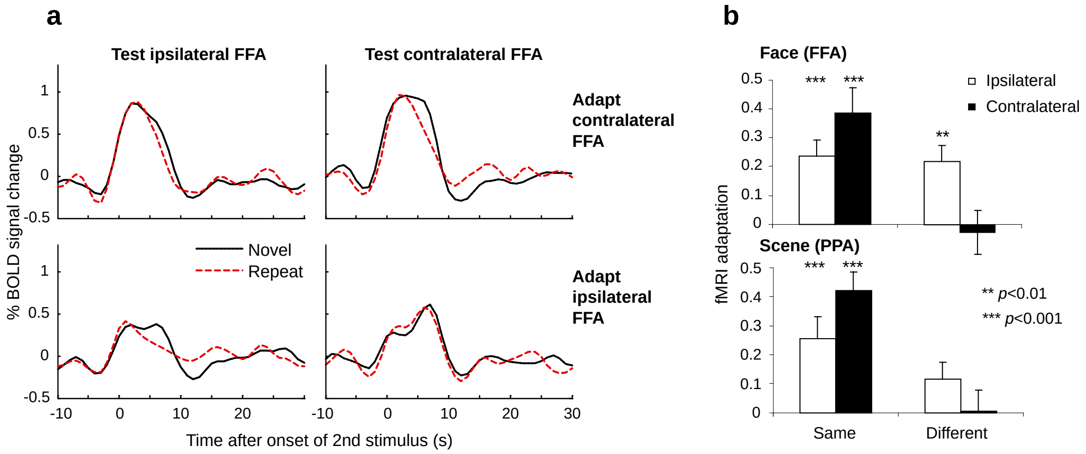

**Figure 39.** Adaptation in the ipsilateral visual field does not attenuate the response to a repeated stimulus in the contralateral visual field.

(a) Event related averages of FFA activity. The adapting face was displayed -4.8 s before the onset of the second face. In the bottom right graph one can visually distinguish the two components of the response. The hemodynamic response to the adaptor and test peaks around 1 and 6 s, respectively.

(b) GLM analysis of the adaptation in each condition. Dark and light bars indicate contralateral and ipsilateral adaptation, respectively. PPA and FFA in both hemispheres selectively adapt if the stimuli appear at the same location (i.e., both contralaterally or both ipsilaterally). Error bars indicate S.E.M. *P* values indicate significance vs. zero (t-test across 15 individuals).

attenuation of BOLD activity for repeat trials compared to novel trials (fMRI adaptation) regardless of the position of the adaptor and the test image. Stimuli were presented at the same eccentricity as the experiment 2.

There was no significant difference between the left and right FFA (similarly, PPA and LO) in terms of the effects of contralateral and ipsilateral stimuli. Therefore, the results of both sides are pooled together for each area and each condition. Figure 39 shows the average results of 15 subjects. The first noticeable finding is the difference between contralateral vs. ipsilateral responses to the adapting stimuli. Both FFA and PPA are considered to be nonretinotopic and stimulation of both hemifields indeed evoked a positive response (response to the ipsilateral adaptors vs. 0: $t_{29}>4.96$, $p<.0001$ 0–5 s with respect to the onset of the second stimulus for both FFA and PPA), suggesting that the receptive field of at least some neurons encompasses both hemifields. Nonetheless, the overall response to the ipsilateral stimulus was weaker than the response to the contralateral stimulus ($t_{29}>4.56$, $p<0.0001$, 0–5 s for both areas).

Remarkably, adaptation was even more contralaterally biased. The responses evoked by the second stimuli (novel vs. repeat) was estimated using a generalized linear model (GLM, see 7.1.1). Adaptation in different conditions were compared using ANOVA (FFA: $F(3,42)=10.8$, $p<0.0001$; PPA: $F(3,42)=15.7$, $p<0.0001$; figure 39b. face selective LO cluster: $F(3,42)=5.46$, $p<0.01$). In all three regions, adapting to the optimal stimuli in the ipsilateral visual field had no significant effect on the activity evoked by a repeated contralateral stimulus (ipsilateral-contralateral condition). PPA and LO were even more spatially selective than FFA and did not show any significant transfer of adaptation to their optimal stimuli from contralateral to ipsilateral visual field.

The results indicate that the representation of faces in FFA is not veridically position-invariant. Nonetheless, FFA results are consistent with a partially nonretinotopic representation. We found an asymmetric transfer across midline (from contralateral to ipsilateral, but not vice versa: post hoc comparison: $p<0.01$). This transfer may be accounted by adaptation of a subpopulation of neurons with receptive fields centered at fovea but subtending both hemifields. In a subsequent experiment, we tested this hypothesis by measuring transfer of adaptation between fovea and periphery in the absence of eye movements.

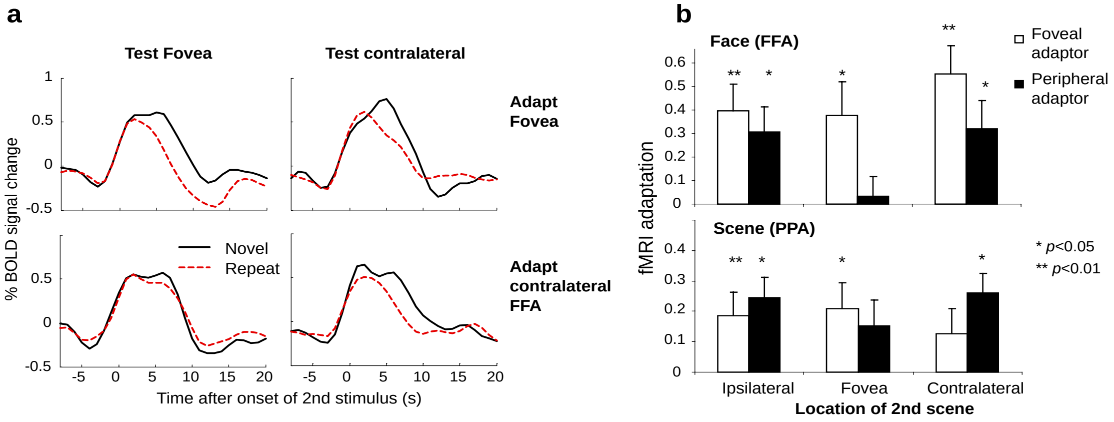

**Figure 40.** Face adaptation transfers from fovea to periphery.

a) Event related averages of FFA activity. Both foveal and contralateral faces activate FFA to the same extent during adaptation.

b) GLM analysis of the adaptation. A foveal face can selectively attenuate the activity evoked by the same face appearing anywhere on the screen. A peripheral face, however, does not attenuate the response to a foveal face. Thus, there may be dissociation between activity and adaptation in FFA. Error bars depict S.E.M. *P* values indicate significance vs. zero (t-test, 10 individuals).

Experiment 5 showed a significant effect of the position of adaptor and test image on adaptation for faces (ten subjects, FFA: $F(5,45)=2.54$, $p<0.05$, PPA: $F(5,45)=0.55$, n.s.). Results demonstrate that FFA adaptation transfers from fovea to periphery but not the other way around (figure 40): adaptation to a contralateral face did not transfer to fovea (adapt contralateral, test fovea vs. adapt fovea, test contralateral: post hoc $p<0.02$). Interestingly, foveal and contralateral faces evoked the same level of activity in FFA; therefore asymmetric transfer of adaptation cannot be attributed to a higher BOLD activation induced in fovea compared to periphery. The foveal bias index (the difference between fovea and contralateral divided by their sum for average activity 0–6 after the onset of the second stimulus) was effectively zero (mean=0.01, 95% confidence interval: -0.05 to 0.08). In comparison, the laterality index—difference between ipsilateral and contralateral divided by their sum—was

0.44 (95% confidence interval: 0.16-0.72). If adaptation was proportional to the activity evoked by the adaptor, then we would have expected similar adaptation to foveal and contralateral adaptors. However, foveal stimuli induced stronger adaptation (in terms of the spatial extent of adaptation) compared to contralateral stimuli presented 6.8° from fovea for the same level of excitation. PPA activity did not show a foveal adaptation bias. Therefore, this dissociation might be unique for face processing.

Experiments 5 confirms that face adaptation in FFA is neither completely local, nor is fully position-invariant. The results of experiments 4 and 5 are hard to reconcile with the psychophysical results which suggest that the identity specific aftereffect is mostly global, and the retinotopic component of the aftereffect is negligible. However, psychophysical results do suggest a spatial component (Melcher 2005). Since in experiments 3–5, the location of the retina was fixed, we are not able to dissociate retinal and spatial component of fMRI adaptation. That is, it is possible that the position specificity observed in experiments 3–5 reflects a representation that is yoked to a frame of reference other than the eye (i.e., head, body, or world). To address this issue, in experiment 6 we asked observers to shift their gaze between the offset of the adaptor and the onset of the test image, so they project onto different retinal hemifield. Both stimuli appeared at the same screen position, so a spatial component (e.g., yoked to the screen position) of adaptation will not be affected. A rectangular frame surrounding the face and the borders of the screen served as external screen coordinate cues.

If fMRI adaptation in FFA, PPA, or LO is spatiotopic, then we expect to find specific attenuation of the repeat trials compared to novel trials. Figure 41 depicts the results. There was no significant adaptation to repeated faces under this condition in either FFA ($F(1,4)=1.5$, $p>0.28$) or face selective LO clusters ($F(1,4)=0.03$, $p>0.88$). PPA did not show

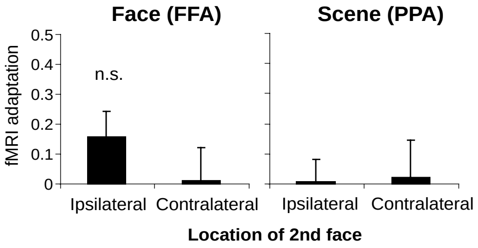

**Figure 41.** Adaptation in FFA and PPA does not transfer with eye movements. Error bars depict S.E.M. Stimuli always appeared at the same location of the screen.

any adaptation to scenes, either (*F*(1,4)=0.06, *p*>0.82). A whole-head GLM group analysis of the differential activity for novel vs. repeated faces failed to find significant clusters in visual areas or anywhere else in the brain.

The attenuation of activity in the FFA contralateral to the second face in experiment 6 was significantly less than the attenuation of contralateral FFA in the experiment 4 in the “same” condition ($t_{18}$=2.25, *p*<.05). Our results show that face adaptation in FFA and LO and scene adaptation in PPA depend on the retinal position of the adapting and test stimuli. This result is inconsistent with the substantial transfer of the psychophysical aftereffect observed in experiments 1–2, indicating for the first time a dissociation between psychophysical and fMRI adaptation.

## 7.2 Discussion

Experiment 1 and 2 show that the representation of the perceived face identity is not retinotopic, and those mechanisms that encode the perceived identity have achieved spatial constancy and position-invariance. If one is exposed to an individual face for a few seconds, then the perception of a subsequent face is biased, regardless of whether the second image appear at a different position or not (both in the retinotopic and the real-world sense). If after adaptation one moves ones eyes, the aftereffect at the original position would not be any weaker than any aftereffect yoked to the eye. In fact, it might be even stronger at the new retinal location that corresponds to the original place in the world.

Psychophysical aftereffect might comprise three possible components: an eye-based (retinotopic) component, a head or body-based (spatial) component, and a position-invariant component. Melcher (2005) reported that the transfer of face adaptation from fovea to the periphery following a saccade is stronger if the test face is presented at the same spatial position. His finding is consistent with the spatial component. The magnitude of the aftereffect was comparable to the aftereffect of a peripheral adaptor at the same retinal position. However, because there is a foveal bias in face processing (Levy *et al.* 2001; Makela *et al.* 2001), it is difficult to interpret the later finding. It was also not clear if the transfer of the aftereffect requires eye movements. We used peripheral adaptation in all conditions and found that the aftereffect transfers to the opposite hemifield, even without any eye movement (experiment 1). Moreover, experiment 2 demonstrates that the contribution of the retinotopic component to face identity aftereffect is small if not absent.

A trend in both experiments 1 and 2 suggests that the aftereffect is enhanced in the hemifield opposite to the direction of the gaze (Melcher 2005). A similar enhancement has been reported for other aftereffects and has been attributed to gain modulation with eye movements (Nieman *et al.* 2005; Nishida *et al.* 2003). Gain modulation is found in visual areas including V1 (Andersson *et al.* 2004; Trotter and Celebrini 1999), V3A (Galletti and Battaglini 1989; Nakamura and Colby 2002), V4 (Tolias *et al.* 2001), MT (Bremmer *et al.* 1997), and MST (Squatrito and Maioli 1996). Recent fMRI studies suggest some degree of modulation in ventral stream (DeSouza, Dukelow and Vilis 2002; Deutschlander *et al.* 2005). Nonetheless, significant transfer of the aftereffect to the opposite hemifield without any eye movement, both psychophysically (experiments 1 and 2) and in fMRI (experiment 4 and 5), suggest that spatial constancy in the object processing pathway is primarily attained via translation invariance rather than gaze modulation.

Experiments 3–6 demonstrate that retinotopic representations in early cortices are transformed to a nonretinotopic representation in category selective areas. The adaptive response for faces in FFA is consistent with the notion that this area is an intermediate representation that achieves partial invariance to the retinal position—although not to the extent that is necessary to account for the psychophysical results.

Foveal and peripheral stimuli evoked selective hemodynamic responses in both hemispheres. Attenuation of both ipsilateral and contralateral responses to a repeated face compared to a novel face indicates that each FFA represents both visual hemifields. FFA adaptation in the contralateral visual field attenuates the response to the same face presented ipsilaterally. Therefore, the representations of contralateral and ipsilateral spaces are not independent, and at least some units receive selective inputs from both visual hemifields.

On the other hand, adaptation in the ipsilateral field did not affect the FFA response to a contralateral stimulus. Similarly, adaptation in the contralateral field did not affect the response to a foveal stimulus. There are two possible explanations for an asymmetric transfer. First, different parts of a receptive field might not excite a neuron to the same extent. Many neurons in the anterior infero-temporal cortex of the monkey exhibit greater position sensitivity than suggested by their receptive fields (DiCarlo and Maunsell 2003). Weaker activity during adaptation is suggested to reduce visual aftereffects (Harris and Calvert 1989; Ishihara 1999) and fMRI adaptation (Avidan, Hasson et al. 2002). Second, different parts of a receptive field of a neuron might not be equally selective. Our fMRI findings are consistent with the hypothesis that a part of the receptive field that adapts the most is confined to the contralateral hemifield and fovea. In particular, the higher resolution (and consequently stimulus selectivity) at the fovea than in the periphery can explain the fact that foveal faces invoked a more extensive adaptation than peripheral faces (Vuilleumier *et al.* 2003) without evoking a stronger response. In summary, the asymmetric transfer in fMRI adaptation can be explained by asymmetries in either neuronal excitation or adaptation, and our results are more compatible with the later explanation.

The contrast between the transfer of face adaptation measured psychophysically and the transfer of fMRI adaptation in FFA implies that fMRI and psychophysical adaptation to the same stimuli (faces) occur at different levels, and focusing on their similarities (Loffler *et al.* 2005) could be misleading. There is no direct evidence that FFA is the site of psychophysical face aftereffect, and our results indicate otherwise. The invariance of the psychophysical aftereffect to the position of the eye is compatible with our phenomenal experience, indicating that the psychophysical aftereffect probes a representation that is at a higher level than FFA. This hypothesis explains the discrepancy between cancellation of face aftereffect under the conditions of binocular suppression (Moradi *et al.* 2005) and the findings showing invisible stimuli may still activate FFA (Moutoussis and Zeki 2002) (but see Tong *et al.* 1998).

Neurons in human medial temporal lobe respond to faces (Kreiman, Koch and Fried 2000a) and a subset of these neurons exhibit remarkable invariance across different stimulus dimensions for highly familiar faces (Quiroga *et al.* 2005). Similarly, face selective neurons are found outside modality specific areas in monkeys, including ventrolateral frontal cortex and amygdala (Gross 1992). Such neurons might compose a final representation of face identity that is directly accessible to awareness. Nonetheless, our failure to localize any adaptive region in the brain in experiment 6 suggests the possibility that face selective neurons outside FFA are not highly clustered.

It is possible that identity is represented by a subpopulation of neurons in FFA, clustered as a distinct sub-region that represents identity invariantly (Pourtois *et al.* 2005). Experiment 2 shows that the psychophysical aftereffect is preserved across eye movements. Thus, any fMRI correlate of such aftereffect should also be preserved across eye movements. However, we found no significant fMRI adaptation under this condition in experiment 6. Therefore, even if there are position-invariant neurons in FFA, their relative contribution to the FFA activity and adaptation is small and does not account for the transfer of fMRI adaptation in other conditions.

We measured fMRI adaptation to faces in face selective voxels in the lateral occipital cortices and found a pattern very similar to FFA: there was no transfer with eye movements. Our results are in contrast to a recent study that found head-based effects in LO using a conventional repetition paradigm (McKyton and Zohary 2006). They presented images of tools every 1 s during 12 s epochs and compared epochs that 2 images were repeated 6 times each vs. epochs that 4 images were repeated 3 times. LO activity was significantly reduced when images were repeated more frequently at the same screen position, even when their retinal position was different due to eye movements. Contrariwise, repetitions at the same retinal position (but different screen positions) had little effect on the BOLD signal. There are two possible explanations for the discrepancy between their results and ours. First, it is possible that rapid repetition effect and slow adaptation involve different neural mechanisms (e.g., an attentional or cognitive effect vs. genuine adaptation). Second, faces and tools might have characteristically different representations ("what" vs. "how," Goodale and Milner 1992; Ress et al. 2000). Remarkably, McKyton and Zohary (2006) also failed to find any evidence of head-based adaptation in the ventral object-related areas.

FMRI adaptation to scenes in PPA was generally similar to faces adaptation in FFA, except that there was no advantage for adaptation to foveal scenes. Lack of a foveal bias in PPA is consistent with a center-periphery organization of the ventral stream (Hasson et al. 2002; Levy et al. 2001). Despite a difference between FFA and PPA in representation of foveal stimuli, and although we were not able to psychophysically measure a scene-selective aftereffect to verify if it exhibits spatial constancy, bilateral representation of scenes in PPA suggest that a reorganization of receptive fields compared to early retinotopic areas is not quite unique to FFA.

In summary, our findings show a transformation toward position-invariance in category specific visual areas. Hemodynamic adaptation in FFA is consistent with expansion and shift of the receptive fields toward fovea and extension of them to ipsilateral periphery (even though one should be cautious about linking fMRI activity and properties of individual neurons rather than emerging network properties). On the other hand, the robust transfer of the psychophysical face aftereffect compared to the limited transfer of adaptation in FFA suggests mechanisms beyond FFA for integration of face identity across space. These findings provide insight into brain organization and the neural mechanisms of perceptual constancy in object recognition.

# 8 VISUAL SEARCH FOR CATEGORIES OF FACIAL EXPRESSIONS

Preattentive processing of facial expressions were studies in a visual search task using morphed images of emotional expressions. Images in such morph continua are perceptually labeled as distinct categories with a sharp transition between the labels. We examined whether the categorical processing of expressions facilitate the visual search by presenting targets and distracters that did or did not span the category boundary while independently varying their distance in the morph space across trials. In all conditions, search time increased linearly with the number of displayed items. We found that the slope of the search is determined by the distance in the morph space. In contrast, category has a small but significant effect on the intercept. In all conditions the search was inefficient (with slopes between 166 and 245 ms/item) and there was no asymmetric advantage of any expression. A patient with bilateral amygdala damage and impaired recognition of fearful expression showed the same pattern of results for fearful-neutral morphs. Findings are consistent with the hypothesis that preattentive processing in visual search is limited to low-level features and the categorical facilitation of visual search does not involve the amygdala.

### 8.1.1 Introduction

In natural vision, most of the retinal input that can potentially evoke a percept never actually reaches conscious awareness (Mack and Rock 1998; Simons 2000; Simons and Chabris 1999). To what extent the brain is able to implicitly processes such information is one of the major open questions in cognitive neuroscience. Retinal input that is not seen may activate a large population of neurons in early cortical areas (Haynes and Rees 2005; Leopold and

Logothetis 1996) and produce measurable aftereffects (Blake and Fox 1974; Lehmkuhle and Fox 1975; Montaser-Kouhsari et al. 2004; White et al. 1978; Young et al. 1996). However, unseen inputs seems to fall short of activating late stages of visual processing involved in object and face recognition (Kanwisher, Tong and Nakayama 1998; Leopold and Logothetis 1996; Moradi *et al.* 2005; Sheinberg and Logothetis 1997).

A number of researchers have speculated that ecologically important stimuli such as faces are processed implicitly even when we do not see them. Rudimentary face perception in newborn infants (Johnson *et al.* 1991) suggests that face perception may have an automatic component. Negative facial expressions or threatening stimuli that are masked or binocularly suppressed nonetheless activate sub-cortical regions and the amygdala (Anderson *et al.* 2003; Morris, Ohman and Dolan 1998; Morris, Ohman and Dolan 1999; Pasley *et al.* 2004; Williams *et al.* 2004). These studies are interpreted as evidence for implicit processing of expressions because the amygdala is involved in orienting toward features that are important for recognition of emotional expressions such as fear (Adolphs *et al.* 2005).

In particular, implicit processing of facial expression is suggested to direct attention toward the stimulus (Eastwood and Smilek 2005; Eastwood *et al.* 2001; Hansen and Hansen 1988; Ohman, Lundqvist and Esteves 2001). This hypothesis is based on the evidence from visual search. Finding an angry face among neutral or happy faces is faster than finding a happy face among an angry crowd (Eastwood and Smilek 2005; Eastwood *et al.* 2001; Fox *et al.* 2000; Hansen and Hansen 1988; Horstmann and Bauland 2006). However, it is not clear if the anger superiority effect in visual search is due to implicit processing of facial expressions or to mechanisms that process other aspects of the angry face.

We probed this question by exploiting the inherent nonlinearity in face perception. One can create a morph continuum between two face categories by linearly interpolating the location and color of the corresponding features. The perceived category of the faces in the morph continuum shows a very sharp transition (category boundary) and it is clearly nonlinear in the morph space. Subjects discriminate most accurately when face-pairs span category boundaries (Beale and Keil 1995; Kiffel, Campanella and Bruyer 2005; Levin and Beale 2000). Categorical perception of faces and facial expressions indicate nonlinear mechanisms at or before the stage of face specific processing. It has been shown that cortical areas involved in face perception at the late stages of the visual processing hierarchy—but not early visual areas—show sensitivity to category change rather than to physical change (Rotshtein *et al.* 2005).

If facial categories rather than low-level image differences attract attention then we predict that the search time should depend more on the perceived difference between target and distracters than on how far apart they are in a morph continuum. Moreover, if a particular category (e.g., fear) attracts attention, search should be faster if the target—but not distracters—belongs to that category (search asymmetry).

### 8.1.2 Methods

Volunteers from the campus community with normal vision who were naïve to the purpose of the experiment participated in one or more experiments.

**Stimuli:** Pictures of facial expressions of six individuals (3 female, all grayscale frontal views) from the Ekman and Friesen set (1978) were used to create morph continua between pairs or expressions or between neutral and expressive faces. Images of the same individual were morphed using SmartMorph program (version 1.55, MeeSoft, http://meesoft.logicnet.dk) to create different strengths of emotional expressions. A 25-step array of morphs between two images was created by manually marking corresponding features. The location and color attributes of each feature in the output of the morph program is given by a linear interpolation of the originals.

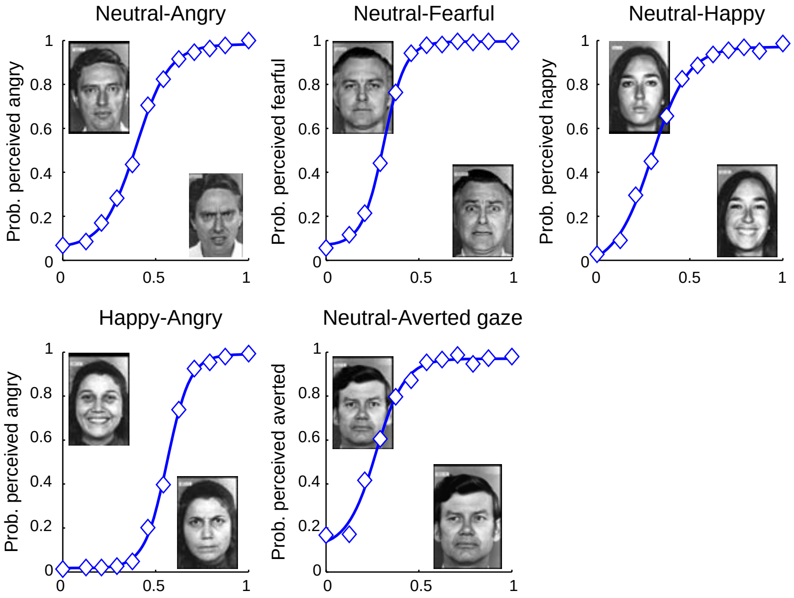

**Figure 42.** Subjective ratings of morphs between two expressions.

Subjective ratings of morphs between two expressions show steep transitions from one category to another one. Abscissa: morph strength. Average data (7 subjects) and the best sigmoidal fit are plotted for each morph continuum. The left and right pictures on each plot represent morph strengths of zero and one, respectively.

**Setup:** Search arrays were displayed on 19" CRT or LCD screens on a PC computer (VisionEgg/Python under Windows XP), placed about 70 cm from the viewer and about the eye level. Participants were sitting comfortably behind a desk and could move their head and change their posture at will. They viewed the images binocularly and responded using a computer keyboard and located the target using a mouse pointer.

**Face rating:** Categorical perception of facial emotions in the morph continua (neutral-angry, neural-fearful, neutral-happy, happy-angry, and neutral-gaze averted) were tested and verified in seven observes (4 male, 3 observers participated in other experiments). Original or morphed images were displayed briefly (100 ms), and then two phrases appeared (e.g., “Calm” and “Angry” for neutral-angry morphs). Observers pressed one of the two keys to indicate which phrase describes the image the best. The average probability of reporting each option was fitted using a sigmoid curve. In all cases, we found a sharp transition between two perceived categories as a function of the morph strength (figure 42).

**Experiment 1:** In each trial, four, eight, or sixteen images were displayed simultaneously at random locations on a 5×5 grid (subtending about 18×18 $deg^2$) on the computer screen. Each face subtended approximately 2×3 $deg^2$. In each search display all images except one (target) were identical. Target and distracters were images of the same individual. Observers were instructed to press a button as soon as they located the target image. Then all the images were masked with a gray rectangle, and observers were asked to point the computer mouse to the location of the target and click. We emphasized accuracy, and then the reaction time for pressing the button. Participants were informed that their response time for pointing to the location of the target did not matter. Visual feedback was given if the wrong location was clicked.

We used a 2×2×2 randomized design to test the effects of distance in morph continuum between target and distracters (0.33 vs. 0.4), category effect (target and distracters on the same side of the category boundary vs. spanning it), and search asymmetry (target more expressive than distracters or vice versa).

**Experiment 2:** The display was similar to experiment 1 except that only in half of the trials a target face (different from the rest of the images) was present. Observers were instructed to press one of the two buttons to indicate whether the target is present or not. They were not required to report the location. Feedback was given for wrong responses. Images remained displayed until the observer made a response.

A 2×2×2 randomized design to test the effects of distance in morph continuum (0.4 vs. 0.5), category effect, and search asymmetry.

**Experiment 3:** The display was similar to experiment 1. In one-third of the trials, there was one target among 4 or 9 simultaneously presented items. In the rest of the trials two possible targets (among 8, 12, 15, or 18 items, 2/3 of the trials) were present. The two targets were always in different hemifields (left vs. right or top vs. bottom). One of the targets was in the same category as the distracters, and the other one was across the category boundary (defined as the midpoint in the morph space). The distance between both targets and distracters in the morph space was equal. Instructions were identical to experiment 1 (report the location of the odd face) and feedback was given for incorrect localization. Observers were not explicitly told about the possibility of more than one target, but after the experiment a few observers indicated that they have occasionally noticed more than one target.

The design of experiment 3 was similar to experiment 1, except that when two targets were present, the outcome of the trial (target selected by the observer) determined whether the trial belongs to the same category or different category group. Other factors (distance in morph space and asymmetry) were randomized.

**Analysis:** inspection of the data revealed a clear linear increase in search time (response latency) with the number of items displayed simultaneously. The trials were binned based on the physical (distance in morph continuum) and perceptual (category effect and asymmetry) effects and the slope and intercept of the search time as a function of number of items were estimated for each bin and subject using regression analysis. The perceptual factors (category effect and asymmetry) were combined together to create 4 groups (target from expression and distracters from neutral category, target from neutral and distracters from expression category, both target and distracter from expression category, and finally, both from neutral category). This was done because the hypothesis that perceived expressions guide attention predicts an interaction between category and asymmetry. The last two groups (both target and distracters from the same category) were combined to increase the statistical power of the analysis. A $2 \times 3 \times N$ ANOVA (where $N$ is the number of observes) was used to establish significant effects.

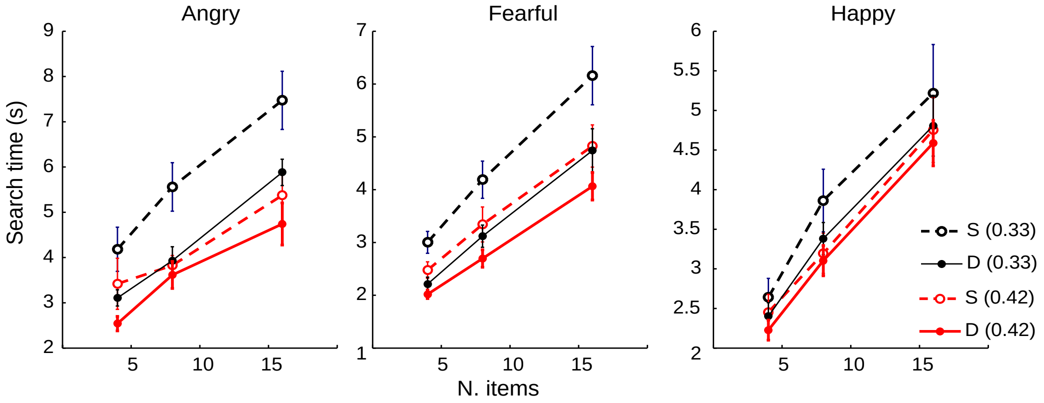

**Figure 43.** Category difference and distance in morph space influence search time. Search time (until the target is found) increases linearly with number of items (experiment 1, n=10). S: target and distracters are on the same side of the natural category boundary. D: target and distracters are on different sides of the category boundary. Black and red curve depict trials in which the distance between target and distracters in the morph space is small (0.33), or large (0.42), respectively.

### 8.1.3 Results

In all experiments search time increased linearly with number of items displayed. Figure 43 shows search time (experiment 1, 10 participants) as a function of display size, distance between target (odd face) and distracters in the morph space, and whether or not target and distracters belong to the same category. Categorical effects in this figure are based on the natural category boundaries (defined as the midpoint in the morph continuum between two original images). Note that the lines are more or less parallel, suggesting that the changes in the slope of the search time as a function of display size are relatively small compared to changes in the intercept.

The effect of face category and distance in morph space on search time (slope and intercept) were assessed using univariate ANOVA. Figure 44 shows contribution of each factor to the search time in experiment 1. The search slope significantly varied with the distance in the morph space between target and distracters for neutral-angry (*F*(1,45)=5.33, *p*=0.026) and neutral-fearful (*F*(1,45)=4.31, *p*=0.044) morphs. A similar trend for slope was observed for neutral-happy morphs which did not reach significance (*F*(1,45)=0.67, *p*=0.42). The effect of morph distance on the intercept of the search function was not significant in any of the conditions, although their trend paralleled the effect on the slope.

Contrariwise, the intercept of the search function varied with the categorical relationship between target and distracters. Search was faster, independent of the number of distracters, when the target belonged to a different category, for both neutral-angry (*F*(2,45)=4.2, *p*=0.02), and neutral-fearful (*F*(2,45)=6.38, *p*=0.004) morphs. A similar trend was also observed for neutral-happy morphs (*F*(2,45)=3.8, *p*=0.056). The effect of category relation on the slope was not significant in any of the conditions. There was no interaction between morph distance and category relation on either the slope or the intercept. This was further verified using a two-way multivariate ANOVA.

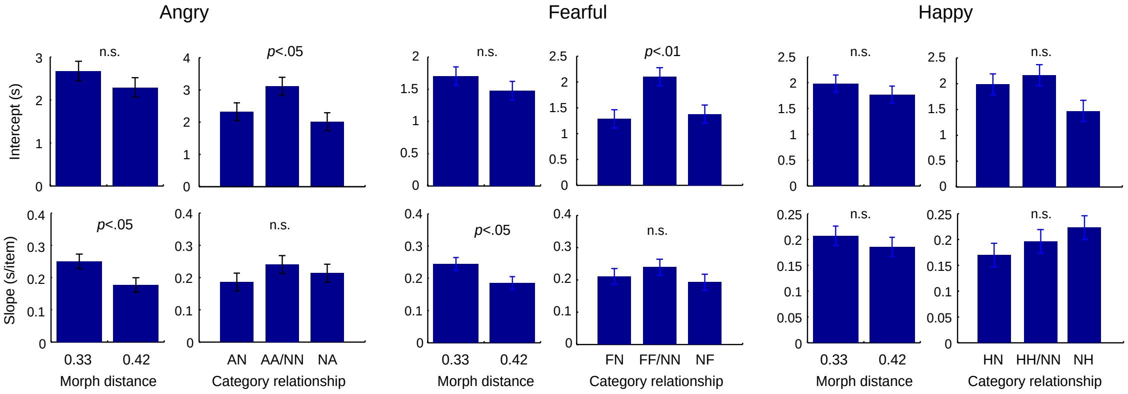

**Figure 44.** The effect of morph distance between target and distracters and categorical relationship between them on the intercept and slope of visual search in experiment 1.

Category relationship is denoted as XY where X and Y denote categories of target and distracters, respectively (A: angry, F: fearful, H: happy, N: neutral). For negative expressions (angry and fearful), distance in morph space affects the slope whereas categorical relationship affects the intercept of the search function.

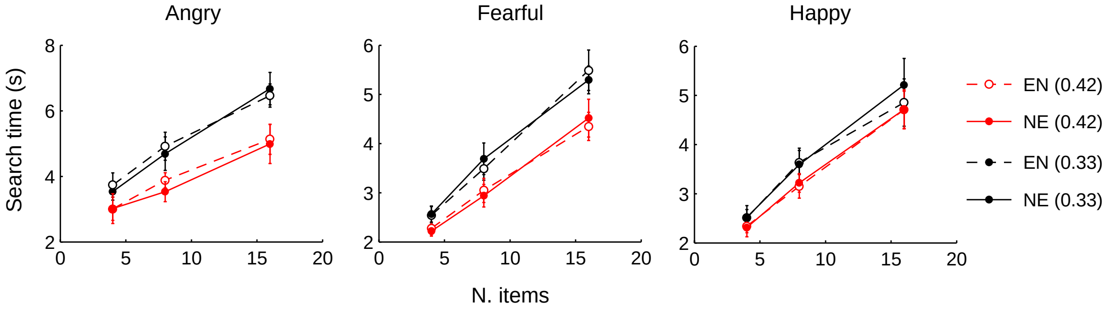

**Figure 45.** No asymmetry in search in experiment 1.

EN: target expresses more expression (anger, fear, or happiness) than distracters (regardless of whether they belong to the same category or not). NE: Target is more neutral than distracters. Black and red curve depict trials in which the distance between target and distracters in the morph space is small (0.33), or large (0.42), respectively.

The linear relationship between search time and display size in experiment 1 is consistent with a serial model of visual search. Remarkably, there was no indication of search asymmetry in our results. Searching for an angry or fearful face among neutral faces were as fast (in terms of both slope and intercept) as searching for a neutral face among angry or fearful distracters (compare AN vs. NA or FN vs. NF in figure 43). Figure 45 illustrates the absence of search asymmetry for all three expression morphs.

The results of experiment 2 (N=9) showed trends similar to experiment 1, but the data were noisier (since in half of the trials the target was absent and therefore those trials were excluded) and the trends did not reach significance. However, when we pooled negative expressions (angry and fearful morphs) together, a significant effect of category relationship could be established (*F*(2,40)=3.37, *p*=0.044). Thus, category relation has an effect on the slope of the visual search even when observers are not required to explicitly localize the target.

There are three explanations for a change in the intercept of the search function. First, implicit knowledge about the presence of a different category might influence the preparation time before the search starts (pre-search latency). Second, the category difference could shorten the search process. Information about the location of category difference might guide attention toward the target. This possibility is often discussed in the context of a change in the slope of the search function. Nonetheless, this account is also consistent with a change in the intercept, assuming that the signal to noise of the implicit information increases with display size (thus there is a smaller effect as the number of items on the display increases). Alternatively, a target belonging to a different category might be registered and terminate the search more quickly than a target from the same category of the distracters. Third, after the search is completed it may take less time to verify the outcome and to evoke a motor response if the target is categorically different from distracters compared to when target and distracters are from the same category (post-search latency).

In experiment 3 we tried to tease apart whether the category relation primarily affects pre-search, search, or post-search latencies. In two-thirds of the trials, two potential targets were displayed on the screen. One of the targets was on the same side of the category boundary as the distracters. The second target always belonged to a different category. Trials were sorted depending on the outcome (whether the reported target belongs to the same category as distracters or to the different category). Pre- or post-search facilitation does not affect the probability that each target is eventually reported. Pre-search facilitation predicts that the reaction time is independent of the outcomes (since a different category is always present in the display), whereas post-search facilitation predicts a shorter reaction time when the target from a different category is reported.

If category difference affects the search process then predictions are nontrivial. Guidance of attention can be modeled as a biased random walk in which attention is more likely to move toward the location of the different category, whereas facilitation of the termination of the search can be modeled as a race between two independent random processes with different distributions. Interestingly, both models predict that subjects are more likely to report the target that belongs to a different category.

Figure 46 illustrates the results of experiment 3. As a control, in one-third of the trials only a single target was displayed (top row). Consistent with experiments 1 and 2 category relationship influenced the intercept. There was a significant effect of category difference in neutral-fearful morphs ($F(2,61)=8.0$, $p<0.001$). Neutral-angry morphs also showed a similar trend.

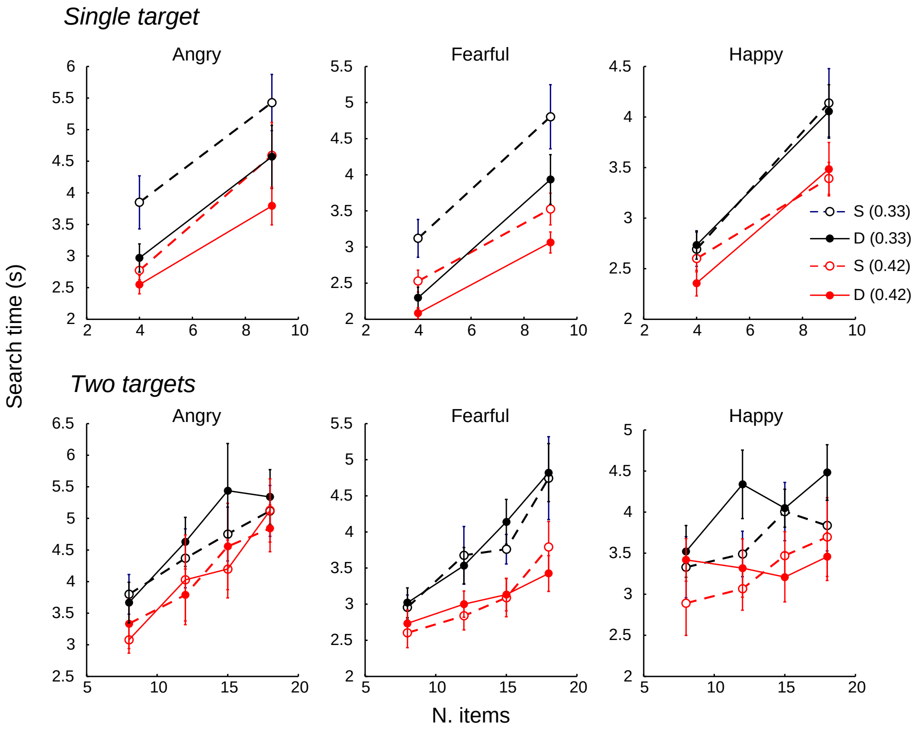

**Figure 46.** Search time as a function of the outcome of the search.

Search time number of items, distance in morph space and category relation of the reported target and distracters in experiment 3 (n=11). Top row shows the results for the control trials (1/3 of the trials) in which only one target was present. Bottom row shows the results for trials in which two targets (one of which was in the same category as distracters, the other one was from a different category) were present. S: target and distracters are on the same side of the natural category boundary. D: target and distracters are on different sides of the category boundary. Black and red curve depict trials in which the distance between target and distracters in the morph space is small (0.33), or large (0.42), respectively.

The bottom row of figure 46 shows the results when two targets were present and trials were sorted based on the outcome. In contrast to the control trials, there is no difference in search time between same and different category conditions. However, the probability of reporting the target with a different category increased for negative expressions (angry: 60±1.77%, *p*<0.001; fearful: 59.2±1.65%, *p*<0.001; happy: 52.4±1.92%, n.s. vs. 50%). These results are compatible with the hypothesis that a category difference facilitates termination of the search. We simulated the race model using the empirical distribution of search times from single target fearful trials. The simulated difference in intercept when two targets were presented and competed was less than 0.1 s (compared to a 0.75 s difference in the single target trials). On the other hand, about 61% of the targets that won the competition and terminated the search in the model were from a different category.

### 8.1.4 Category boundaries in search vs. Perceptual categories

The analyses of the effect of the category on search time in the previous chapter were carried out using a fixed category boundary of 0.5. The midpoint in a morph continuum serves as a natural category boundary for the two original images in terms of low-level similarities. However, in figure 42 it is evident that the actual perceived category boundaries for expression morph continua are different from the midpoint (neutral-angry: 0.39±0.03, *p*=.02, neutral-fearful: 0.32±0.01, *p*<.001, neutral-happy: 0.29±0.04, *p*<.001, two tailed t-test vs. 0.5). It can be argued that the boundaries estimated from subjective ratings rather than the midpoint should be used for analyzing the effect of facial category on visual search.

Remarkably, when perceptual category boundaries estimated from subjective ratings were used, we found either a weaker or no effect of category on the search time for angry and fearful morphs, or even an opposite effect for happy morphs (search was faster if target and

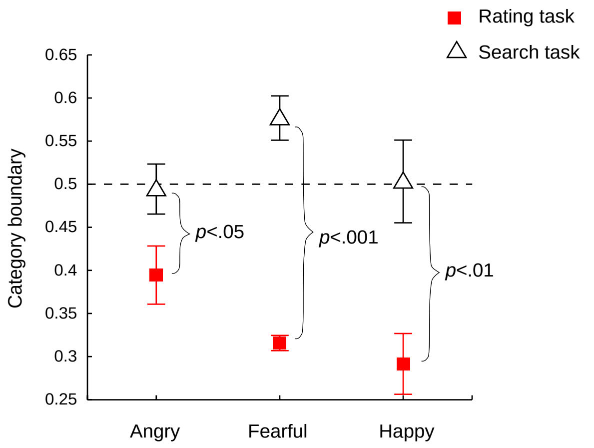

**Figure 47.** Optimal category boundaries depend on the task.

Optimal thresholds estimated from search experiment 1 vs. thresholds from direct rating by observers. (*p* values are based on two-tailed *t*-test between normal observers, not corrected for multiple comparisons.)

distracters belonged to the same “perceived” category in experiment 1). These results suggest that the category boundaries utilized by subjects for the search task are be different from perceptual category boundaries measured from a subjective labeling task.

In order to quantitatively compare the category boundaries in search with perceptual category boundaries we tried to estimate category boundaries from the search data by fitting a simple regression model to the reaction time data. The expected reaction time was assumed to be a linear function of number of items, distance between target and distracters in the morph space, and the difference between category of target and distracters. Category of an image in the morph continua was modeled using the following function:

$$C(x) = \mathbf{tanh}\ 6(x-\theta),$$

where $\theta$ is the category boundary, and $x$ is the relative distance of the morphed image from the neutral image. Using a smooth boundary instead of a step function enables us to

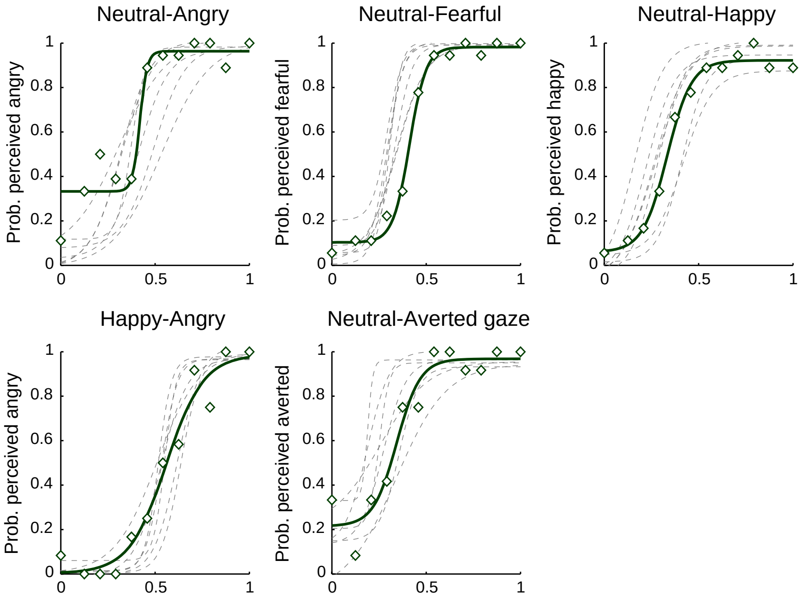

**Figure 48.** Categorical perception in SM compared to healthy individuals.

SM shows sharp category boundaries for all morphs continua. Her category boundaries are within the control range, except for fearful morphs in which she has a significantly higher threshold in reporting fear. Dotted curves depict the best fit for each control subject. Open symbols and the solid curve depict raw data and the best fit for SM, respectively.

estimate the boundaries robustly. The slope of $C(x)$ is approximately equal to the slope of the psychometric curves from the rating experiment. Category boundaries in each observer were calculated by minimizing the fit error of the linear model.

Figure 47 illustrates the differences between category boundaries estimated from the two tasks. These results suggest that categorical facilitation of search and categorical perception are not the same.

## 8.2 Visual search in amygdala patient

Amygdalae are almond-shaped bilateral masses of gray matter in the anterior portion of the human medial temporal lobes and are considered part of the limbic system. Functional imaging studies demonstrate that human amygdala is involved in judging facial expressions such as fear (Breiter *et al.* 1996; Morris *et al.* 1996; Whalen *et al.* 2001). Behavioral studies in rare cases of bilateral amygdalae damage in humans often demonstrates impairment of recognition of negative facial expressions (Adolphs *et al.* 1994; Adolphs *et al.* 1999; Broks *et al.* 1998; Young *et al.* 1996). Recently, it has been suggested that the primary deficit which causes poor perception of facial expressions in such patients is a lack of proper orienting toward relevant features such as eyes (Adolphs *et al.* 2005).

Here we set to examine visual search for facial expression categories in patient SM, who has complete bilateral amygdala damage and profound but very selective deficits in recognition of negative expressions and particularly fear from photographs of faces. Our motivations for studying visual search in SM are threefold: First, our results in normal controls show a significant advantage in visual search time (experiments 1 and 2) and probability of reporting (experiment 3) for category differences for fearful and angry, but not happy expressions. This pattern matches the role attributed to amygdala in perception of facial expressions. Second, negative facial expressions or threatening stimuli that are masked or binocularly suppressed nonetheless activate sub-cortical regions and amygdala (Anderson *et al.* 2003; Morris *et al.* 1998; Morris *et al.* 1999; Pasley *et al.* 2004; Williams *et al.* 2004). We would like to know if implicit processing of facial expressions in the amygdala underlies facilitation of the search. Third, amygdala is suggested to be involved in orienting toward features that are more distinctive for fearful expressions and in particular, the eyes (Adolphs *et al.* 2005). That is, amygdala might be involved in guiding attention during the visual search.

Figure 48 depicts subjective labeling for morphed faces in SM compared to healthy controls ($N$=7). For fearful expressions, SM had a significantly higher threshold than the controls ($z = 4.1$, $p<.0001$). For other morph continua, SM's thresholds were similar to controls.

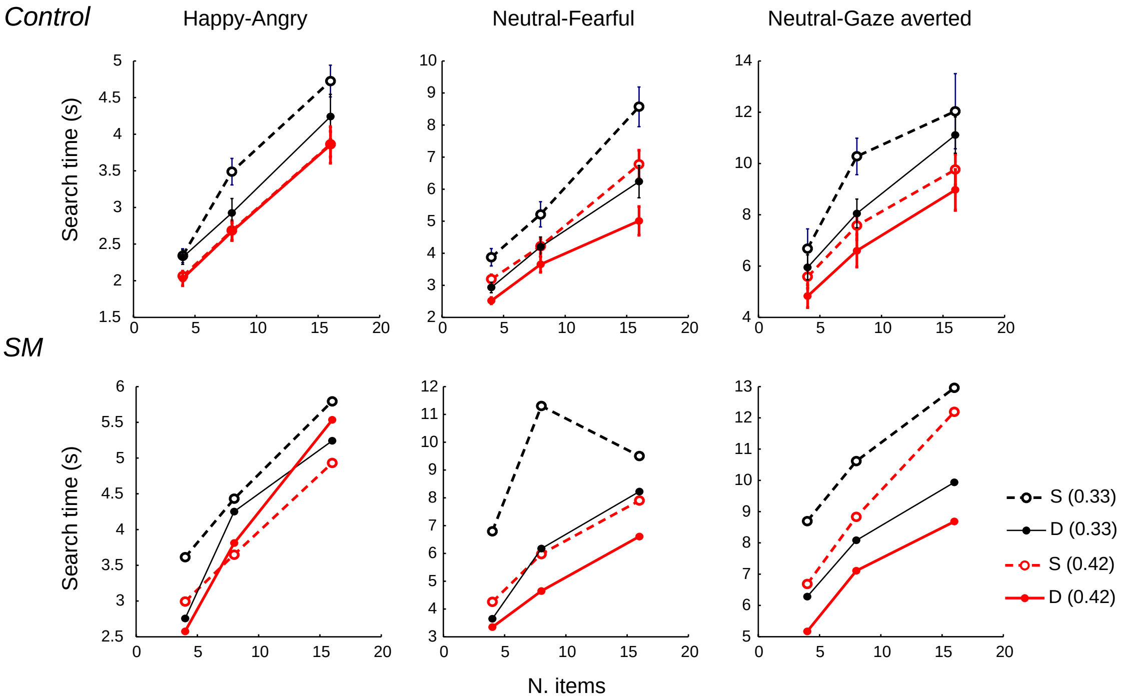

**Figure 49.** Search time in SM.

Search time as a function of number of items, distance in morph space and category relation of the reported target and distracters in normal controls (n=13, top) and patient SM who has bilateral amygdala damage (bottom). S: target and distracters are on the same side of the natural category boundary. D: target and distracters are on different sides of the category boundary. Black and red curve depict trials in which the distance between target and distracters in the morph space is small (0.33), or large (0.42), respectively.

We tested SM and 13 healthy individuals using a paradigm similar to experiment 1: happy-angry, neutral-fearful, and neutral-averted gaze morph continua were used. The motivation for using gaze morphs was to test whether SM's ability to notice subtle differences in the gaze direction from photographs is impaired or not.

The control group replicated the findings in experiments 1 and 2. Category relation had a similar effect on the intercept in all three conditions even though the effect reached statistical significance only for neutral-fearful morphs ($F(2,49)=4.62$, $p=0.012$). There was no significant search asymmetry and no effect of category relation on the slope of the search.

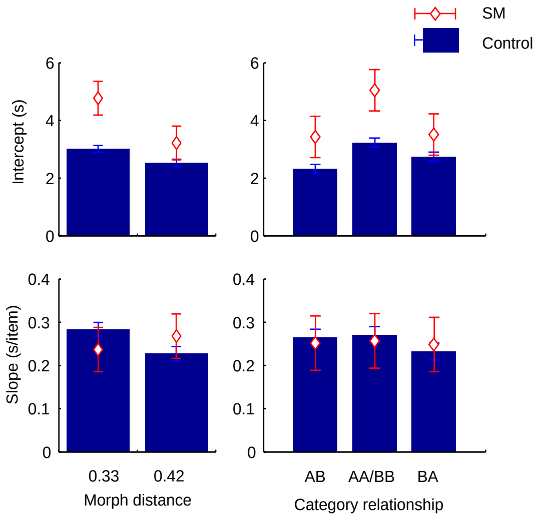

**Figure 50.** The effect of morph distance and categorical relationship on intercept and slope in SM vs. normal controls.
Category relationship is denoted as XY where X and Y denote categories of target and distracters, respectively (A: angry, fearful, or looking away, B: neutral or happy).

Notably, a similar effect was also observed for SM. Although her reaction time was slower than controls, she showed the same category effect in all conditions (figure 49). In all three conditions the effect of category on the intercept in SM was equal or larger than the average effect in the control group. Results were also verified using average search time (which is not sensitive to the errors in estimating the slope of the search function) instead of the intercept.

A larger effect in SM might be partially due to a possible general impairment of her ability to discriminate small changes in facial expressions. In the absence of an age and IQ matched control group, however, this impairment is difficult to attribute to the amygdala damage. Nonetheless, the improvement across category boundary suggests that she is able to utilize categorical information in visual search.

Figure 50 illustrates the effect of category relation and distance in morph space pooled across all three morph continua. The intercept significantly varied with both category relation

(*F*(2,60)=8.44, $p<0.001$) and distance in morph space (F(1,60)=7.16, $p<0.01$). The interaction between them was not significant. The distance in morph space also significantly affected the slope (*F*(1,60)=6.16, $p<0.05$). On the other hand, the slope of the search did not vary with category relation (*F*(2,60)=1.08, p=0.35).

Finally, figure 51 shows that the category boundaries in visual search for SM are similar to the control group and they are different from perceptual categories obtained from the rating task.

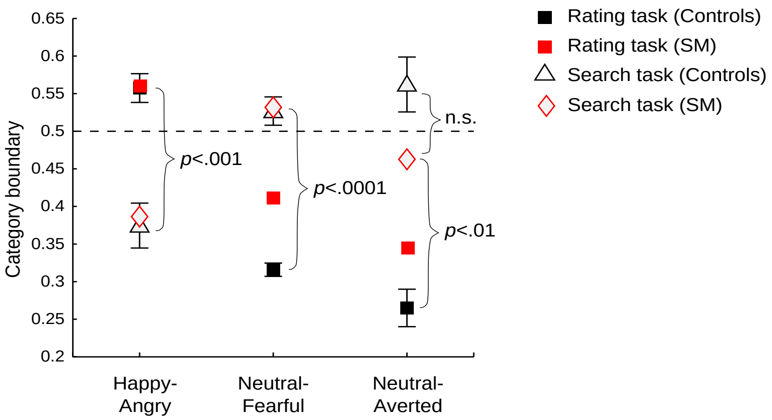

**Figure 51.** Optimal category boundaries for search in SM are similar to normal controls and different from rating task.

*p* values are based on *z*-statistics, uncorrected for multiple comparisons.

### 8.3 General discussion

We studied visual search for facial expressions in normal individuals and patient SM with bilateral amygdala damage using realistic morphs of facial expressions. Our results demonstrate that the visual system utilizes categorical processing, particularly for negative expressions: search was more efficient in terms of the intercept of the search function when the target of the search is categorically different from distracters. In contrast, the slope of the search, which is the conventional measure of the efficiency of the search, varied significantly with the distance in the morph space but not with the categorical content of the display. There was no evidence of search asymmetry or an advantage for finding an angry or fearful face among neutral distracters vs. finding a neutral face among angry or fearful distracters.

The results of the amygdala patient show that the categorical processing of negative facial expressions in visual search is possible without involvement of the amygdala. Even though SM was impaired in perceiving and labeling fearful faces, her search results paralleled results of the normal controls. This finding casts doubt on the hypothesis that the amygdala modulates orienting toward negative expressions in visual search.

Absence of search asymmetries in our results is in contrast to a sequence of previous studies that show an asymmetric advantage for threatening expressions in visual search (Ashwin, Wheelwright and Baron-Cohen 2006; Fox *et al.* 2000; Hansen and Hansen 1988; Horstmann and Bauland 2006; Ohman *et al.* 2001). It has been argued that a target defined by the presence of a preattentive feature is easier to find than a target defined by the absence of that feature (Treisman and Gormican 1988). Faster search time for an angry target among neutral or happy distracters compared to a neutral or happy target among distracters might indicate that anger (or some coincidental feature or image primitive in the angry face) is processed pre-attentively. Absence of such an asymmetry, on the other hand, indicates that anger itself is not a preattentive feature. Our results show no asymmetry, while at the same time the paradigm used is sensitive enough to show that categorical information is processed and facilitates the search. Thus we concluded that anger is not a preattentive feature. Horstmann and Bauland (2006) recently pointed out that the asymmetry is stronger when cartoon drawing of faces are used compared to realistic photographs of faces. This might indicate that the mechanisms underlying such an asymmetry in visual search have a low sensitivity to expressions, and the morphed faces used in our experiments might be too similar for such mechanisms even though perceptually they depict distinct emotional expressions.

The category boundaries utilized in visual search were different from perceptual category boundaries obtained by asking subjects to label expressions in both normal controls and the amygdala patient. Different category boundaries could indicate dissociable mechanisms with different tunings for processing facial expressions: mechanisms that are involved in recognition of emotion from photographs of facial expressions (rating experiments) appear to be more sensitive and have a lower threshold than mechanisms that facilitate the visual search. It can be argued that the category boundaries are sensitive to cognitive biases (such as a response bias) imposed by the structure of the task and frequency of exposure to stimuli or choices. However, the boundaries are difference even the exposure and response are balanced (figure 51, happy-angry morphs). Moreover, the perceptual category boundary for fearful expressions is shifted in SM, suggesting that the amygdala is involved in recognize fear, whereas her search boundary is the same as normal controls.

Experiment 3 demonstrates that the change in the intercept of the search cannot be attributed to acceleration of pre-search mechanisms (or any preattentive mechanism that uses implicit knowledge about the presence of category difference in the display) or to a faster response after the target is found. When two targets are present—one categorically similar to distracter, the other one different—the second target is preferentially found. This finding is compatible with the hypothesis that a category difference at the attended location facilitates termination of the search. It is also possible, but less likely, that the category difference is implicitly processed and consequently guides attention. However, since this causes a change in the intercept and not the slope of the search in single target displays, we argue that the implicit guidance should decrease with the number of distracters. Thus, the implicit processing of facial categories is not preattentive, but could occur in the penumbra of attention and awareness. This view is consistent with the behavioral results that show face categorization can be efficiently done while attention is split (Reddy, Reddy and Koch 2006; Reddy, Wilken et al. 2004).

In summary, our results indicate the implicit categorical processing of facial expression has little effect on the slope of the search, there is little asymmetric advantage for fearful and angry expressions, and damage of the amygdala has little or no effect on a categorical facilitation of the intercept. These findings contradict the hypothesis that emotional expressions are processed preattentively in the amygdala and guide attention toward ecologically significant facial expressions.

# 9 SUMMARY

In normal vision, retinal inputs enter the cortical stages of visual processing and evoke specific percepts. However, the same inputs may occasionally evoke a different percept or fail to evoke any percept. What happens to the retinal inputs when we fail to see them?

Figure 52 illustrates the hierarchy of areas in the visual system (Felleman and Van Essen 1991). The visual stimuli activate retinal ganglion cells (bottom of the hierarchy). Activation of those cells could in turn result in activation of neurons in the lateral geniculate nuclei, V1, V2, and other areas, in a serial fashion. A volley of excitation travels along the visual processing hierarchy (feedforward sweep), eventually entering brain areas involved in motor function, memory, and planning. Following activation of these areas the observer reports seeing the stimulus, later remembers seeing it, and modifies her subsequent behavior accordingly.

Alternatively, the wave of activity that is evoked by stimulation of the retina might gradually subside and fail to activate the areas that are involved in motor function, memory, and planning. If so, the subject neither reacts to the stimulus nor does she form any memory about it. In other terms, the she does not see the stimulus.

Figure 53 depicts propagation of firing activity in feedforward network with random excitatory connections between layers (Moradi 2004). Activation of the input layer either evokes a robust volley of synchronous neuronal excitation propagating along the network, or subsides and dissolves to the baseline level of activity after traveling for only a few layers (Moradi 2004).

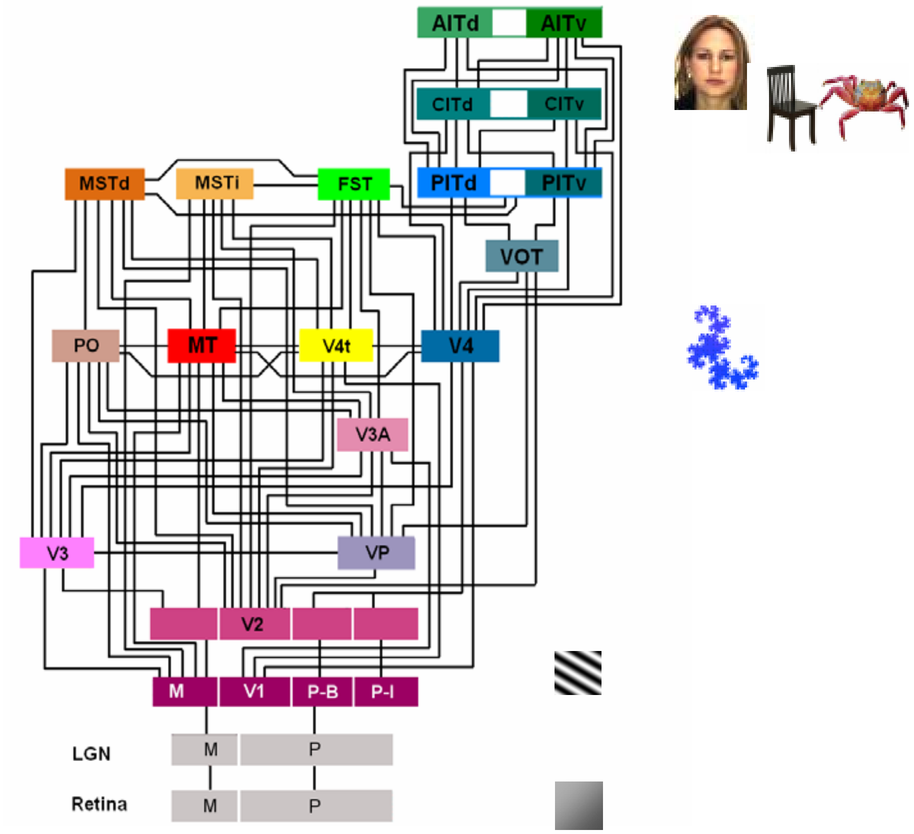

**Figure 52.** Hierarchy of visual areas (after Felleman and Van Essen 1991). The activity propagates from the bottom of the hierarchy (early areas that respond to simple features such as contrast or orientation) toward the top (areas that respond to complex images of objects, faces, etc).

The probability of excitation of the whole network depends on the connectivity between layers and the thresholds of individual neurons. In the visual processing hierarchy, adaptation increases the threshold of neurons responding to the adapting stimulus, whereas a sudden visual transient attracts attention and evokes mechanisms that adjust the gain. Disappearance of the subsequent stimulus following the combination of adaptation to sustained low-contrast pattern and the transient flash but not following each one individually shows synergy between changes in threshold and in gain.

This theoretical framework can be easily generalized to multistabile perceptual illusions.

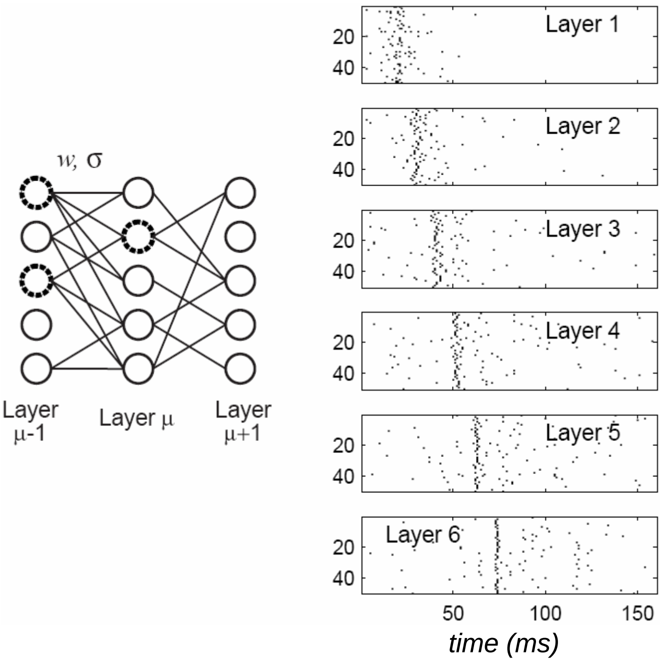

**Figure 53.** Propagation of firing activity in a network of integrate-and-fire neurons.

Left: Firing of a subpopulation of neurons in layer μ–1 (dotted circles) results in excitation of neurons in the next layer (μ). Depending on the connectivity (*w*) and prior membrane potential some of the neurons in layer μ may reach threshold (σ) and fire, which in turn results in activation of the subsequent layer (μ+1). If a neuron does not reach the threshold, its membrane potential decays to the resting potential.

Right: An illustration of the propagation of a wave of excitation along the network. Each dot represents the firing of one neuron (50 neurons/layer).

Transient changes contingent upon prior adaptation frequently elicited perceptual alternations in structure from motion, binocular rivalry, Necker cube, and ambiguous apparent motion. Alternative percepts are represented by parallel and competing synfire chains. Representations of different percepts mutually inhibit each other and therefore only on of them is registered at any moment. Adaptation affects neurons that encode the dominant percept. Once the dominant percept is suppressed by the synergetic effect of adaptation and visual transient, the visual input may activate the competing synfire chains and consequently evoke an alternative percept.

Bistable inputs (i.e., inputs for which the synfire network sometimes but not always converges to full excitation) have one remarkable property: Even when they fail to traverse the whole network (and consequently are not seen), they still excite the first few visual areas in the hierarchy. The activity decays gradually, thus the correlation between activation and the outcome (visibility) is rather weak in V1 and improves in subsequent areas.

Chapter 4 used visual aftereffects to probe activation in two stages of the visual processing hierarchy: an early stage that responds and adapts to oriented patterns (possibly as early as V1) and a later stage that encodes complex visual information such as face identity. Consistent with the synfire chain metaphor, binocular suppression and inattention did not interfere with the orientation-specific aftereffect which could occur in early stages of the visual hierarchy. In contrast, face identity-specific aftereffect was found to depend on the visibility of the inducing face.

The competition between incompatible or interfering visual inputs to reach awareness is resolved before those aspects of information that are exploited in face identification are processed. The neuronal circuitry underlying face identity processing is not fully understood, but faces selectively activate an area in the human fusiform cortex (Kanwisher et al. 1997). Face identity aftereffect is invariant to eye movements. We found that the fMRI adaptation in face-selective region of the fusiform cortex is not fully invariant (chapter 7). Therefore identity aftereffect is likely to originate subsequent to the level of face processing in the fusiform area.

Attention can influence perception by permitting some aspects of the visual input to be processed while preventing other aspects to go through and interfere with the processing. Gating of information processing in a synfire chain can be best realized by adjusting the gain of the neurons in early layers of the network. After the first initial layers, the activity either has converged to a stable pattern, or has substantially decayed. At this point, modulating the gain is unlikely to have a significant effect on the outcome. Changing the gain at an early level, however, can significantly influence the evolution of the activity in the synfire chain (it might be necessary to modulate the gain at higher stages of processing as well because complex stimulus properties relevant to the gating of the information are not always represented at the earliest areas).

Failure of adaptation to the identity of unattended faces suggests that attentional selection is early (with respect to the level of face identity processing). The results of visual search for facial expressions (chapter 8) are incompatible with preattentive processing of emotional categories. Thus, recognition of facial emotional expressions occurs after the level of attentional selection.

When a stimulus is not attended, it still evokes a BOLD response in early visual areas (chapter 6). The measured fMRI response becomes weaker in subsequent stages of visual processing hierarchy and the evolution of the fMRI activity from V1 to V4 is compatible with a simple gain cascade model. Attentional modulation of the gain of neurons at multiple levels of the visual hierarchy determines how far the retinal input is processed and whether or not a high-level representation of the input will be constructed.

In conclusion, our results point to a simple scheme in which the evolution of the feedforward activations in the visual processing hierarchy is affected by top-down attentional signals that modulate the gain of neurons, and by prior adaptation of those neurons. The outcome of this feedforward chain closely correlates with the subjective experience of seeing.

# 10 APPENDIX: BINDING AND PREATTENTIVE SURFACE SEGREGATION

Visual input is segregated in the brain into subsystems that process different attributes such as motion and color. At the same time, visual information is perceptually segregated into objects and surfaces. Here we demonstrate that pre-attentive segregation of visual entities based on a transparency cue precedes and affects perceptual binding of attributes. Adding an irrelevant transparency cue paradoxically improved the pairing of color and motion for rapidly alternating surfaces. Attributes are registered over the temporal window defined by the perceptual persistence of segregation, resulting in asynchrony in binding. While the segregation is early (i.e., before the visual stream subdivides into specialized areas) and does not require top-down feedback, attention is necessary for correct registration of attributes in the presence of ambiguity[1].

## 10.1 Temporal asynchrony in binding

Neurophysiologists have shown that different aspects of visual stimuli (e.g., color, motion, etc.) are registered in separate cortical subsystems (Felleman and Van Essen 1991; Livingstone and Hubel 1988; Milner and Goodale 1995; Mishkin, Ungerleider and Macko 1983; Ungerleider and Mishkin 1982; Zeki 1978) (but see Lennie 1998). Localized brain damage in human patients can result in isolated deficits in perception of a single attribute (Damasio *et al.* 1980; Goodale and Milner 1992; Meadows 1974; Zeki 1991; Zihl, von

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[1] This chapter is published in Vision Research (Moradi, F., and S. Shimojo (2004a). Perceptual-binding and persistent surface segregation. *Vision Res* **44**, 2885-2899.)

Cramon and Mai 1983). Recent functional brain imaging studies also support specialization of cortical functions (Hadjikhani *et al.* 1998; Kanwisher *et al.* 1997).

Although various visual attributes are processed and represented in functionally distinct brain regions, they are rarely perceived as separate. We perceive various visual attributes as belonging to segregated surfaces and objects. Mechanisms must exist that integrate attributes into a coherent percept. Otherwise, it would be impossible to distinguish, for example, between one display consisting of a red square on a green background and another one containing a green square on a red background. Two types of computation are required in order to integrate different aspects of visual input into a unified percept. The visual system should be able to partition the visual scene into individuated entities such as surfaces and objects (segregation). Segregation (also called "parsing") is often discussed in the context of development of the visual system (Spelke, Gutheil and Van de Walle 1995). It should also determine which combination of attributes is associated with each entity (feature binding).

Observation suggests that binding and segregation are related. Spatial or temporal coincidences of attributes are significant only if they come from the same entity. Even if attributes are superimposed, there is no guarantee that they come from the same single object[2]. Figure-ground segregation can influence how attributes are bound. For example, when a figure (e.g., red square) moves on a uniform background, local motion signals at the

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[2] For example, if an object casts a shadow on a surface the visual system discounts the shadows in perceiving the lightness of the surface. Thus, the shadow and the surface are perceived at the same location, but are not bound together. One can easily think of other examples in which transparency, occlusion, or figure-ground segregation should be considered before binding.

figure-ground boundary are bound to the object perceived as the figure, and not the background[3] (Ramachandran and Anstis 1986; Tommasi and Vallortigara 1999).

It is not known if segregation is interlinked with binding or if it is only necessary when there are ambiguities in the scene (when attributes can bind in different ways). We address this issue by examining whether an explicit segregation cue (motion or depth transparency) can facilitate color-motion (or color-disparity) binding. Color and motion are processed in distinct cortical areas (Zeki 1978). Cells in the area MT of the monkey show high sensitivity for motion direction, whereas their sensitivity for color is low. In contrast, few cells in area V4 are direction selective (Cowey 1994; Felleman and Van Essen 1987). Consider a display containing red dots moving left, and green dots moving right (either simultaneously or at different times). Observers are asked to report the direction of the red dots. The task itself does not necessitate segregation of red and green dots into distinct surfaces. However, if observers require an explicit segregation cue (e.g., transparency) to do the task, then we have established that binding and segregation are related. This issue is examined in experiments 1–3.

The dependence does not imply that binding and segregation are the same process. Presumably there are certain aspects that dissociate segregation and binding. Experiments 4-6 address whether segregation precedes binding (i.e., the scene is first segregated, then attributes are assigned to each object), or if binding and segregation occur concurrently at the same level of processing. We also examine if either segregation or feature binding could occur pre-attentively. There is a rich literature about feature binding and attention. We would

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[3] This display is ambiguous: it is also possible that a green surface with a square-shaped hole moves on a red background. Alternatively, red and green may both move. However, in the absence of other cues the dominant percept is red moving and green stationary.

like to know if attentional mechanisms in feature binding are also involved in surface segregation, and to what extent.

### 10.1.1 Observers and apparatus

Volunteers with normal or corrected-to-normal vision from the Caltech participated in the experiments. Participants were naïve to the purpose of the study. Subjective equiluminant green (CIE x = 0.29, y = 0.59) was measured for maximum red intensity (CIE x = 0.62, y = 0.63, 54 cd/$m^2$) using a technique based on minimizing the flicker between red and green at 14 Hz (Wagner and Boynton 1972).

Experiments were programmed using the Psychophysics Toolbox extensions (Brainard 1997; Pelli 1997) on a Windows PC. The visual stimuli were presented on the 17" CRT monitor (Dell Trinitron Ultrascan 1000HS) at 85Hz viewed binocularly from a distance of 54cm. In each trial, the stimulus was displayed for about 1.2 s. The participant was asked to press a key to indicate the direction of movement of the red dots (experiment 1-2) or the color of the moving dots (experiment 4-6). Conditions were randomized within each block. No feedback was given to the observers. The procedure will be described separately for each experiment in each section.

### 10.1.2 Experiment 1: Color-motion pairing and perceptual transparency

On some occasions attributes can bind in more than one way, and segregation is necessary for correct interpretation of a scene. This may be caused by a top-down influence or contextual effect for resolving ambiguities, or a high-level selection of alternative outcomes of a binding process. Conversely, segregation itself might be directly involved in the binding process. To verify the latter possibility, we study a case in which the stimulus is not ambiguous, and consequently binding is computationally separate from segregation.

### Experiment 1a

We tested whether explicit segregation (motion transparency) facilitates binding. Observers were asked to view displays of either two transparent surfaces interleaved with blank periods (figure 54a), or two alternating single-colored surfaces (figure 54b). They were required to report the direction in that the surface defined by red dots moved. This task requires binding of color and global direction of motion. Both surfaces appear at the same location, thus location cannot be used to pair motion and color. When two moving surfaces are superimposed, transparency subserves as an explicit cue for segregation (Nakayama, Shimojo and Ramachandran 1990; Watanabe and Cavanagh 1993) In the alternating condition one surface is displayed at a time and it seems that segregation is not perceptually as strong as in the transparent condition.

In theory, segregation is not necessary for performing the task. Computationally, segregation is less efficient than directly looking for the correspondence between color and direction of motion. Observers might alternatively be able to selectively attend to a particular color or direction to do the task. However, if binding requires segregation then we predict that color-motion pairing will be impaired if the segregation between the two surfaces becomes weak.

### Stimuli and Procedure

Stimuli are illustrated in figure 54a,b. Random dot patterns (red/green) were presented inside a 5.7° x 5.7° square area on a black background. Each surface consisted of dots (3.5 arcmin) with 2.5% density moving coherently with velocity of 4.85° /s on the black background. Observers (*n* = 14, all naïve) binocularly viewed the display for 1180 ms from a distance of 54 cm.

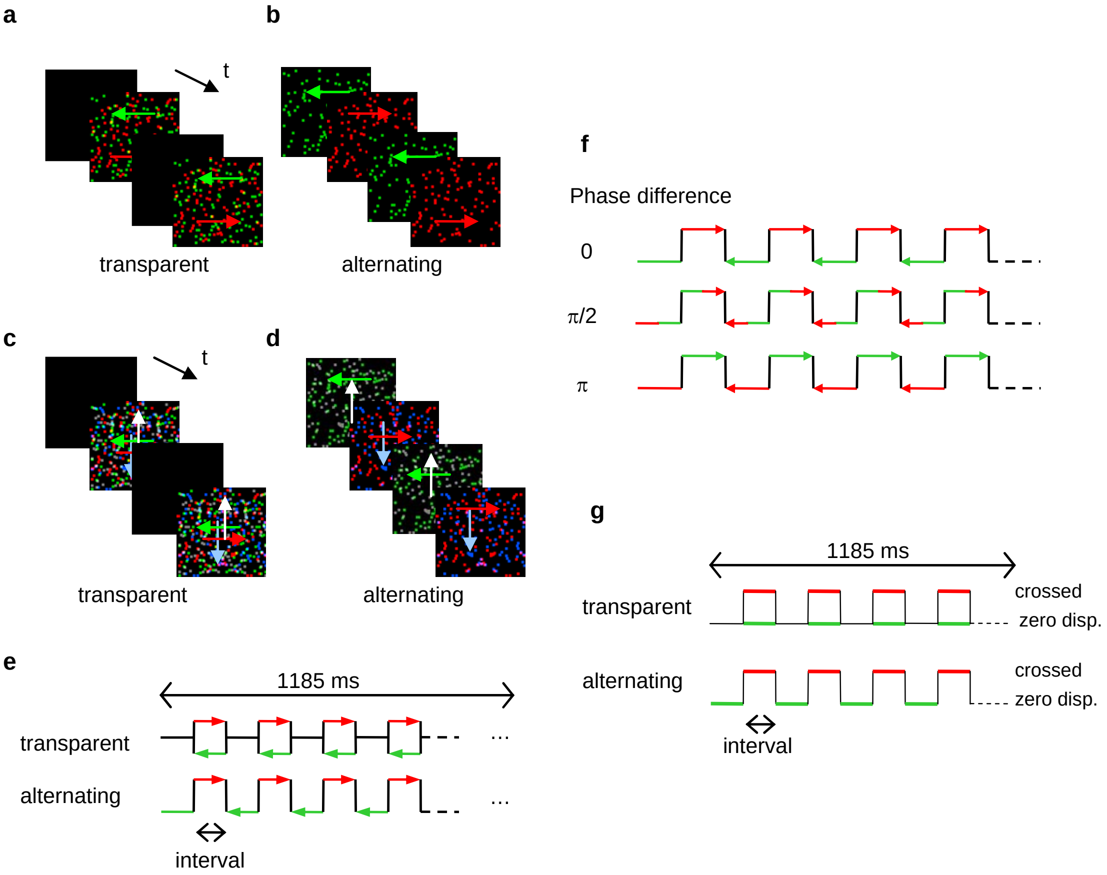

**Figure 54.** Experimental paradigms.

a,b) Color-motion binding for transparent (a) and alternating (b) surfaces in experiment 1. Observers were asked to report the direction of the red dots.

c,d) Experiment 2: the two additional surfaces (gray, blue) are irrelevant to the task. Participants were asked to report the direction of the red dots. In ***c*** all four surfaces were superimposed (transparent). In ***d*** two superimposed surfaces were alternated.

e) Experimental paradigm.

f) Temporal asynchrony between color and motion (compare to Moutoussis & Zeki 1997). In this example, observer should report red is moving right.

g) Binding between disparity and color information (experiment 3). Two surfaces were presented at zero or 20' disparity planes.

The red and green dots were turned on and off either simultaneously (transparent condition) or in opposite phase (alternating condition). Participants were asked to press a key to indicate the direction of the red dots (left vs. right) after each trial. Trials were randomized for direction, transparency, and interval (SOA of 60, 120, 240, 360 ms). Each participant performed 40 trials per condition.

**Results**

Observers correctly reported the direction of the red surface in most trials (>98%) for transparent surfaces, regardless of the frequency of alternation (figure 55a). In contrast, subjects performed near chance (50%) when two surfaces were alternated every 120 ms. The interaction between transparency and interval was highly significant (3-way ANOVA, $F(3,40) = 19.56$, $p < 0.0001$). The pattern of results was consistent across observers (figure 55b). There was significant difference between transparent and alternating condition ($F(1,40) = 81.35$, $p < 0.0001$), and between different intervals ($F(3,40) = 17.2$, $p < 0.0001$).

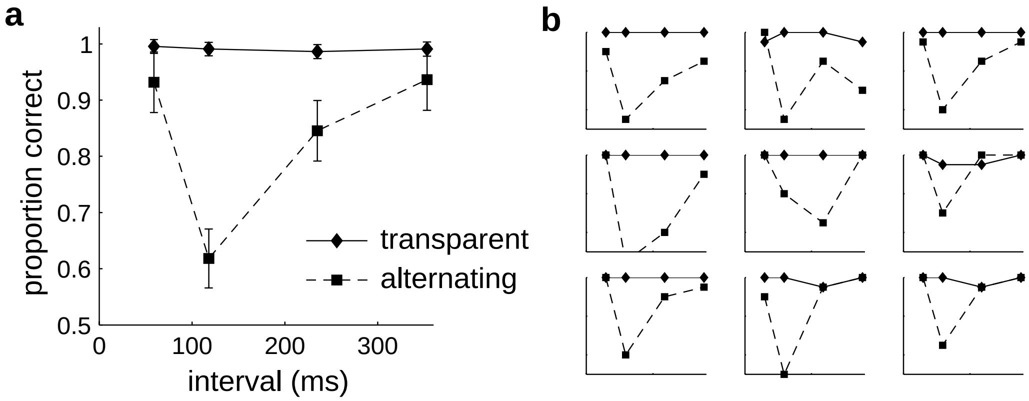

**Figure 55.** Binding in alternating and transparent displays.

a) Average performance plotted as a function of rate (interval between alternations) in experiment 1.

b) Individual plots of nine participants (same axes as in a). Each dot is the average of 20 trials.

In the transparent condition, both surfaces are displayed at the same time. The relative motion between the two surfaces may confound the task. Can the higher performance in the transparent condition be attributed to the presence of relative motion in this condition? To rule out this possibility we introduced relative motion in the alternating condition. Nine naïve observes were tested in a separate experiment in which a fixed gray random dot surface was superimposed over the original alternating stimuli. The average performance for the 120 ms interval was 59.4 ±4.8 % (mean ± S.E.M.), which did not show any significant improvement compared to the original experiment (57.2 ± 5.8 %, $p > 0.38$, one tailed t-test).

### Experiment 1b

Can observers' failure in the case of 120 ms interval be due to asynchronous processing of color and motion (Moutoussis and Zeki 1997)? If color is processed faster than motion then alternating motion before color (figure 54f) should compensate the difference in latencies and consequently should improve pairing.

To test this possibility, we varied the phase between color and motion. Four naïve observers participated in this experiment. Stimuli and setup were similar to the alternating condition in experiment 1, except that color and motion were alternated with different phases (20 trials/observer for each data point). Three intervals (94, 120, and 140 ms) were tested. The order of trials was randomized. Observers were asked to report the direction of the red surface.

### Results

The performance was around chance level for all phases and intervals, and did not improve by changing the phase between color and motion (figure 56). Evidently, impaired pairing cannot be attributed to a fixed latency difference between disparity and color processing.

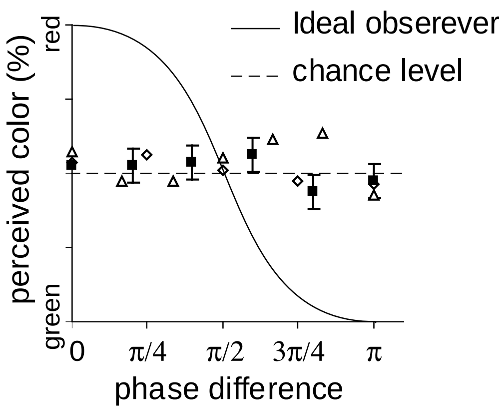

**Figure 56.** Impaired binding in rapidly alternating displays.
Asynchronous presentation of color and motion (experiment 1b) did not improve pairing for 94 (diamond), 120 (square), or 140 ms (triangle) intervals. The performance of an ideal observer (based on temporal information) is depicted as an ogival curve.

**Discussion**

Color-motion pairing was impaired in the alternating condition for the 120 ms interval, whereas it was intact in the transparent condition. For longer alternation intervals, colors and directions appeared separable to some extent (based on temporal cues), but observers still failed to correctly pair them in a significant number of trials.

The results support the claim that if binding and segregation are related, then providing an additional segregation cue should facilitate binding. Apparently, alternating the two surfaces does not provide a strong cue for surface segregation compared to transparency, although rapid alternations can be accompanied by a sense of transparency (Holcombe 2001). For the 60 ms interval, observers reported that the alternating surfaces were perceived as transparent. Consequently, the performance was high and comparable to the transparent condition.

What causes the impairment of veridical motion color binding? Misbinding of alternating features cannot be attributed to a fixed neural latency difference for color and motion (Moutoussis and Zeki 1997), as performance was high for the shortest interval (60 ms), never dropped below the chance level, and presenting one attribute in advance did not improve the pairing for the 120 ms interval. The performance increased with longer alternation intervals (figure 55a), suggesting that observers could utilize temporal cues at lower rates (Nishida and

Johnston 2002). They suggest that observers simply note which color and which direction appear at the same time, but at higher rates they fail to keep track of the order of the attributes.

Nonetheless, in the absence of temporal binding cues in the transparent condition observers performed almost perfectly. Our results indicate that temporal cues are not necessary for feature binding in general, even though they may play a role for slowly alternating stimuli.

It is worth emphasizing the significance of the difference between performance in the transparent and alternating conditions. Previous studies have reported dependencies between pairing and frequency of alternations (Clifford, Arnold and Pearson 2003; Holcombe and Cavanagh 2001; Moutoussis and Zeki 1997; Nishida and Johnston 2002), and suggested different mechanisms to explain the dependencies. However, none of the suggested models mentioned earlier address the role of transparency or segregation in binding.

### 10.1.3 Experiment 2: Transparency cues improve binding

#### Experiment 2a

The results of experiment 1 suggest that segregation cues improved the performance associated with feature binding. There are two possible arguments against this interpretation: First, binding mechanisms for transparent surfaces might be inherently different from sequential alternation. This was partly ruled out by the control experiment in 3.1.2. Second, although a fixed latency difference by itself cannot account for the results, in experiment 1 we cannot rule out a contribution of the different temporal dynamics for color and motion pathways (Clifford *et al.* 2003). Thus, the different temporal relation between the two surfaces in the transparent and alternating conditions is a possible confounding factor.

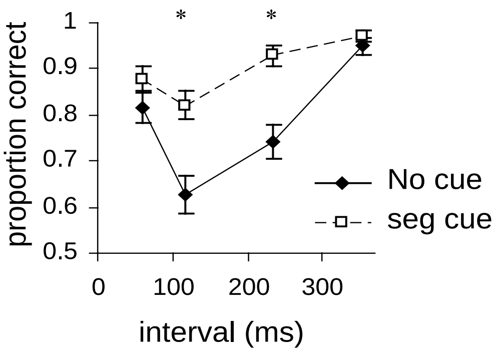

**Figure 57.** Results of experiment 2a. Adding a transparency cue (5% of the dots) significantly improved pairing in the alternating condition. * $p < 0.05$

To address these issues, we introduced transparency in the alternating condition. We have already shown that the performance in the absence of transparency is low for the 120ms interval. Does surface transparency without modifying the temporal structure of the stimuli improve pairing? More specifically, how does pairing performance improve when transparency serves as a cue for a) direct segregation between red and green surfaces, or b) indirectly (i.e., transparency is irrelevant to the task) as a constraint for segregation. The latter case is interesting because it requires an internal representation of multiple surfaces.

### Stimuli and Procedure

Two horizontally moving random dot patterns (red, green) were presented alternatively, similar to alternative condition in experiment 1a. Six naïve observers were asked to report the direction of the red dots. In half of the trials (no cue condition), no transparency cue was included in the stimuli. In the rest (segregation cue condition), 5% of the dots on each surface were gray and remained visible during the whole trial (1.2 s). Trials were randomized for direction, transparency, and interval (SOA of 5, 10, 20, or 30 frames).

### Results

The stimulus in the no cue condition was identical to the alternating condition in experiment 1a. As expected, in the absence of any explicit surface segregation cue the pairing was impaired for the 120 ms and 240 ms intervals (figure 57). Adding a transparency cue significantly improved performance (3-way ANOVA, $F(1,15) = 34.35$, $p < 0.0001$). There was also a significant interaction between the interval and presence of a cue ($F(3,15) = 3.59$, $p < 0.05$). Results confirm that explicit surface segregation can facilitate binding.

### Experiment 2b

experiment 1 was modified by adding two vertically moving (orthogonal to the target) or stationary surfaces with different colors (blue and gray, figure 54c,d). One target-distracter pair was alternated with the other target-distracter pair with a variable interval (figure 54d). The transparency cue is irrelevant for discriminating between red and green surfaces. We claim that the segregation constraints posed by transparency facilitates feature binding. If the addition of the irrelevant transparent surfaces indeed improves the performance of motion-color binding (compared to experiment 1), our claim would be supported.

### Stimuli and procedure

The stimuli and procedure were identical to experiment 1 except that distracter surfaces with the same dot density were added in order to introduce a transparency cue (figure 54c, d). The two additional surfaces had a color of either blue or gray at near equiluminance moving vertically (up or down). In the alternating condition, the red and green surfaces were presented alternatively superimposed on one of the distracter surfaces. In the transparent condition, all four surfaces were simultaneously displayed, followed by a blank screen for the same duration. The sequence was repeated for 1180 ms. Fourteen naïve participants (same as experiment 1a) were asked to press a key to indicate the direction of the red dots (left vs. right) after the trial. The order of the experiments 1a and 2b was counterbalanced between these participants.

The coincidence of the orthogonal patterns may arguably provide an additional cue for binding, that is, the target direction can be inferred from the direction of any of the distracters. To avoid this possibility, we randomized the sequence in which distracting colors appeared in each trial for a subset of observers, so that the distracters did not contain information about the target. In another control experiment, we used stationary dots in the alternating condition. In experiment 1b we showed that adding stationary dots per se has little effect on pairing performance. This experiment was conducted on five (4 naïve) participants.

### Results

In the transparent condition, the performance was slightly lower compared to experiment 1, demonstrating the increased difficulty of the task. Overall, observers still performed better in the transparent condition compared to the alternating condition (3-way ANOVA, $F(1,27) = 21.27$, $p < 0.0001$). The performance depended on the interval ($F(3,27) = 4.5$, $p < 0.011$), although this effect is smaller compared to figure 55a. Although the patterns of results seem different in the transparent and alternating conditions, the interaction between transparency and interval was not significant ($F(3,27) = 1.59$, $p > 0.2$).

Despite the increased complexity of the stimulus, observers performed significantly better in the alternating condition for the 120 ms interval compared to experiment 1 (figure 58a, $p<0.0001$, HSD post hoc test). The higher performance due to additional segregation cues corroborates our interpretation of experiment 1 that segregation cues improve feature binding. Furthermore, the results show that feature binding is improved by transparency, regardless of its task relevance. Figure 58c depicts the performance of each subject in experiment 2 compared to experiment 1. We analyzed results of both experiments together and found significant interaction between number of surfaces, interval, and transparency (4-way ANOVA, $F(3,37) = 7.34$, $p<0.001$). That is, adding irrelevant distracter surfaces significantly affected the difference between transparent and alternating conditions. In this case, pairing was improved for the alternating condition, and slightly deteriorated for the transparent condition.

It can be argued that orthogonal motion increases the saliency of the target surface, thereby enhancing performance. In the control experiment, alternating red and green surfaces were displayed with and without irrelevant stationary transparent surfaces. The results are shown in figure 58b. Irrelevant stationary distracters also resulted in improvement in feature binding. Observers performed significantly better for the 120 ms interval ($p$=0.0028, one-tailed $t$-test). The control experiment eliminates the possibility that orthogonal motion contributed to the better performance of feature binding.

### Discussion

Although observers carried out essentially the same task in experiments 1 and 2, and the pattern of presentation of red and green surfaces were identical, the correct feature binding for the alternating condition was considerably higher in experiments 2a and 2b. Transparency between distracter and target surfaces provides a cue for segregation in the alternating condition. Even though this cue is not directly relevant to the task in experiment 2b and increases the complexity of the stimulus, it facilitates pairing presumably by imposing a constraint for parsing input. Experiment 1 indicates that in the alternating condition (120 ms interval) the target surface cannot be effectively segregated from the subsequent surface which moves in the opposite direction (thus perception of the same surface moving back and forth). In experiment 2b, the target is tailed by either opposite motion, or orthogonal (stationary). However, the target cannot be grouped with both (transparency constraint). If the target direction is even briefly grouped with dots that are not moving in the opposite direction then the observer would be able to infer the correct direction. This would nicely account for the result obtained here.

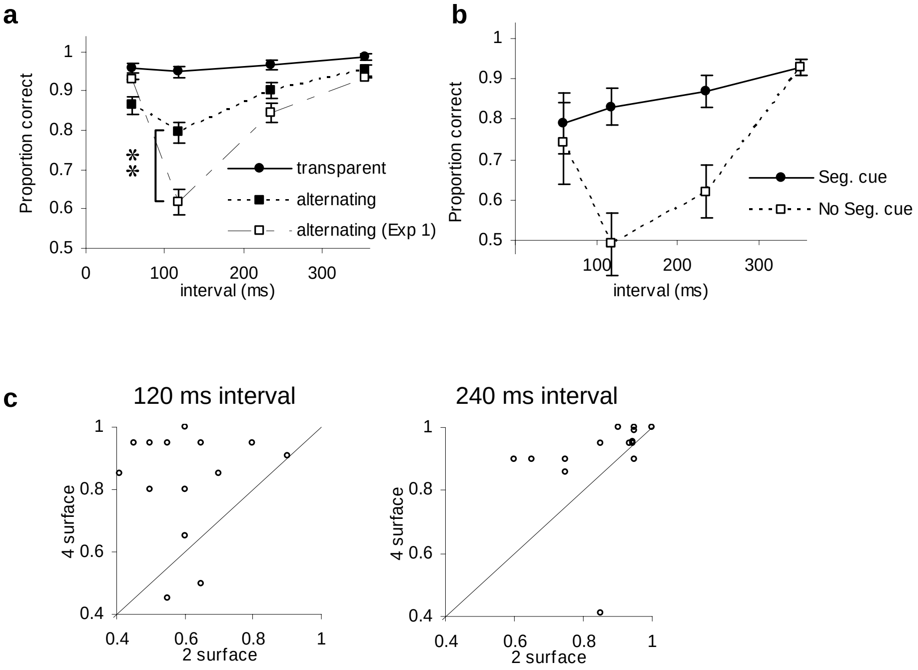

**Figure 58.** Pairing is more reliable when an irrelevant segregation cue is present. Participants were asked to report the direction of red dots.

a) Increasing attentional load can improve feature binding between color and motion. Four surfaces are displayed instead of two in experiment 1. Open squares in the graph depict the performance in the 2-surface condition for comparison.

b) A similar result was obtained in five observers using stationary surfaces.

c) Results of 14 participants (a) are plotted against their performance in experiment 1a for the 120 ms and 240 ms alternating conditions.

### 10.1.4 Experiment 3: Pairing color and disparity

In the previous two experiments, we showed that the binding between motion and color is facilitated in the transparent condition compared with alternate presentation of each surface. Is this a general principle in binding or limited to color and motion? To examine the generality of the effect, we examine the binding between depth and color. Unlike direction of motion, many cells in area V4 are selective to disparity (Felleman and Van Essen 1987;

Watanabe *et al.* 2002). Hence, binding disparity and color might involve a different mechanism than motion-color binding. We segregated the two surfaces by putting them in different depth planes. Two random-dot stereograms (green vs. red) were superimposed to form perceptually transparent surfaces, or were presented in alternation (figure 54f).

### Stimuli and procedure

Participants viewed two superimposed random dot stereograms (6.7 deg × 6.7 deg, density = 4%, dot size = 2 arcmin, disparity = 0 vs. 20 arcmin) through a mirror stereoscopic system. The distance between each image and the observer's eyes was 46 cm. To help fusion and provide a reference, a static zero-disparity black-and-white random dot pattern (width = 1.65 deg) surrounded the stimuli. Observers were asked to report whether the red surface was in front of the background or not. Trials were randomized for depth, transparency, and interval. Three naïve observers and the author (FM) participated in this experiment.

### Results and discussion

Observers performed almost perfectly in the case of transparent surfaces. In the alternating condition, the error rate was small when rapid alternation of the planes induced perceptual transparency (except for one subject), but the responses deteriorated significantly for longer intervals (figure 59). It is worth mentioning that the red and green planes are presented at *spatially* (depthwise) distinct locations. Yet, observers could not fully exploit the depth cue when the interval between alternations was about 100 ms or more.

In general, the results show a similar pattern to experiment 1. Pairing between color and disparity is efficient when the pairing is supported by a transparency (segregation) cue. In contrast, pairing is impaired when the same stimuli are presented for the same duration but there is no explicit segregation cue.

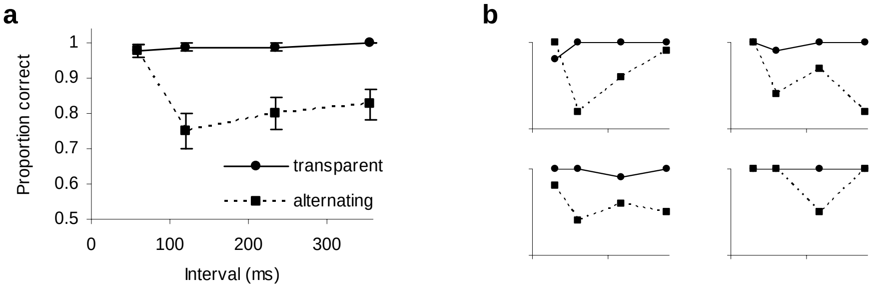

**Figure 59.** Binding between disparity and color information.

a) Average results (experiment 3, n = 4). Two surfaces were presented at zero or 20' disparity planes.

b) Individual plots of each participant.

### 10.1.5 Attention and conjunctive representation of attributes

Experiments 1–3 demonstrate that binding is easy when an explicit cue for surface segregation is present. Thus, we argue that binding and segregation are related. In the following experiments we examine whether feature binding and segregation occur at the same level of visual processing, or they involve different (but perhaps serially linked) processes.

#### Binding and attention

Illusory conjunctions can occur in normal observers under increased attentional load (Treisman 1977). Spatial (Treisman 1988; Treisman and Gelade 1980), feature (Saenz, Buracas and Boynton 2002; Saenz, Buracas and Boynton 2003; Simons and Chabris 1999; Treue and Martinez Trujillo 1999), surface (Mitchell *et al.* 2003; Valdes-Sosa, Cobo and Pinilla 2000), and object-based attention (Duncan 1984; Duncan 1993; Duncan and Nimmo-Smith 1996; Kahneman and Henik 1981) have been suggested to mediate binding of high-level feature representations. In these accounts, segregation is imposed by top-down attention. Evidence from patients with parietal damage (Ashbridge, Cowey and Wade 1999; Friedman-Hill, Robertson and Treisman 1995; Robertson *et al.* 1997), transcranial magnetic stimulation (Ashbridge, Walsh and Cowey 1997; Walsh *et al.* 1999), and functional brain mapping in normal observers (Corbetta *et al.* 1995; Shafritz, Gore and Marois 2002) indicate the involvement of the parietal lobe in feature binding. Thus, top-down mechanisms mediated by the parietal cortex appear to be important for segregation or feature binding, or both.

### Preattentive mechanisms in feature binding

There is evidence suggesting the possibility that a weak form of feature binding can be executed pre-attentively, based on coarse location cues (Cohen and Ivry 1989; Keele *et al.* 1988), or implicit mechanisms (DeSchepper and Treisman 1996; Egly *et al.* 1995). Neurons in inferior temporal cortex respond to complex combinations of features such as shape and color (Tanaka 1993). These studies indicate a complex representation of visual entities in which combination of multiple attributes is explicitly represented. Such representation is suggested to be pre-attentive and early (with the exception of inferior temporal neurons) before different attributes of visual input diverge into distinct cortical areas.

We suspect that some of the controversy surrounding the role of attention in feature binding might reflect the difference between binding and segregation. In the following experiments we therefore dissociate segregation and binding. In experiment 4 we verify that surface segregation is early and pre-attentive. In experiment 5, we provide evidence that binding between different features (motion and color) follows surface segregation with considerable temporal delay. In experiment 6, we will show that the registration of feature-conjunctions requires top-down attention. Results of experiments 4-6 contrast early pre-attentive surface segregation and late attentive feature binding.

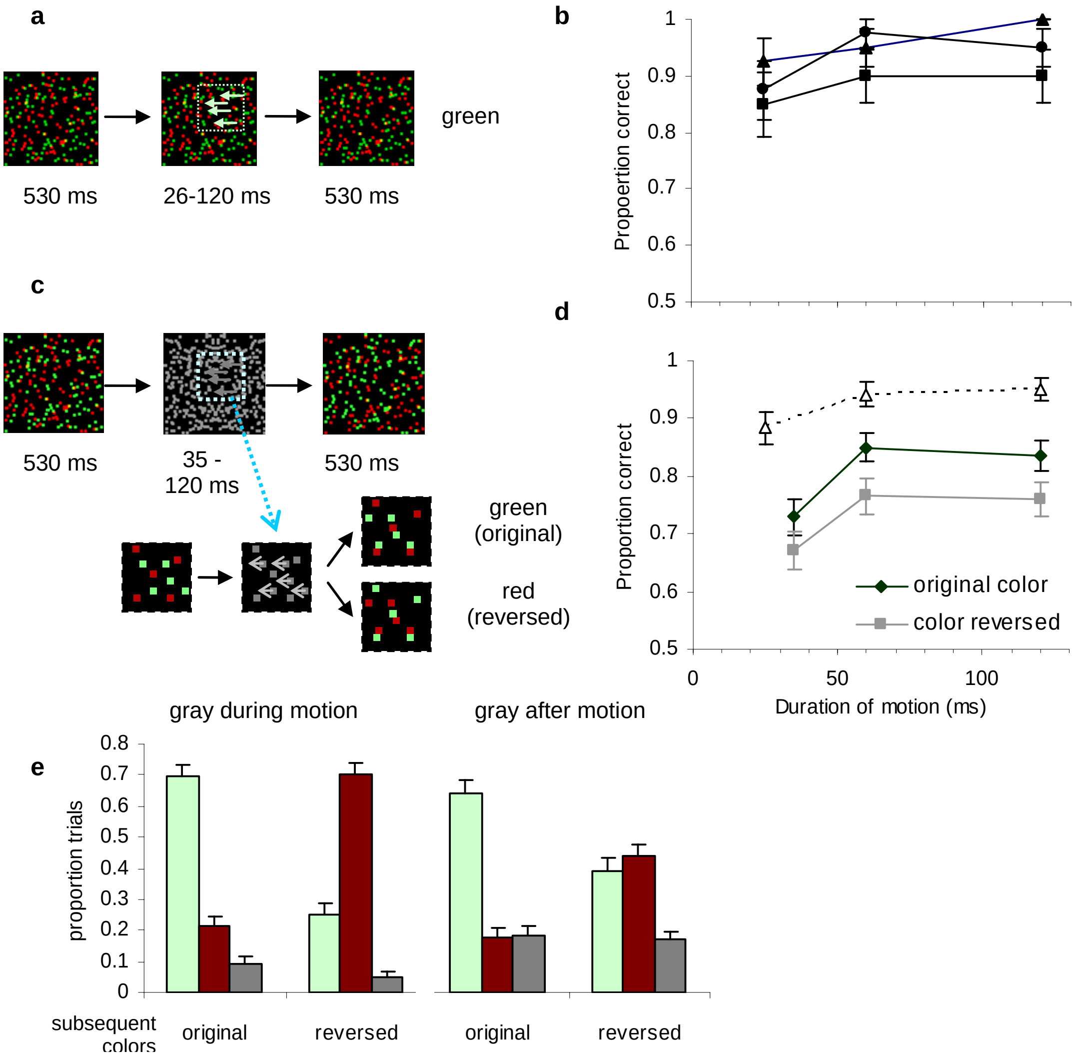

**Figure 60.** Persistence of surface after motion.

(a) After 530 ms, all green dots inside a square (invisible boundaries) move left for 26-120 ms (experiment 4).

(b) Performance vs. duration of motion for three observers. The performance is high even for the shortest duration.

(c) Experiment 5: all dots turned gray before motion onset. The dots that were originally green moved left. After the motion, dots either turned back to their original color or switched colors.

(d) Observers nearly always reported the final color of the dots (considered as the correct response). Dotted line depicts performance in experiment 4.

(e) Four naïve observers were asked to report the color of the moving pattern. The moving dots were turned gray for 60 ms during or after motion. The green bar represents the trials in which the original color was reported, the gray represents trials in which observers reported gray.

### 10.1.6 Experiment 4: Brief motion display

Two similar random dot patterns are superimposed, and one of them briefly moves. When both surfaces are stationary, observers cannot distinguish between them (figure 60a). However, the two surfaces become perceptually separable when one starts moving. As the motion stops, the separation disappears.

If top-down attention is necessary for segregation of the surfaces and registration of the different attributes of each surface, then motion needs to be presented long enough for attention to select one of the surfaces (or its points). If the representation is pre-attentive, then the target surface will be detectable even for short display durations, even when the location of the pattern is not known.

#### Stimuli and procedure

Initially, two stationary random dot patterns (red, green) were superimposed on the display. Around 520 ms after the onset of the trial, dots of one of the two surfaces inside a randomly located square region (2.8 deg × 2.8 deg) moved (4.85 deg/s) briefly and then stayed at their final location for another 520 ms (figure 60a). Four naïve participants were asked to report the color and direction of the motion (4 choices). The duration of motion was varied from 24 ms to 120 ms (including the first and last frames). Location, color, and direction of motion were randomized and were not known beforehand.

**Results**

Direction was accurately reported (>98%) for all durations. Observers also accurately reported the color of the dots for all durations as well (figure 60b, chance level is 50%). The location of the target was not known before motion began. A shift in attention conceivably requires 50 ms or more (Shepherd and Muller 1989). Yet, all participants performed better than 85% correct for the shortest duration (24 ms), which was a one-pixel displacement. Thus, segregation of the target does not seem to require involvement of top-down attentional mechanisms. Performance was slightly increased for longer presentation times (60–120 ms). An increase in performance can be attributed to the increased saliency of the motion for 60 ms compared to 24 ms.

There are at least two possible explanations for these results: either the brain can bind color and motion information pre-attentively (Holcombe and Cavanagh 2001), or the surface could form a trace in observer's brain (similar to iconic memory). In the later case, the internal representation of the surface lasts longer than the attribute (i.e., motion) that had defined it.

### 10.1.7 Experiment 5: Persistence of motion-defined surface

Here we examined if color and motion attributes are paired and encoded together pre-attentively. It may seem counterintuitive that while a presentation duration as short as 24 ms was sufficient for correct binding in experiment 4, a 120 ms interval in the alternating condition in experiment 1 was not. A critical difference in these two experimental conditions is that in the alternating condition in experiment 1, a new surface was presented at every interval. Thus, the persistence of the same dots on the screen after the motion (or the presence of the dots before the motion onset) might have contributed to the results in experiment 4.

We assessed such contributions by modifying the paradigm as follows. During the motion the patterns turned gray (preserving luminance and dot locations). After the motion, colors were presented again. Participants were asked to report the color and the direction of motion of the moving dots. During the motion, the two patterns are perceptually segregated. If binding is early then we predict that color would be perceived as gray. However, if the representation of the target surface persists after motion offset then it would be affected by subsequent colors and that would be reflected in the responses.

### Stimuli and procedure

The stimuli were the same as in experiment 4. Dots of one of the two surfaces inside a square region moved for 60 ms. To discourage attending to local features, the location of the square was randomized across trials. Dots turned gray either during or after motion. In half of the trials, dots turned back to their original color. In the remaining trials (reversed condition), the colors were swapped (i.e., dots that were originally red become green and vice-versa, figure 60c).

Four naïve observers were asked to report the color of the moving dots, ignoring the color that appears before or after the motion (3-AFC: red, green, or gray). Observers were explicitly informed that the color may change before or after motion. In a separate experiment, we varied the duration of motion (36, 60, or 120 ms). Five naïve observers were asked to report the color (2AFC: red, green) and direction (left, right) of the dots that had moved.

### Results

Figure 60e depicts the results of the experiment. Observers failed to notice that the moving dots were gray. In fact, gray was mostly reported (in less than one-fifth of trials) when it appeared after motion offset. The phenomenally perceived color often matched the color physically presented following the motion. There was significant interaction between reversal and perceived color (3-way ANOVA, $F(2,36) = 13.67$, $p < 0.0001$), regardless of whether gray appeared before or after motion ($p > 0.3$).

A similar pattern was observed for other durations. In the majority of the trials, the reported color of the target "dots" matched the color that appeared after motion offset (i.e., the new color). Observers reported the new color significantly better than chance ($p < 0.0001$, figure 60d), although their performance was somewhat worse than figure 60b. The performance depended on the duration of motion ($F(2,22) = 9.76$, $p < 0.001$), and was lower for 36 ms duration ($p < 0.005$ HSD post hoc test), but was the same for 60 ms and 120 ms motion ($p > 0.9$). Even for the shortest duration, observers still performed significantly better than chance in reporting the color that was applied to the surface after motion offset.

The probability of reporting the new color was lower when it was not the same as the old color for all durations studied ($F(1,22) = 11.13$, $p < 0.003$), indicating that the color of the surface before motion onset influences its perceived color. The direction of the target was reported correctly in almost all trials, regardless of the reversal of the color. Surprisingly, participants did not notice that the moving surface was gray when they were questioned after the experiment.

### Discussion

These results demonstrate that the perceived color of the target is mostly determined by what is displayed a hundred milliseconds or so later. Positional cues cannot account for such result, because the location of the target was not known a priori, and moving dots were superimposed on non-target stationary dots. Even if observers could individualize a single dot (i.e., as a single object), they clearly misbound color and motion. Overall, experiment 5 suggests that color information is integrated over a temporal window which extends over a considerable period of time and is biased toward later times relative to motion (i.e., the perceived color at time $t_0$ is influenced by inputs in the interval $[t_0, t_0+a]$, the temporally weighted average is perceptually projected back in time to $t_0$). Thus, in the absence of segregation cues (transparency), the subsequent colors presented on the screen affect the perceived color of each surface. This temporal shifting and smearing presumably contributes to the reported perceptual asynchrony in other studies (Moutoussis and Zeki 1997) and the failure of observers to pair correctly in the alternating condition in experiment 1.

### 10.1.8 Experiment 6: Conjunctive search for motion-color

Although visual entities can be segregated pre-attentively (experiment 4), attention may be still necessary to access the attributes of the surface. This was examined using a visual search paradigm. Four items (moving surfaces) were presented on the screen. Three items had the same color. Participants were instructed to locate the odd one. To examine whether conjunctive search for motion-color is serial or parallel, we varied the duration of the presentation. Experiment 4 demonstrates that observers could report the color even for stimuli as brief as 24 ms. If the search is parallel, then the performance should not be affected by increasing number of targets for the short motion display. If binding is pre-attentive as proposed by (Holcombe and Cavanagh 2001), then the search should be easy and parallel. If the task requires serial deployment of attention to the four items, then the observers' performance will be low for 24 ms display, and increase if presentation time is increased.

It has been suggested that the visual system can direct attention to stimuli with common motion (Driver, McLeod and Dienes 1992; McLeod *et al.* 1991). One may expect then that performance increases when all patterns move in the same direction compared to trials when each item moves in a different direction (that is, if attention to a particular direction of motion is involved in binding).

We contrast the odd color search with a guided search task to control for the particular stimulus parameters. In a separate experiment (guided search), the target was always moving upward and distracters were moving horizontally. Observers were asked to report the color of the target dots. Thus, the direction of motion provides the cue for the location of the target. Since the upward motion pops out, attention needs to be directed to only one location, unlike the search task in which at least three locations should be examined to find the odd target. Because the stimulus parameters are the same in both experiments, any difference in the performance should be attributed to the difference in attentional requirements of the two tasks.

### Stimuli and procedure

Experiment 6 was similar to experiment 4, except that dots moved in four 2.3° x 2.3° square regions in the four quadrants (figure 61a). In each square, all dots with a specific color moved coherently. The rest of the dots (different color) remained stationary. In one of the quadrants, the color associated with moving dots was different from others, and five naïve participants were instructed to report that quadrant (4AFC). One of the patterns always had a different color than the other three. In half of the trials, dots moved in the same direction in all four squares. In the remaining trials, each location moved in a different direction.

In the control experiment, dots moved vertically inside one square and horizontally inside the others. Participants were asked to report the color of the dots moving vertically. The stimulus parameters were the same as in the search experiment.

The two superimposed random dot patterns were displayed for 520 ms before and after motion. The duration of motion was varied from 24 ms to 355 ms. Observers were asked to report the location of the odd pattern.

### Results

In the visual search task, participants performed near chance for the shortest duration. Their performance increased with longer search display durations, consistent with a serial

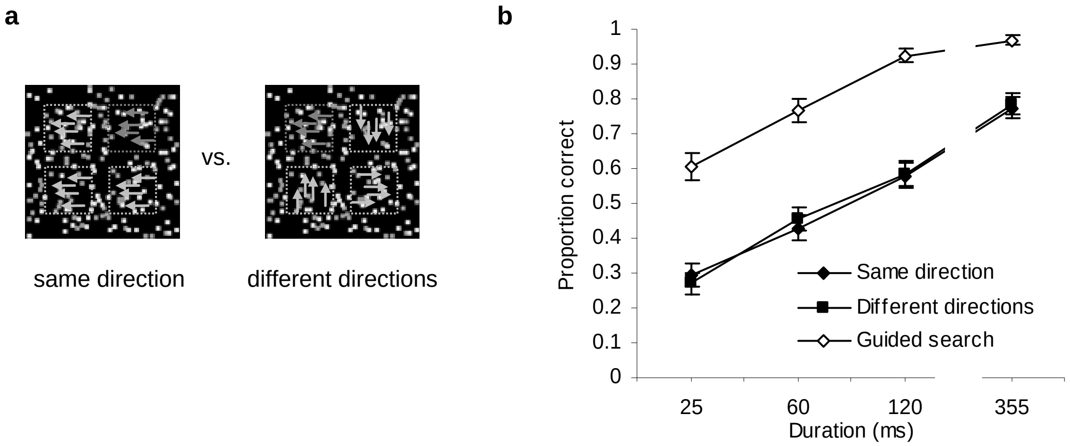

**Figure 61.** Color-motion conjunction search.

a) Visual search stimulus (experiment 6). In one of the quadrants, moving dots have a different color.

b) The serial nature of the search, as marked by an increase in performance with time, suggests that attention is necessary to register surfaces' color. Open circles (o) depict the performance of subjects in reporting the color of the target defined by upward motion (control experiment).

strategy for searching (figure 61b). Observers correctly reported the target location in about 78% of the trials for the longest duration (355 ms), and only in 58% when the motion duration was 120 ms. In the control experiment observers could accurately report the color of the target in more than 92% of the trials for the same motion duration (given this performance observers should have been able to perform better than 77% in the search task for 120 ms motion if one assumes that binding does not require attention).

Earlier reports suggest that visual search for shape is performed in parallel among stimuli with a common motion (McLeod, Driver and Crisp 1988; McLeod *et al.* 1991). However, we did not find any difference between the condition in which all targets moved in the same direction, and the condition in which each item had a different direction. In both conditions, the conjunction search for color-motion requires considerably longer exposure for four items than one item (experiment 4), compatible with a serial search strategy. Thus, attention to the common direction of motion does not facilitate binding between color and motion.

A similar argument can be made about grouping. When all dots move in the same direction, they can be grouped together as one surface. If observers could attend to this surface then the odd location would have become immediately apparent, independent of the set size (Nakayama and Silverman 1986). However, the result indicates that search was serial. Thus the segregation trace observed in experiments 4-6 is local, presumably before stimuli are grouped into a surface.

### 10.2 General discussion

We examined the role of spatiotemporal segregation cues and attention to a particular feature, in binding feature and spatiotemporal properties. Participants were asked to pair color and direction of motion for two alternating or superimposed surfaces, at the same location. While subjects could hypothetically use temporal cues or attend to a particular feature, they were severely impaired when shown alternating surfaces at a presentation rate of 4.25 Hz. Visual stimulus synchrony has been suggested to facilitate binding (Usher and Donnelly 1998). Our results indicate that binding cannot be solely based on temporal coincidence. However, with a low rate of alternation (~2 Hz or less), temporal cues can be used to segregate alternating stimuli in a sub-optimal way. Pairing improved at a higher rate (8.50 Hz) and when surfaces were presented simultaneously. A similar result was demonstrated in the case of disparity and color.

Impaired pairing of color and motion for alternating (4.25 Hz, experiment 1b) surfaces indicates that visual attributes that appear synchronously at the same location and time are not necessarily bound together. Transparency by itself had little effect on binding (experiment 1a control). Nonetheless, pairing improved when the transparency cue invoked segregation of the scene into target and distracter surfaces (experiment 2a,b): different attributes were consistently redistributed to two or more apparently superimposed layers (Watanabe and Cavanagh 1993). Thus, the visual system is able to construct reference representations (i.e., of visual entities such as objects and surfaces) that encode combinations of attributes, after which binding becomes possible. We propose this conclusion is applicable to surface segregation cues in general, not just transparency. Directing attention to one surface facilitates access to its attributes, and reduces interference from attributes that belong to others. Although attention might be necessary for registration of surface attributes (experiment 6), experiment 4 suggests that segregation of surfaces and their attributes precedes attentional binding (Nakayama, He and Shimojo 1995).

These representations are presumably formed in low-level visual areas, before location, color, motion, disparity, etc. diverge into distinct and separate functional processing cortical areas. It has been shown that the late response profile of neurons in V1 reflect figure-ground separation (Lee *et al.* 1998). Thus, dynamic neural assemblies in V1 might be a possible candidate for the online representations of objects and surfaces. Such representations are presumably created by top-down feedback from specific areas such as MT (Castelo-Branco *et al.* 2002; Muckli *et al.* 2002) which process the segregation cues.

Feature binding improved when distracting surfaces were added to the alternating condition. Pairing attributes for alternating surfaces is computationally easier than pairing transparent surfaces, and is definitely easier without distracting surfaces. Yet, observers performed better in the more difficult task than the easier one (figure 58). Despite increasing the attentional load, the distracters improved subjective segregation between target stimuli, facilitating subsequent binding of color and motion.

It can be argued that in experiment 1 observers rely on the color and direction of a few dots rather than the whole surface. One could see leftward-moving red dots in some local areas, and rightward-moving green dots in other local areas. Although this argument may explain how the participants performed accurately in the transparent condition, it fails to account for the difference between the alternating and transparent conditions. Local cues are present for the same duration in both conditions. Yet, participants performed significantly better in the latter case. It is therefore unlikely that observers used local cues (i.e., a few dots) for pairing.

We further examined the relationship between surface segregation and binding by presenting two static superimposed surfaces and moving one of them briefly. Observers could correctly discriminate the color of the target surface, even when motion was too brief for feedback from top-down mechanisms. Therefore, segregation based on motion transparency appears to be early and pre-attentive. However, we demonstrated that the color does not even need to be present during the motion (experiment 5). Color and motion are bound together as long as they are perceived as attributes of the same object. Experiment 5 indicates that feature binding occurs later in time, after segregation. Experiment 6 also demonstrates that unlike segregation, attention is necessary for binding in the displays used. Probably, the persisting low-level representation preserves interesting visual events for later analysis by attentional mechanisms.

### Temporal asynchrony and neural latency

It is suggested that high-level selective representations (such as those in color-selective and motion-selective areas) suffer from different latencies (Arnold and Clifford 2002; Arnold, Clifford and Wenderoth 2001; Moutoussis and Zeki 1997), or different temporal dynamics (Clifford *et al.* 2003) of independent streams of visual information. Moutoussis and Zeki (1997) reported a 50–100 ms bias where a color change is perceived to occur earlier than a motion change. They argued that the bias reflects the differences in the latencies of color and motion processing that precedes binding. In contrast, early-representations (e.g., V1) are immune to such perceptual asynchronies and therefore, are efficient for high rates of presentation. Holcombe and Cavanagh (2001) tried to dissociate early (pre-attentive) and late binding by examining the temporal asynchrony in binding different aspects of visual stimuli. Using rapidly alternating colored orthogonal gratings, they found that color and orientation can be paired correctly for very short periods. Since their finding is not compatible with a model with late binding and different latencies for color and orientation they conclude that these features are encoded in combination.

Our results offer an alternative view which is not based on the latency difference. Experiment 1b and 5 indicate that in the absence of transparency or other explicit segregation cues color is integrated over time. In both cases, the visual system fails to prevent the integration of consecutive stimuli. At higher alternation rates (8 Hz), surfaces become segregated based on apparent transparency from motion. At lower alternation rates (2 Hz), binding can be based on the temporal pattern of stimuli. We propose that in the alternating condition the reversal of the direction of motion is the main cue used by the visual system for segregation of the target surface—observers seem to be able to accurately report if changes in color and direction are synchronous or not (Bedell *et al.* 2003; Clifford *et al.* 2003; Nishida and Johnston 2002). Therefore, they have access to the temporal information. We, however, assume that changing color, at least near equiluminance, is not salient for segregation. Experiment 5 indirectly supports this claim: most observers never or rarely observed the gray color when retrospectively asked). Segregation resets integration of colors, which necessitates that perception be delayed (Eagleman and Sejnowski 2000). Such temporal aspects of segregation and binding seem to explain impaired performance of the observers during 4 Hz alternation compared to the transparent condition.

Clifford et al. (2003) suggest a complex model which results in neural simultaneity for very short intervals (60 ms). Neural simultaneity exists in the transparent condition for all features, yet observers do not misbind color and motion. Furthermore, in experiment 1b we manipulated simultaneity by asynchronously presenting color and motion, yet the performance was independent of input asynchrony for the 120 ms interval. So, it is unlikely that simultaneity plays a role in such short intervals.

### Postdiction vs. different neural latencies

Experiment 5 demonstrates a perceptual lag between individualization of an object, and perceiving its attributes. A related effect has been described earlier for the location of a moving object at the time indicated by flashing a stationary marker (flash-lag illusion) (Eagleman and Sejnowski 2000; Nijhawan 1994; Nijhawan 1997; Sheth, Nijhawan and Shimojo 2000). The notion of different latencies has been used to explain the flash-lag illusion (Baldo and Klein 1995; Purushothaman *et al.* 1998; Whitney and Murakami 1998). However, the latency difference cannot reconcile the flash-lag illusion and color-motion asynchrony first reported by Moutoussis & Zeki (1997). The apparent latency for moving objects in flash-lag illusion is shorter than stationary objects (consistent with a processing advantage for the moving stimuli), whereas in color-motion binding, pairing improves if the direction of motion reverses 50–100 ms before changing the colors. That is, the apparent latency for motion is longer than color.

Conversely, the postdictive account is consistent with both phenomena. It has been suggested that in the flash-lag illusion, the perceived location of the moving object at the time of flash (temporal cue) is determined by the position of the moving object in a temporal window after the flash (Eagleman and Sejnowski 2000). Similarly, experiment 5 demonstrates that the perceived color attributed to motion is contaminated by subsequent colors in a 50–150 ms time window after motion offset. The surface defined by the motion persists and consequently permits integrating subsequent colors after motion has stopped. In our view, the lag between segregation and binding and the persistence of the surface after motion can account for the reported asynchrony between color and motion. We do not need to assume anything about different latencies for color and motion to explain asynchrony in binding.

It is worth mentioning that the persisting representation discussed here is different from shape from motion (Shioiri and Cavanagh 1992). Inferring a subsequent color camouflaged by random dots requires more than shape boundaries: the visual system should be able to individualize dots that moved from those that didn't. The short time-scale and the spatial specificity suggest that this representation is low-level. Indirect evidence for such low-level representation comes from transcranial magnetic stimulation of the occipital cortex: visual input to the stimulated cortex is not perceived. The location of the scotoma is well predicted by V1/V2 retinotopic organization. Interestingly, the scotoma is filled in with the color that follows the stimulation (Kamitani and Shimojo 1999). Thus, when occipital activity is disrupted, the new visual input overrides the old representation.

## Conclusion

We have dissociated segregation of visual input and perceptual binding. Combinations of visual attributes can be pre-attentively segregated and assigned to persisting low-level representations. Since features are encoded for each object separately, further asynchronous processing of color and motion by separate cortical pathways does not pose a binding-problem.

The results reveal that surface segregation precedes binding of color and motion. However once the visual scene is segregated, attributes that belong to the same visual entity (i.e., surface/object) are encoded concurrently as parts of the same representation that is formed in low-level areas. Such representations might not be readily available to visual awareness, and attention is employed for conscious registration of the corresponding attributes.

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