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Involvement of single unit activity in inferotemporal and perirhinal cortices in recognition memory of visual objects in the macaque

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Abstract. Recognizing objects from the past is a vitally important ability for everyday live. The studies of brain mechanisms responsible for visual recognition memory suggest that the modulation of single unit activity in the inferotemporal and perirhinal cortices could be an important part of the neuronal substrate of recognition memory. In this review, I will describe Stimulus Specific Adaptation (SSA) - the reduction in neuronal response to previously viewed objects. The experimental tasks in which SSA is observed will be presented, along with the possibility that SSA may be enhanced by saccadic exploration of visual scene. Next, I will demonstrate that under special circumstances (partially split-brain preparation) monkeys could recognize the re-presentation of visual images without the concomitant appearance of SSA. The most promising alternative candidate for neuronal mechanism involved in recognition memory is delay activity - an increased frequency of cell firing in the time between the initial presentation of an image and its subsequent re-presentation. In order to determine if delay activity is important for recognition we have started to investigate the effects on recognition memory of disrupting delay activity by electrical stimulation. Preliminary results indicate a positive correlation between a reduction in delay activity and a decrease in recognition performance.

Mini-review

Key words: recognition memory, single unit, saccadic eye movement, adaptation, visual learning, macaque, inferotemporal cortex, perirhinal cortex, split brain monkey

INTRODUCTION

Historical background

Studies of patients with brain lesions show that bilateral ablation of temporal lobe produces severe memory disturbances. The best known example is patient HM (Scoville and Milner 1957), who underwent bilateral resection of the anterior medial temporal lobe to relieve his intractable epilepsy. After this operation his ability to keep information about new objects and recent events in working memory was severely impaired if any distraction was introduced. Interestingly, many other memory functions such as immediate memory, semantic memory, the ability to learn and retain new skills and the priming effect were fully preserved. Recently Corkin (see Corkin et al. 1997), who has studied memory functions of this patient for many years, showed that the lesions were not exactly in hippocampus and amygdala. Part of hippocampus was preserved, whereas some other neighboring structures were removed. This case started the search for an animal model of amnesia, which could be used to study working memory. Mishkin (1978), for example, found that combined bilateral lesions of hippocampus and amygdala severely disturbed working memory in non-human primates, whereas lesions limited to each of these structures alone did not. Later studies showed that these bilateral resections of hippocampus and amygdala were always accompanied by lesions in the rhinal cortex. It seems now that it may have been just rhinal cortex (perirhinal and entorhinal cortices) lesions, which were responsible for the observed disturbances in working memory (Gaffan and Murray 1992, Murray and Mishkin 1998).

Brain structures involved

Lesions of inferotemporal and perirhinal cortices abolish a monkey's ability to recognize the novelty of images (Gaffan 1994, Brown 1996) and studies of the activity of single units in these structures show a substantial decrease in response to previously seen objects (Baylis and Rolls 1987, Brown et al. 1987, Miller et al. 1991, Riches et al. 1991, Li et al. 1993, Rolls et al. 1993, Sobótka and Ringo 1993,1994). Therefore, it would seem, that inferotemporal and perirhinal cortices play a particularly critical role in recognizing whether a visual object is new or has been seen previously. These structures belong to a larger recognition memory system. They receive input from visual cortex and send reciprocal projections to other brain structures like entorhinal cortex (and from there to hippocampal formation), amygdala, prefrontal cortex, thalamus, basal forebrain and basal ganglia (Suzuki and Amaral 1994, Suzuki 1996, Brown and Xiang 1998). Especially strong connections are with entorhinal and prefrontal cortices.

Terminology: stimulus specific adaptation

Different laboratories have used different terms to describe the phenomenon of decreased cell response to a repeated presentation of a visual image when compared to the first presentation. This effect has been called repetition-sensitive response or decrement response (Brown et al. 1987, Brown 1996, Brown and Xiang 1998) and adaptive mnemonic filtering or response suppression (Miller et al. 1991, Desimone 1992,1996, Miller and Desimone 1994). In our laboratory, we use the term: stimulus specific adaptation (Sobótka and Ringo 1994,1996, Ringo 1996). The term stimulus specific adaptation describes two main characteristic features of this effect. First, stimulus specific - indicates that this effect depends on which image is used. It occurs only for a particular class of images, those which have previously been seen. Second, adaptation - the response to previously presented images is less pronounced than that elicited by previously unseen images.

METHODOLOGY

Tasks

The two tasks described below have been used in experimental studies of stimulus specific adaptation.

RUNNING RECOGNITION TASK

A series of single visual images is successively presented on a screen in front of a monkey (Gaffan 1977). In one version of this task the monkey is actively involved in the recognition of stimulus novelty, in the other version the animal is not. In one case, the monkey is rewarded for signaling with one type of motor reaction (hand or eye movement) that current image is a new one and with another type of motor reaction that the image has been already seen. In the other case the monkey can be involved in a task in which its response is not related to the recognition of novelty. For example, she could be

involved in discrimination between two groups of visual images, signaling the presence of images belonging to different groups with different types of motor reaction (Sobótka et al. 1993).

DELAYED MATCHING (OR NON-MATCHING) TO SAMPLE TASK

In this task a sample is initially presented to the animal and then removed (the "sample" period). After some delay period, two images are shown (the "test" period). One of the images from the test period is identical to that of the sample; the other image is different. Reward is given if the subject displays the correct motor reaction (hand or eye movement) to the same image in the delayed-matching-to-sample version of the task. Alternatively, if the animal is performing the delayed-non--matching-to-sample version of the task the response to the new image is rewarded.

A variation of this approach involves the presentation of only one image during the test period. The animal then signals the novelty or familiarity of the image by a go or no-go reaction.

In another popular version of the delayed matching to sample task, a string of visual images is presented. Each trial starts with a sample image, then several non-matching images are presented and finally a matched image identical to the sample is shown. Only a sequence of correct reactions to all presented images is rewarded. It is possible that among the non-matching images two of them be identical, thus permitting a comparison of stimulus specific adaptation between the situation when the recognition of stimulus novelty is critical with the situation when it is incidental to the task (Miller and Desimone 1994).

Among the variations of the task used in studies of stimulus specific adaptation, some involve:
- changing the ambient light intensity in which the experiment takes place.
- informing the monkey about a new trial (with a warning tone or the onset of a fixation point), or forcing the animal to initiate the trial itself (by an eye movement which shifts gaze into a response window or by an appropriate motor reaction like pulling a bar).
- repeating the sample image once or several times.
- presenting sample and match images in a fixed or random position on the screen.
- rewarding the animal after each correct reaction or only after a series of correct response.
- rewarding the animal immediately upon a correct response or delaying the reward for a period of time.

Visual images

Varieties of two-dimensional visual images (flat presentations of real objects or computer generated abstract stimuli) as well as real three-dimensional objects have been used to study stimulus specific adaptation. In a typical experiment employing two-dimensional stimuli, a colored, single visual image is presented on a screen located in front of the monkey.

Sometimes the monkey has previous experience with some of the stimuli used in the experiment. For example, in one experiment in which different views of abstract three-dimensional objects were used as images, one set of these objects was put into the monkey cage and the monkey played for prolonged periods of time with these objects and saw them frequently from different angels. The other set of objects has never been shown to the monkey.

Visual images can represent real objects (like fruits, body parts, elements of laboratory equipment, etc.) or can be abstract (drawings, textures, geometrical shapes, fractal, gratings with different spatial frequency, hues, etc.). One advantage of using abstract stimuli is that they can be new to the monkey and their parameters can be precisely controlled during the process of image generation. For example, in the studies of Sobótka et al. (1996, 1999) images were built from three elements randomly positioned in space (with the limitation that each element had at least one common point with each of the other two elements). The shape, size and color of each element were randomly chosen from among several available combinations. In this way, an almost infinite number of new images could be generated. The use of abstract stimuli is not without disadvantage as such images can be more difficult to differentiate (because they usually share some common features) and remember (because they usually do not have emotional associations).

Entire visual scenes can be used as an alternative to single images. In the study of Sobótka et al. 1998 the scenes were built from several visual images (see description above from studies of Sobótka et al. 1996,1999 on how objects were created). These images were randomly placed in different locations in the scene with the constraint that objects did not overlap one another. Thus, a monkey could explore a new scene with saccadic eye

movements and gradually become familiar with new portions of the scene.

CHARACTERISTICS OF CELLS WITH STIMULUS SPECIFIC ADAPTATION

Incidence

Stimulus specific adaptation has been found primarily in inferotemporal and perirhinal cortices. Lesions of these structures produce profound disturbances in the recognition of novelty in visual stimuli. Single unit recordings in both these regions suggest that these cells have the capacity to process complex features of the visual image that could be essential for image recognition. Such a capacity is not available in cells at earlier stages of visual processing (in primary visual cortex and the posterior portion of associative visual cortex). On the other hand, cells at later stages of image processing (involved in association with emotions, preparation of motor reaction, etc.) have recognition response latencies that are longer than those seen in inferotemporal cortex and therefore can not give rise to the effects seen in inferotemporal cortex.

Our study (Sobótka and Ringo, 1993) showed that responses elicited by a very familiar set of images are substantially smaller than those evoked by a much less familiar visual set. This stimulus specific adaptation was present in about 75% of the visually responsive cells from inferotemporal cortex. The averaged cell response to the familiar set of images was about 7 spikes/s (30%) smaller than the averaged response to the less familiar set. This robust stimulus specific adaptation occurred despite the fact that the task did not require the monkey to detect the novelty of presented items. The difference between the responses elicited by a visual image when it was presented for the first time and when it was repeated shortly after the first presentation depended strongly on the number of intervening images. Stimulus specific adaptation was most prominent when there was no intervening image, decreased when one intervening image separated the repeat from its first presentation and disappeared when ten images intervened between presentations of new and repeated stimuli.

Stimulus specific adaptation is also present (but much more scattered) in cells of other brain structures involved in the recognition memory system, especially in entorhinal and prefrontal cortices (see introduction). This mechanism was also found in several other areas which, as was shown in ablation studies, were not essential for recognition memory (see Brown and Xiang 1998).

Coding recency and familiarity

In principle, a cell can signal, through a decreased response to a previously seen visual image, at least two different aspects of the relationship between current and previous image presentations. Cells displaying stimulus specific adaptation may provide information about the "familiarity" - the frequency with which an item has been seen in the past. Alternatively, stimulus specific adaptation may provide information about the "recency" of a prior presentation - when an item was previously seen. Studies of recognition memory suggest that recency and familiarity may be coded in separate groups of cells (Fahy et al. 1993, Brown and Xiang 1998).

Responses of recency cells are substantially smaller to recently seen images as compared to the same images which have not been seen for longer period. These responses are similar for familiar and unfamiliar images. In contrast, responses of familiarity cells are substantially smaller to familiar images than to unfamiliar images and they are similar to images recently seen and not seen for a longer period. Recently Brown and Xiang (1998) described a new response pattern they termed a "novelty" response. Units displaying this pattern of activity only respond strongly to the first presentation of new (unfamiliar) images. They display a weaker response to subsequent representations of these unfamiliar images. These cells also produce only a very short burst of activity in response to familiar images.

Presence in excitatory but not in inhibitory responses

Stimulus specific adaptation has been studied almost exclusively in cells that show an excitatory response to the onset of visual image. In a typical experiment a single unit electrode is slowly lowered (with a microdriver) into inferotemporal cortex or perirhinal cortex until a unit is encountered. If the cell is found to produce an excitatory response to visual stimuli the recording session starts. If the cell does not respond to visual images or exhibits an inhibited response, it is disregarded and the electrode is lowered further. Unfortunately, with this method of data collection a significant subset of cells which could play an important role in visual processing and memory is not

analyzed, as about one quarter of all cells show such inhibited response to visual images. Sobótka and Ringo (1994) published the first study addressing the question about whether stimulus specific adaptation was present in inhibited cells. We showed that stimulus specific adaptation was present only in cells with excitatory response to visual images. There are, however, some difficulties in studying inhibited responses due to the possibilities of a floor effect (where responses can not fall to a rate less than zero spikes/s), whereas the maximal rate of response of excitatory cells is limited only by the cell refractory period. In order to address the problem of these different response ranges Sobótka and Ringo compared the responses from inhibited cells with those from units displaying only a moderate excitatory response. Stimulus specific adaptation was still found to be exhibited by the set of units displaying only a moderate excitatory responses. Thus, although stimulus specific adaptation could not be found in inhibited cells it would appear to be present across a range of excitatory responses.

Incremental response

In most cases cells that code recognition memory decrease their response to a repeated presentation of a visual image (as compared with the first presentation of that image). However, in special conditions a small subset of cells increase their response to a repeated presentation. Miller and Desimone (1994) for example used a delayed matching to sample task in which the monkey saw a sample (A), then several (0 to 4) successively presented images (B, C, etc.) and finally a match image (A). The monkey's task was to signal the appearance of the match image (identical to the sample image). The authors found that among cells which showed recognition memory, approximately one third of them had increased cell activity with a match (repeated image A). On occasion, the image presented between sample and match was repeated (B, B). Interestingly, under this condition the cell response to such intervening image was smaller for the repeated presentation than for the first presentation (showing typical stimulus specific adaptation). The effect of increased cell activity to the match stimuli could be explained by the assumption that information about the sample image is actively held in memory. This process could facilitate the cells response to an identical and potentially rewarded match image (while the monkey could ignore other intervening images not relevant for reward). Different task requirements could cause the lack of incremental response in the running recognition task. In the running recognition task the animal has to remember many different items whereas in the task of Miller and Desimone the working memory task can in principle be accomplished by reciting a single target.

MODULATION OF STIMULUS SPECIFIC ADAPTATION

Incidence and strength of saccadic modulation in darkness

In 1994 we conducted an experiment (Ringo et al. 1994) in which we recorded cell activity in the ventral temporal lobe triggered by spontaneous saccadic eye movements. The rhesus monkey, which had an eye coil implanted permitting us to record eye position, was not engaged in any specific task. We recorded while she sat quietly in the experimental chair. On average, the monkey made about 3 saccades/s in the light and about 2 saccades/s in the dark. Many cells produced a robust response to each saccade. In the light, cell responses to saccadic eye movements could be explained by a slip of the retinal image across the retina. Unexpectedly however, we found that a substantial percentage of cells (about one fourth) responded in total darkness (where retinal slip is not an issue). Also, we found that in light about one fifth of cells responded with a very short latency, starting before information about the retinal image had time to reach the ventral temporal lobe. Therefore, we concluded that the saccade itself, produces a robust extra-retinal modulation in a substantial portion of cells. We estimated that in the ventral temporal lobe an extra-retinal signal of about 10 million action potentials accompany each saccade. Taking into consideration the robustness of the cell responses and their neuroanatomical localization in areas, which are strongly involved in visual perception and memory, we hypothesized that this saccadic modulation could play an important role in these cognitive processes. Each saccade produces a break in the flow of visual data into the cortex and defines a new starting point for object identification and learning. The synchronized firing of many cells, caused by the inflow of saccade controlled visual information and at the same time extra-retinal saccadic modulation, could use a Hebian mechanism to form neuronal connections and generate long term potentiation – currently the most popular candidate for memory coding.

Spontaneous and guided saccadic eye movements

It is possible that cell activity around the moment of spontaneous saccadic eye movement is influenced by different internal factors which could generate or accompany the saccade. For example, a saccade could be initiated when there is substantial buildup of motivation. Therefore, in subsequent experiments we analyzed saccadic modulation when a monkey was involved in a task that guided saccadic eye movements (Sobótka et al. 1997, Sobótka 1999). Saccades were triggered by the brief presentation of a small dot on a computer screen. The timing and location of this dot externally determined the temporal and spatial parameters of saccades. Similar to the situation for spontaneous saccades, many cells in the ventral temporal cortex showed robust saccadic modulation to these directed saccades.

Full adaptation after a few seconds of viewing visual scene

In most of the experimental studies of stimulus specific adaptation visual images are presented in a somewhat artificial way. A monkey is required to fixate her eyes at a point located on a screen in front of her, after which an image is flashed on the screen to motionless eyes. In most normal situations, however, a visual image is brought onto the fovea of the retina through an active, abrupt shift of gaze, called a saccadic eye movement. Influence of both types of image presentation (through abrupt image onset when gaze is fixated and through saccade) on stimulus specific adaptation would be comparable if we assume that the only effect of a visual saccade is the shift of the visual image on the retina. The saccadic eye modulation described above suggests, however, that presentation through saccadic eye movement might be involved in memory processes. Two our studies showed that saccades could indeed play a significant role in memory processes. One of these studies (Nowicka et al. 1995) suggests that stimulus specific adaptation is significantly enhanced (approximately doubled) when an image is acquired through an active saccade as compared with the situation when it is presented to fixated eyes. In this study, stimulus specific adaptation was found only in cells with stimulus selectivity, i.e., which responded differently to different visual stimuli (similar result to Li et al. 1993). In another study, (Sobótka et al. 1998) large visual scenes were successively presented on the screen in front of the monkey. Each scene (consisting of many geometrical objects) was shown for about half a minute and was abruptly replaced with a new scene. Characteristically, monkeys actively explored the scenes making from 2 to 5 saccades per second. Cells in the ventral temporal cortex which showed a strong response to saccades that placed gaze in new portions of the scene did not produce any response when gaze was directed toward previously visited portions of the scene. Such an effect of full stimulus specific adaptation could allow the animal to allocate all brain resources (cell activity) to the process of searching for new objects, as fast discovery and recognition of new objects could be critical for animal survival in the natural environment.

Implications of split-brain results

While SSA is a promising candidate as a neuronal basis for recognition memory, Sobótka and Ringo 1997 showed that stimulus specific adaptation can under some conditions be disassociated from recognition memory. We recorded neuronal activity in inferotemporal cortex of the partly split-brain monkey in which the optic chiasm and splenium of the corpus callosum were transected, leaving the anterior commissure as the sole path of interhemispheric transfer of visual information. In such preparations, the visual image presented to the eye contralateral to the recorded IT neuron (with the other eye closed) is processed through a cascade of brain areas. Visual information travels through ipsilateral primary visual cortex, inferotemporal cortex and then through the anterior commissure to reach the inferotemporal cortex of the opposite hemisphere. In our experiment, monkeys performed a running recognition task in which they were required to respond to repeated images with a panel press, withholding any response to new images. It was found that cells in inferotemporal cortex decreased their response to repeated images presented to the ipsilateral eye (hemisphere), showing typical stimulus specific adaptation. However, there was an unexpected dissociation of behavior and stimulus specific adaptation when the same images were represented to the contralateral eye (hemisphere). Cell responses did not show stimulus specific adaptation. Nevertheless, the monkey could identify (though with some difficulty) repeated images as repeated. This dissociation of behavior and cell response suggests two possible explanations. First, it is possible, that stimulus specific adaptation in other cortical areas (outside inferotemporal cortex) is responsible

for the correct recognition of an image presented to the opposite hemisphere. It is also possible that an entirely different cell mechanism is responsible for this recognition. One candidate for such an alternative cell mechanism is delay activity. Recently, we began experiments testing each of these alternative hypotheses.

Delay activity as another possible single unit memory mechanism

Delay activity was first described by Fuster and his collaborators (see Fuster 1995). Using the delayed matching (or non-matching) to sample paradigm, they found a number of cells in inferotemporal cortex (Fuster and Jervey 1981) and prefrontal cortex (Fuster and Alexander 1971), which showed stimulus specific activity during the delay period between the presentation of a sample and its match. It is possible that something like a reverberation of information about the sample image could generate this delay activity. If the visual images used in the experiment are chosen from very limited stock, this reverberation is more important for correct recognition and delay activity is usually more pronounced.

Further research with electrical stimulation during delay period

Recently, we started testing the hypothesis that delay activity could act as an alternative neuronal mechanism to stimulus specific adaptation for the recognition of novelty. In partly split brain monkeys (see description above of Sobótka and Ringo 1997), the delay activity could explain the retained memory of an image as already presented even when stimulus specific adaptation is not present. To test this hypothesis we recently started experiments in which we use an electrical stimulation, which disturbs both delay activity and the monkeys performance in the delayed matching to sample task. A parallel decrease in performance and delay activity (proportional to an increase of stimulation level) would support the hypothesis that delay activity could play a role in recognition memory. Alternatively, a dissociation between performance and delay activity would suggest that recognition memory is based on a cell mechanism other than delay activity. Our preliminary study supports the first possibility (Sobótka et al. 1999).

In conclusion, the effect of stimulus specific adaptation seems to be the strongest candidate for a neuronal mechanism used for the recognition of novel visual images. This effect is substantially enhanced if the images are actively brought onto the fovea through saccadic eye movements (as compared with their presentation to motionless eyes). However, in special circumstances, stimulus specific adaptation is not present and another neuronal mechanism, delay activity, may be involved in novelty recognition.

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