Eszter Turi, Yoni Smolin, Ilana Malekan

Short-term Adaptation of Primary and High-order Visual Areas – Psychophysical Experiments

Visual adaptation is a known phenomena induced when the visual system is exposed to the same stimulus for a prolonged time. When the stimulus is turned off one of the systems' calibration mechanisms are caught off-guard and visual perception is briefly perturbed. There has been a lot of research done regarding long-term adaptation and its effect but there is little known about short-term adaptation. In our study, we conducted for the first time a psychophysical experiment on short-term adaptation of primary and high-order visual areas. We generated adaptation by re-exposing the subject to the same image over and over. Subjects were instructed to perform a 'one-back-match' task, responding as accurate and as fast as they could by pressing the appropriate yes/no response button for indicating differences in the images shown. Both accuracy and response time aspects were analyzed. Our results indicate that short-term adaptation effect was achieved, and showed a high correlation with the results achieved by previous long-term adaptation experiments.

1. Introduction

Vision is the most dominant sensory modality of primates. Information passes from the retina to the lateral geniculate nucleus (LGN) from which it is sent to area V1 that is linked with area V2. Beyond these two large visual areas there is a large number of smaller cortical areas that contain neurons with selectivity to different parameters such as color, direction of motion etc.

Visual information is then divided into two paths known as the ventral and dorsal stream. The ventral "what" stream controls recognition, object representation and memory while the dorsal "where" stream runs motion and object locations.

A variety of experimental procedures has been developed for demonstrating the cortical architecture and the unique pattern of activation for each group of cells. In their pioneering electrophysiological studies of

Ezster Turi (1987), Csorna (Hungary), Hunyadi u. 23, Réva Miklôs Gimnázium, 4th grade

Yoni Smolin (1988), Nazareth Illit. (Israel), 2 Ziporen 6/8.

Ilana Malekan (1989), Muttontown NY 11791 (USA), 171 Woodhollovct.

SUPERVISOR: Anat Herbet-Grinfeld, Technion – Israel Institute of Technology, Haifa, Israel

monkeys and cats, Hubel and Wiesel worked out the appropriate light stimuli for various cortical cells (Hubel and Wiesel 1968). It was found that V1 has neurons with elongated receptive fields which respond best to simple stimuli such as bars, lines and edges. V1 neurons also have spatial-frequency selectivity and respond to luminance changes. Visual cortical neurons are highly tuned and specialized for processing a certain aspect of visual information such that any given neuron only responds to a subset of stimuli in its receptive field.

Recognizing an object in the human brain takes only a fraction of a second. The neural mechanisms underlying this remarkable ability are not well understood. Until the mid-1990s, little was known about the functional organization of human visual cortex. This landscape has changed dramatically with the invention of functional magnetic resonance imaging (fMRI), a powerful tool for the non-invasive mapping of the normal human brain.

Recent studies have shown that there are regions in the cortex which specialize in specific visual stimuli recognition. Using fMRI techniques, Malach and colleagues delineated an area that showed a preferential activation to images of objects, compared to a wide range of texture patterns (Malach *et al.* 1995). This area was termed the lateral occipital cortex (LOC).

Kanwisher and co-workers have suggested that this area, and some other regions located at the ventral temporal cortex, contain a limited number of modules specialized in specific category recognition such as faces (fusiform face area; FFA), places (parahippocampal area; PPA), and body parts (extrastriate body part area; EBA). (Kanwisher *et al.* 1997; Epstein & Kanwisher 1998; Downing *et al.* 2001)

The visual system is almost constantly exposed to new images and thus it is forced to adjust the visual coding to the characteristics of the image currently presented. Visual adaptation is a known phenomena induced when the visual system is exposed to the same stimulus for a prolonged time. Processes of visual adaptation manipulate the sensitivity of the cells in the visual cortex. Exposure to an adapting pattern for several seconds causes a decrease in the sensitivity of neurons tuned to the pattern's specific properties. This phenomenon lasts for a few more seconds after the stimulus is turned off, and thus defines the adaptation effect. In that period, the exposed subject recalls striking changes in perception of shape, color and motion. Adaptation involves a variety of visual attributes and stages of visual processing.

Long-term visual adaptation and its effects have been extensively studied for many years. It is known that due to adaptation our brain is forced to bias any new information to alternative non-adapted neurons which is why our perception is briefly perturbed. However, very little is known about short-term adaptation.

In our project, we intend to contribute to a better understanding of the phenomena of short-term adaptation, especially in primary visual areas and high order face-related regions. As we can see clearly, there is a hot debate on the neural mechanisms that are fundamental to face perception and yet, a major consensus regarding cortical areas that are most activated by viewing faces. Not even perception of simple stimuli such as bars is well understood. We, therefore, used 2D geometrical shapes with grayscale grating pattern and 2D grayscale face images as the most captivating and tuned stimuli. Our main assumption was that short-term adaptation affects the ability to receive and analyze new coming stimuli. In order to prove it, we conducted a psychophysical experiment testing the impact of short-term adaptation on subjects' ability to distinguish changes in contrast and figural properties of a stimulus.

2. Methods

Two psychophysical experiments were conducted which were aimed to find out the influence of short-term adaptation on the ability to note minor changes in the presented stimuli. It is important to note that without adaptation those modifications could be easily detected. The experiments were conducted serially as the order was controlled.

2. 1. Participants

Twenty subjects (eight males and twelve females) participated in the experiment, five of them were eliminated (two males and three females) due to some environmental factors while conducting the experiment. All of them were students at the age of 16-33 years. All were regular users of computers and had normal or corrected-to-normal vision. Except for one, all the subjects were right-handed. The amount of sleeping hours during the night before the experiment varied between 4-9 hours. Three of them have participated in psychophysical experiments before.

2. 2. Stimuli of the experiment on primary visual areas

To examine the effect of short-term adaptation in primary visual areas, stimuli were chosen which most activate the primary visual cortex. While constructing our experiment we used motives resembling to those found in previous research dealing with long-term adaptation. These kinds of stimuli are proved to activate mainly primary areas in visual cortex. We used four different shapes; each had four different types of modification (Figure 1): the original image, one with modified spatial frequency, both with original and different level of contrast. All modified parameters were controlled such that in each image the modification level is comparable to the other.

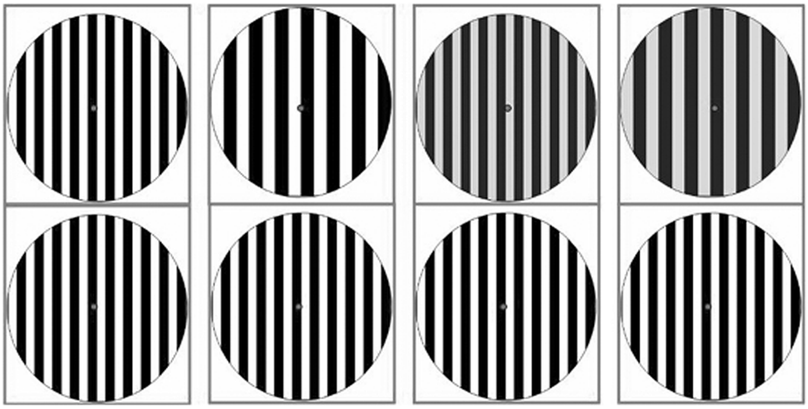

Figure 1.
Stimuli presentation – Primary Visual Areas
The four different "events" that were used. Bottom row-original images, upper row-different modifications that were applied to those images: (a) no modifications, presenting the same image again. (b) Spatial frequency modification. (c) Contrast modification. (d) A combined modification of both contrast and spatial frequency.

2. 3. Stimuli of the experiment on high-order visual areas

As our aim was to examine the effect of short-term adaptation in high order visual areas, we chose stimuli which most activate the high order visual cortex. As social primates, faces are the most common stimuli which we are exposed to in our life span. These kinds of stimuli are proved to activate mainly secondary areas in visual cortex. We decided to use unfamiliar faces to avoid any other effect. Four different images were used; each had four different types of modification (Figure 2): the original image, a modified face, both with original and different level of contrast. Face modification was performed using 'Morphases' program (www.morphases.com). All modified parameters were controlled such that in each image the modification level is comparable to the other.

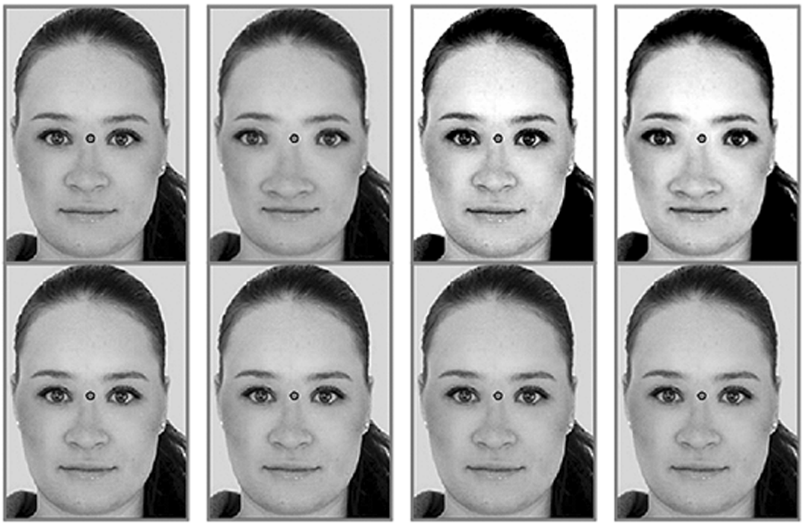

Figure 2.
Stimuli presentation – High Order Visual Areas
The four different "events" we used. Bottom row-original images, upper row-different modifications that were applied to those images: (left to right) no modifications (presenting the same image again), face properties modification, contrast modification, a combined modification of both contrast and face-properties.

2. 3. Presentation

The experiments were conducted using 'Presentation©' program package.

2. 4. Procedure

We were interested in the viewer's performances both in accuracy and speed aspects. Since there is a trade-off between the two, our instructions were to pay attention to both of them but accuracy should be more important than speed. Eight images were presented in a pseudo-random block sequence. Image presentation within each block was controlled in a way that preserves a constant ratio between different "events" (Figures 3-4). Subjects were asked to perform 'one-back-match' task.

Four different images were presented in four block types; in the first block adaptation was acquired by exposing the subject to the same image eight times. The second block was composed of images with only minor changes. The third one contained pictures with different aspects of modifications; original (non-modified), spatial frequency modifications, contrast modifications and with modifications both in contrast level and in spatial frequency. The purpose behind this approach was that these changes interrupted the adaptation so we could use the fourth block (which was quite similar to the second one concerning the types and numbers of different events) as a control. A fixation point was shown during the whole experiment. Visual epochs were alternated with 5-s blanks. Four cycles of the stimulus were shown (one for each image). Total time was 336 s.

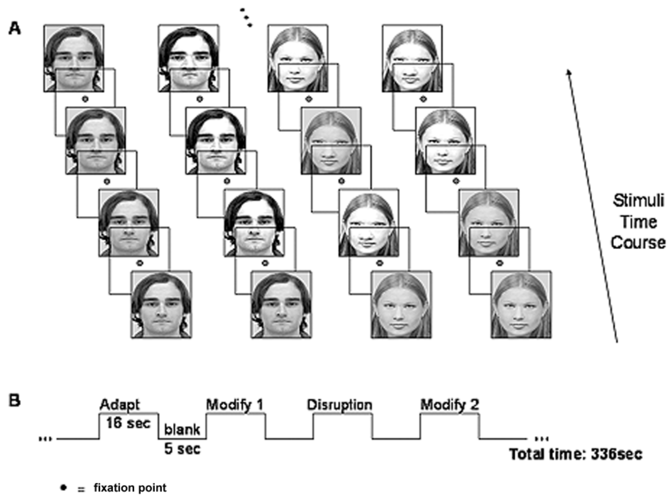

Figure 3.
Experimental paradigm – Primary Visual Areas Experimental paradigm. (A) Four types of blocks (left to right): adaptation, control_1, adaptation interruption, control_2. (B) A segment from the time axis of the experimental run of an overall duration of 336 s.

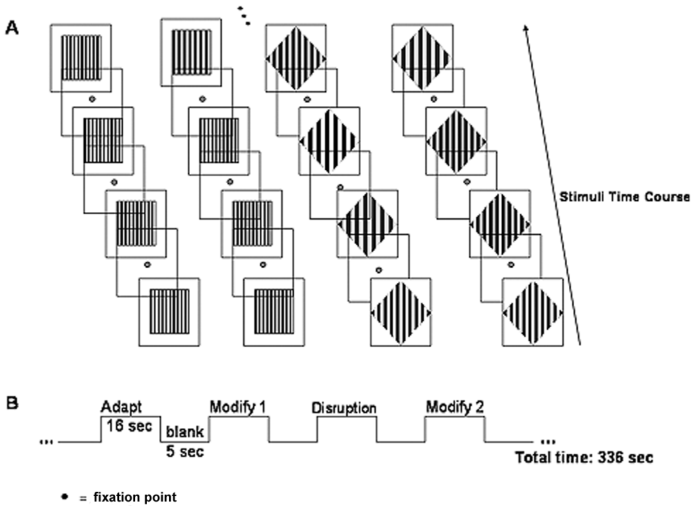

Figure 4.
Experimental paradigm – High Order Visual Areas.
Experimental paradigm. (A) Four types of blocks (left to right): adaptation, control_1, adaptation interruption, control_2. (B) A segment from the time axis of the experimental run of an overall duration of 336 s.

3. Results

Data analyses included several different aspects which refer to the accuracy and response time of performances.

3.1 The influence of adaptation / interruption (to adaptation) on response accuracy

The first block was designed to generate adaptation and the third one to interrupt adaptation. The second and fourth blocks were similar which enabled us to use them as internal controls. We, therefore, focused on the responses given in the second and fourth block, assuming that significant differences in performances between these two homologue blocks result from the primer block. As we can see from the results of the experiment on primary visual areas, in 73% of the events, the subjects' ability to note minor changes in the displayed picture is increasing after the interrupting block. In 9% of the events, the value of accuracy remained the same and

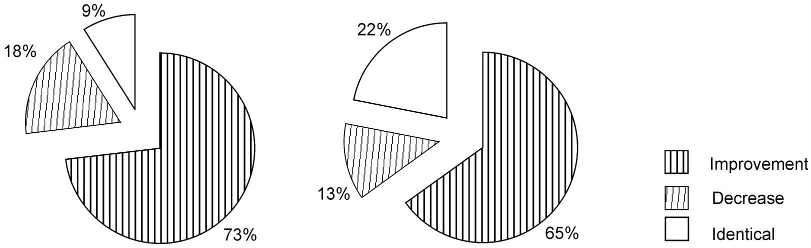

Figure 5.
Distinction of accuracy – Primary and High Order Visual Areas.
The percentage of change in accuracy between the second and the fourth blocks. A significant improvement in performances was indicated after interrupting adaptation.

in 18% of the events accuracy level decreased. The same analysis was done on the data derived from the experiment on high-order visual areas, where we found that in 65% of the events, the subjects' ability to note minor changes in the displayed picture is increasing after the interrupting block. In 22% of the events, the value of accuracy remained the same and in 13% of the events accuracy level decreased (Figure 5).

Calculating the averaged response time in every block type, a high correlation to our previous findings from accuracy analysis was found. We paid attention especially of the differences between the response times measured in the second and fourth block. According to our paradigm response times after interrupting adaptation should decrease which can be detected from our data (Figure 6).

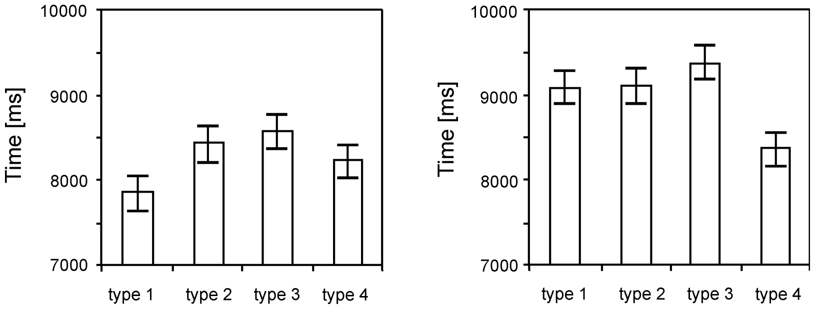

Figure 6.
Averaged response time of the block types – Primary and High Order Visual Areas
The averages of response time measured in the different kinds of blocks. A significant decrease in speed aspect was indicated in both of the experiments.

3.2 Error analysis

Tracing the most confusing event, we examined the distribution of error types in both kinds of experiments. From these results it can be clearly seen that most of the errors were due to contrast modifications and the amount of errors caused by showing the same image without any modification was the lowest (Figure 7).

Further analysis was done also on the response time data. There is no significant differences between the averaged response time for hits and errors neither between the response times in event types A-**A** and A-A' (comparing original images to modified contrast and to modified picture

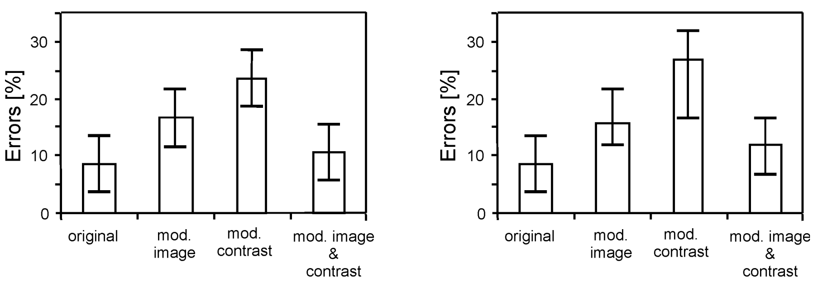

Figure 7.
Distribution of error types. The total number of errors was analyzed according to its "event" type. The percentage of each group was calculated for each subject separately, and was averaged across subjects.
Distribution of error types – Primary and High Order Visual Areas

minor changes) consistent with our findings in the accuracy aspect analyses. A-A' generally induced a slower but more accurate response. Both accuracy level, and averaged response times of the event type A-A (showing the same image without any modification) were found to be the lowest (Figures 8-9).

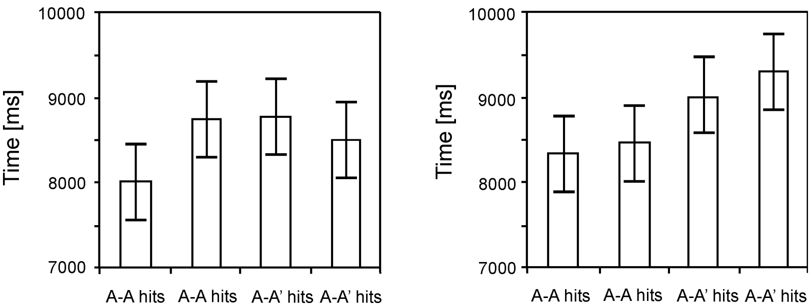

Figure 8.
Distribution of response time for hits – Primary and High Order Visual Areas
Distribution of response time for hits. The total number of the hits' response time was analyzed according to its "event" type. An average was calculated for each subject separately, and was averaged across subjects. (A-A showing the same image, A-A modifying contrast, A-A' modifying face properties or spatial frequency, A-A'

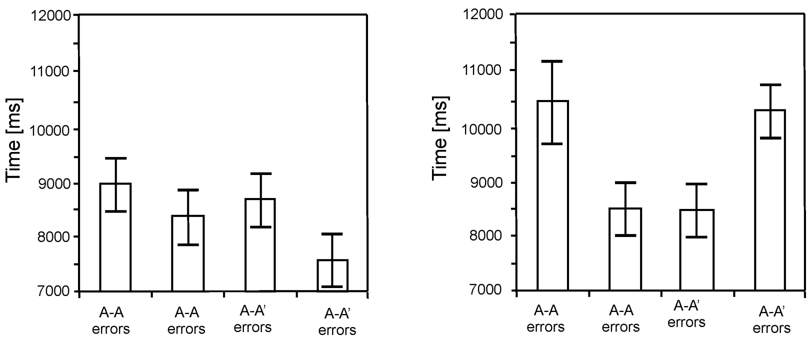

Figure 9.
Distribution of response time for errors – Primary and High Order Visual Areas
Distribution of response time for errors. The total number of errors' response time was analyzed according to its "event" type. An average was calculated for each subject separately, and was averaged across subjects. (A-A showing the same image, A-A modifying contrast, A-A' modifying face properties or spatial frequency, A-A' modifying both contrast and face properties or spatial frequency)

The properties of the first error after adaptation effect were investigated. It was found that errors due to changes in contrast level were the most dominant (Figure 10).

3.3. Comparison with adaptation effect between the experiments on primary and high-order visual areas

As we conducted two experiments simultaneously involving both primary and high-order visual areas, it allowed us to make some more analyses. First of all, we compared the number of errors in the two experiment types. The average percentages of total errors did not show any significant differences.

We also compared the average percentages of errors due to different contrast levels. As it can be seen, the errors due to contrast levels in both the primary and high-order experiment had no significant difference (Figure 11).

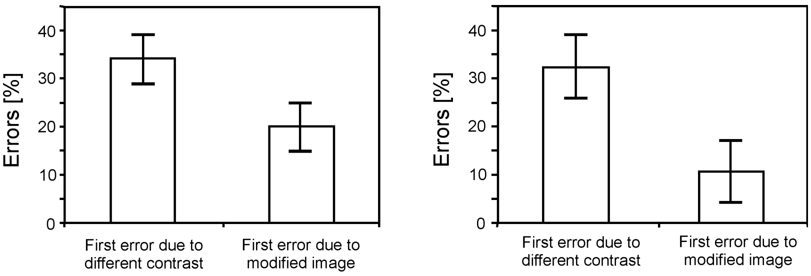

Figure 10.
Properties of the first error after adaptation – Primary and High Order Visual Areas.
Percentage of the errors in first exposure to modified image after acquiring adaptation (block 2). Two different optional error types: caused due to an image modification or a contrast modifications.

A comparison dealing with averaged response time was also performed. The averaged response time in the experiment on primary visual areas was found to be about 600ms shorter compared to averaged response time in high order visual areas' experiments (Figure 12). This result might refer to a weaker adaptation though subjects were asked to pay more attention to accuracy than speed.

3.4. 'Training' effect

Half of the subjects were first exposed to the high-order adaptation experiment, and half of the subject participated first in the primary-visual-areas adaptation experiment. For each subject the total accuracy level was calculated for both experiments and a total average was calculated. Accu-

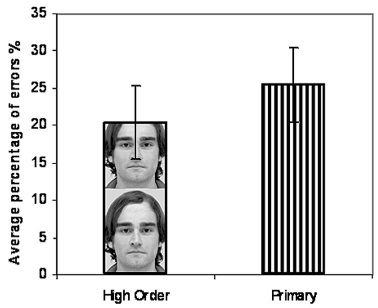

Figure 11.
Incorrect answers due to contrast changes
A comparison between the percentage of errors due to contrast changes in both primary and high order experiments.

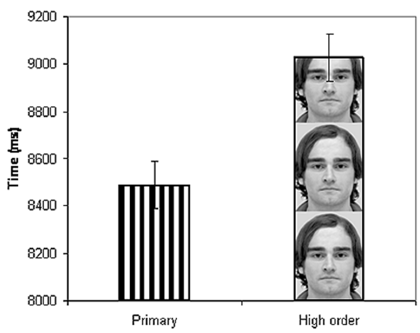

Figure 12.
Comparison between the averaged response time of the experiments on high order and primary visual areas
Comparison between the averaged response time of the experiments on high order and primary visual areas (including hits and errors as well.) Averaged response time was calculated for each subject separately, and was averaged across subjects.

racy analyses indicate a minor improvement trend that was demonstrated in the second experiment, regardless of experiment-type. This might be due to some 'training' effect in which the subjects are more familiar with the task, less tense, and thus achieved better performances. However the response times analyses did not support these findings.

4. Discussion

There have been many studies on adaptation effects using fMRI but hardly any psychophysical experiments on short-term adaptation. The study of short-term adaptation is of a huge importance due to the potential influences of understanding these neuronal mechanisms better from both physiological and cognitive aspects. Using short-term adaptation scientists are capable of distinguishing between different functional properties of cortical neurons, and thus use this feature as a tool in human brain mapping. The behavioral analysis performed in this experiment, which successfully showed adaptation, can be carried out through fMRI for a more detailed description of underlying neuronal activity. The experiment approved that adaptation indeed occurred as subjects responded to the second block of images less accurately and much slowly after looking at a repeated image than after looking at a block with altered images. This adaptation, indicated by other scientists, was due to fatiguing neurons responding less than normal.

5. Conclusion

We showed successfully for the first time that short-term adaptation behavior achieved by psychophysical experiment is correlated with the results achieved by long-term adaptation experiments, and consistent with results achieved in fMRI-adaptation experiments.

This aspect of the results is compatible with our basic assumption: Short-term adaptation causes a decrease in the accuracy of reaction to changes in stimuli and raises the needed time for doing the task as accurate as possible.

The most ambiguous behavior was demonstrated after contrast modifications. It was found that errors due to changes in contrast level were most dominant, and here the most time was needed thus imply that the system is aware of some change but fails to specify it.

Conducting two parallel researches, one dealing with "complex" stimuli, activating high order cortical areas, and the other with "simple" stimuli, stimulating primary visual areas, we correlated the results of the studies. This unique comparison revealed a vast resemblance in the results of the two. We therefore suggest that the behavioral mechanisms underlying short-term adaptation effect are similar in both types of visual areas.

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