

Adaptation of PMLS neurons to prolonged optic flow stimuli

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Changes in neuronal responses during and after adaptation to prolonged optic flow stimulation were investigated by extracellular single-unit recording in the posteromedial lateral suprasylvian area (PMLS) of the cat. In comparison with translation stimuli, the complex optic flow patterns (radiation and rotation) produced more pronounced adaptation and after-effects by inducing larger response reduction, and altered the direction selectivity of many neurons obviously as well.

Generally, the adaptation effects were direction-specific for radiation/rotation, but independent of the direction of test stimulus for translation. These results suggest that PMLS may play an important role in the perception of motion after-effects to complex optic flow fields, while the adaptation to simple translation might be generated at a relatively earlier level of the visual system. *NeuroReport* 12:4055–4059 © 2001 Lippincott Williams & Wilkins.

Key words: Adaptation; Cat; Direction selectivity; Motion after-effect; Optic flow; PMLS

INTRODUCTION

Prolonged viewing of a stimulus moving in one direction makes following stationary patterns appear to drift in the opposite direction. This visual motion after-effect has been suggested resulting from a temporary imbalance in the activity of cortical neurons sensitive to movement in different directions [1–3]. It is generally accepted that prolonged stimulation would fatigue the neurons that respond most strongly to the stimulus pattern and it takes a short period for them to recover from this effect after the adapting stimulus is withdrawn. While these fatigued neurons reduce their responsiveness obviously, the activity of other neurons decreases much less or even increases, so that visual perception is biased away from the adapting pattern.

This explanation for the visual motion after-effect (MAE) is supported by a number of neurophysiological studies through the years [4–6]. Specifically, in the striate cortex of the cat [7–10] and area MT of the primate [11], many neurons were found showing direction-specific adaptation, i.e. the decrease in responsivity was dependent on whether the test stimulus matched the prior prolonged stimulation in drifting direction. Consequently, the direction-specific adaptation often produced changes in the degree of direction selectivity of the neurons and sometimes even reversed the preferred direction. These results suggest that the neural basis of MAE may arise from the primary visual cortex. On the other hand, many psychophysical studies indicated that MT and certain areas upstream from it are closely involved in the perception of MAE to complex pattern motion [12–15]. However, little has been done to

explore the contribution of single neurons in the extrastriate cortical areas of either the primate or the cat.

It is notable that the relevant neurophysiological studies usually took moving bars, gratings or textures as stimuli for single-unit recordings, while optic flow patterns with complex organization of various moving directions (such as radiation and rotation) were only used in several psychophysical experiments. Previous findings have shown distinction between MAEs caused by translation and radiation/rotation [13,16], but it is not known whether there is difference at neuronal level which may underlie the perceptual phenomena. PMLS of the cat is commonly considered as functionally analogous to primate MT [17,18] and thus a likely candidate subserving the perception of MAE. In the present study single neurons in this extrastriate area were tested with different optic flow patterns for changes in their responses caused by prolonged stimulation. The results demonstrate that the adaptation effects are dependent on the mode of optic flow fields and, for radiation/rotation stimuli, direction specific.

MATERIALS AND METHODS

Experiments were carried out by single-unit recordings in PMLS of six normal adult cats using glass-coated tungsten micro-electrodes. The general procedures for animal preparation, maintenance and recording have been described previously [19,20]. Adequate measures were taken to minimize pain and discomfort, in compliance with the NIH guidelines on the care and use of laboratory animals. Briefly, the cats (weighing 2.5–4.0 kg) were initially anesthetized with ketamine (20–30 mg/kg, i.m.) and surgery

was performed to implant a foreleg venous cannula for continuous infusion of Ringer's solution and a tracheal cannula for artificial ventilation. During recordings, appropriate anesthesia and paralysis were maintained with urethane and gallamine triethiodide (20 and 10 mg/kg/h, i.v., respectively). Rectal temperature, end-tidal CO₂, electrocardiogram, and sometimes, electroencephalogram were continuously monitored. Pupils were dilated with homatropine and nictitating membranes were retracted with phenylephrine hydrochloride. The eyes were protected using contact lenses of appropriate refractive power. The locations of area centralis and optic disks were checked frequently with a reversible ophthalmoscope. Neuronal activity was amplified and filtered with a programmable amplifier, then fed on-line into a computer via a laboratory interface. The analog signals were selected through a window-discriminator to isolate the action potentials of a single unit. Occasionally electrolytic lesions were made for histological identification of the electrode tracks.

Visual stimulation: Receptive fields of isolated units were first estimated and plotted on a tangent screen using hand-held stimuli. The visual stimuli used in quantitative measurements were self-programmed, generated on-line by a PC compatible computer and displayed on a 21-inch monitor with a resolution of 800 × 600 pixels and a refresh rate of 85 Hz. For each cell, a preliminary test was performed to determine its preferred direction to translating random-dot patterns (12 drifting directions separated by 30° steps were included in the test) and its preferred optic flow pattern to radiation/rotation (expansion, contraction, clockwise and counterclockwise rotation were included in the test, for details of these stimuli see [20]). All these stimulus patterns, and a blank control for measuring the spontaneous activity, were pseudorandomly interleaved and presented for 8–10 trials for averaging the data.

The cell was then tested with a series of adaptation-test stimuli of either translation or complex optic flow (radiation or rotation, the one elicited better responses was used) mode. The general repertoire was similar to that adopted by Petersen *et al.* [11]. Normally, an adaptation phase of 20 s was followed, after an 1 s delay (blank background only), by a test phase lasting ≥ 2 s and subsequently a recovery period with no stimulation. In the adaptation phase, a random-dot pattern was presented moving either in the preferred direction (PD) or opposite to the preferred direction (i.e. non-preferred direction or NPD), or as a stationary field (control). The three adaptation fields were paired with either of the two test conditions: motion in the preferred or non-preferred direction of the same stimulus mode (translation or radiation/rotation). In a complete adaptation-test series, each of the six combinations was presented five times in a pseudorandomly interleaved sequence.

RESULTS

A total of 64 PMLS neurons were successfully recorded for their response changes during and after prolonged optic flow stimuli, of which 44 cells with translation in the preferred/non-preferred direction, 60 cells with the two possible patterns of either radiation or rotation mode. Normally, the firing rate of a cell declined steadily soon

after the onset of adaptation stimulus and reached a relatively stable plateau after a few or up to 10 s. In comparison with the control, most cells showed some extent of reduction in responsiveness to test stimuli of both directions, especially after adaptation in preferred direction. To show the relationship between these effects and the direction of adaptation and test stimuli statistically, the data obtained from the whole sample were averaged and plotted in Fig. 1.

Response decrement during prolonged stimulation: time course of adaptation: As shown in Fig. 1, the mean response decrement curves during adaptation phase could be approximately fitted with a single exponential decay

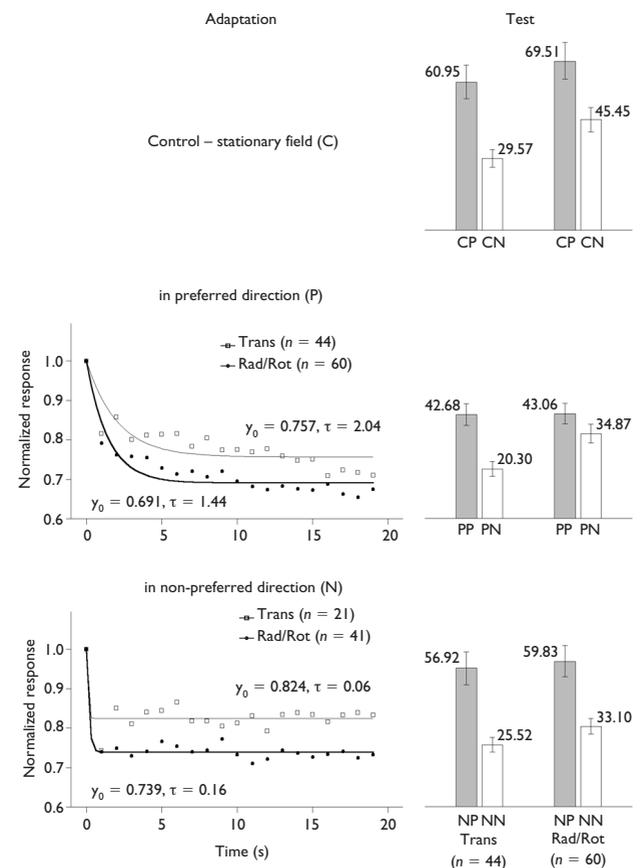


Fig. 1. Effects of prolonged translation (Trans) and complex optic flow (Rad/Rot) stimuli on responsiveness of PMLS neurons. (Left) Average time course of adaptation. Before averaging, responses of each cell were collected with a binwidth of 1 s and then normalized to its initial value in the first second. The mean response decrement curves were fitted by a single exponential decay function in the form $y = y_0 + (1 - y_0)e^{-t/\tau}$, where y_0 = the asymptotic response level and τ = the time constant for the exponential. (Right) Mean response strengths and standard errors to test stimuli presented after adaptation phase. For each cell and each condition, the neuronal activity within 0–2000 ms after stimulus onset was collected and converted into firing rate (R, in spikes/s). In the abbreviations, the first letter (C, P or N) indicates the condition of adaptation; the second (P or N), the direction of test stimulus. Since the normalization of response decrement may produce uncontrollable error if the initial response was absent or weak, the cells of which R_{CN} was smaller than half of R_{CP} were excluded from the statistics for the time course of adaptation in non-preferred direction.

function, in which the parameters y_0 and τ characterize the effects of different adaptation conditions. No matter the adaptation was in the preferred or the non-preferred direction, the radiation/rotation stimuli always resulted in lower asymptotic response level (y_0) than translation, which means a larger extent of response reduction during prolonged exposure to the complex optic flow fields. In addition, the time constant τ was lower when adaptation was conducted in the preferred direction of radiation/rotation than in the preferred direction of translation, indicating faster decay in responsiveness in the former case. Both differences suggest that the radiation/rotation stimuli containing complex organization of various directions produced stronger adaptation effects to the PMLS neurons in comparison with translation along a single direction.

Compared with adaptation in preferred direction, the response decrement curves for adaptation in the non-preferred direction had higher y_0 and very small τ values. The smaller reduction in responsiveness indicates that the adaptation mechanism was less effective when the cells were exposed to their non-preferred stimuli. As for the τ values close to zero, they reflect the very rapid drop of responsiveness at the beginning of adaptation phase. In other words, it took a much shorter time for the response strength to go down from its initial level to the plateau (see Fig. 1). It should be noted that, considering the possible errors, the difference between the two τ values for translation and for radiation/rotation would not make much sense.

Response changes after adaptation to prolonged stimulation: after-effects: The mean response strengths of PMLS neurons to their preferred and non-preferred stimuli presented after adaptation phase are also displayed in Fig. 1. Similar to what had been reported previously [20], the cells had higher mean response strengths to radiation/rotation than to translation. The difference was small in the preferred direction but significant in the non-preferred direction (Mann-Whitney U-test, $p < 0.05$), implying a better direction sensitivity to planar flow fields (also see Fig. 2 for results about direction indices and Fig. 6 in [20]).

A comparison with the control (CP, CN) demonstrates that all the mean response strengths decreased obviously and significantly after adaptation in preferred direction (Wilcoxon test, $p < 0.0001$), but in general much less after adaptation in the non-preferred direction (a small subset of cells even had their activity enhanced). On the other hand, the decrease of mean response strengths was relatively smaller for translation than for radiation/rotation stimuli. These results are consistent with the above-mentioned differences between the mean response decrement curves, indicating that the adaptation mechanism was still effective during the test phase and led to some kind of after-effects at the neuronal level.

The bar plots in Fig. 1 provide only a rough view on the extent of response change after adaptation phase. A further quantitative analysis by normalizing the responses measured after adaptation to the control on the basis of cell by cell can reveal more details of this issue. The statistics shown in Table 1 (higher mean values for Trans than for Rad/Rot, for NP than for PP, for NN than for PN) coincide

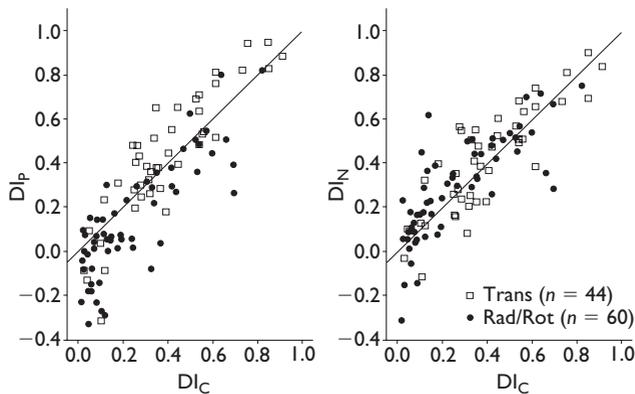


Fig. 2. The direction index $((R_{PD} - R_{NPD}) / (R_{PD} + R_{NPD}))$ measured after adaptation in preferred direction (DI_P) or in non-preferred direction (DI_N) is plotted against the value obtained in control (DI_C). The mean (\pm s.e.) values are 0.379 ± 0.033 and 0.243 ± 0.028 (DI_C), 0.424 ± 0.044 and 0.144 ± 0.033 (DI_P), 0.406 ± 0.037 and 0.277 ± 0.030 (DI_N), respectively, for translation and radiation/rotation stimuli. The line with a slope of 1 is drawn as a reference showing no change in direction selectivity after adaptation in respect to the control.

with what have been summarized above very well except for the unexpected high value obtained in condition of Rad/Rot combined with PN. Thereby it turns out that, when radiation/rotation patterns were used as stimuli, the mean response ratio for condition PP was significantly lower than that for PN (U-test, $p < 0.0001$), and the value for NN lower than that for NP ($p < 0.0002$). These differences indicate that the decrease of response strengths was more obvious, i.e. the after-effects induced by adaptation process was more remarkable, when the test stimulus was conducted in the same direction as the adaptation stimulus than in the opposite direction. Nevertheless, it should be noted that no such significant difference has been found among the mean response ratios for translation ($p > 0.05$).

Changes in direction selectivity: Since the variations of response strengths to preferred and non-preferred stimuli may lead to changes in the degree of direction selectivity, a direction index (DI) was calculated for each cell and each adaptation condition and plotted in Fig. 2. When radiation/rotation patterns were used as stimuli, most neurons became less direction selective after adaptation in preferred direction (represented by points falling below the line with a slope of 1), and the mean value of the whole sample was significantly lower than the control (DI_P vs DI_C , Wilcoxon test, $p < 0.0001$). For a number of cells the preferred direction was even reversed and the DI value became negative. In contrast, the mean value for DI_N was higher than that for DI_C ($p < 0.02$), indicating that the cells were in general more direction-sensitive after adaptation in non-preferred direction. The situation was very different for translation: both the mean values for direction indices measured after adaptation were slightly higher than the control, but the differences were insignificant (DI_P vs DI_C , $p > 0.02$; DI_N vs DI_C , $p > 0.15$).

Since the adaptation effects turned out to be direction-specific for complex optic flow fields (Table 1, Fig. 2), it would be interesting to check whether the decrease of

Table 1. Mean response ratios and standard errors in different conditions of adaptation and test.

	PP	PN	NP	NN
Trans ($n = 44$ or 21)	0.743 ± 0.026	0.752 ± 0.051	0.971 ± 0.031	0.870 ± 0.043
Rad/Rot ($n = 60$ or 41)	0.649 ± 0.019	0.834 ± 0.034	0.875 ± 0.025	0.728 ± 0.027

The data were obtained by normalizing the response strengths of each neuron to the corresponding control (R_{CP} or R_{CN}) and averaging the normalized values. To minimize the potential errors introduced by weak responses to non-preferred stimuli, the cells of which R_{CN} was smaller than half of R_{CP} were excluded from the statistics on non-preferred responses (conditions PN and NN).

responses after adaptation was dependent on the degree of direction selectivity. However, only a very weak, if any, negative correlation could be found between the response strength ratio PP and the initial direction index DI_C (for translation, $r = -0.171$, $p < 0.25$; for radiation/rotation, $r = -0.281$, $p > 0.02$). Although the cells with obvious direction selectivity to radiation/rotation stimuli tended to reduce their responsiveness to a relatively lower level after adaptation, inspection on individual samples shows that many direction-insensitive units exhibited pronounced direction-specific adaptation to the complex optic flow patterns.

DISCUSSION

The optic flow patterns taken as stimuli in our experiments were as same as those used in an earlier study [20], and the normal response properties of PMLS neurons were generally similar to those reported before. However, it was the first time, to our knowledge, that investigation on motion adaptation and MAE was conducted in this extrastriate visual area and radiation/rotation stimuli were used in such work at neuronal level. Previous studies have suggested that PMLS is mainly involved in higher functional aspects of visual motion processing and analogous or even homologous to primate MT [17,18]. Our findings, especially the direction-specific adaptation effects to radiation/rotation, indicate that PMLS may play an important role in the perception of MAE to complex motion in the cat, possibly similar to MT in the primate as revealed by some psychophysical experiments [13–15].

Statistically, the PMLS cells displayed a higher degree of direction selectivity to translation than to radiation or rotation (also see [20]). Therefore it sounds somehow controversial to find that, as compared with planar motion, prolonged radiation/rotation stimuli were more effective in reducing responsiveness of single neurons and the adaptation was more direction-specific. However, the more pronounced adaptation effects induced by complex optic flow patterns were demonstrated by the extent of neuronal response decrement during prolonged stimulation and also after that (see Fig. 1), and they are consistent with a number of psychophysical findings. For example, Steiner *et al.* [13] reported that the MAEs in cortical areas beyond V1 are stronger for expansion and rotation than for translation. A similar conclusion was also derived by Bex *et al.* [16] using three different methods. All these results suggest that the MAEs to complex optic flow stimuli might be generated in higher cortical areas while the primary visual cortex is possibly involved in adaptation to simple translation, and may add evidence to support the existence of multiple stages of motion processing for optic flow fields

[21,22]. PMLS and MT, lying at an intermediate level in the hierarchical structure of visual cortex, may serve as the preliminary neural substrate for complex motion perception and adaptation, and some even higher extrastriate areas may contribute to further processing.

The present results are alike to what have been found in the cat striate cortex [4,7–10] in some points. During and after adaptation in the preferred direction, almost all neurons showed some reduction in response to motion in the preferred direction and most showed some reduction in the non-preferred direction. Adaptation in the non-preferred direction induced less overall changes in responsiveness. In addition, the correlation was very weak between the decrease of response and the degree of direction selectivity, and many direction-insensitive neurons exhibited clear adaptation effects after prolonged stimulation. The major difference is that in PMLS the adaptation to translation was generally independent of the direction of test stimulus, while obvious direction-specific adaptation has been observed for many striate neurons by different authors using various moving stimuli (bar, grating or texture). These similarities and differences may reflect the continuity and hierarchy in visual motion processing.

Although PMLS is supposed to be functionally analogous to MT, there might be some dissimilarities between them. Petersen *et al.* [11] claimed that direction-selective MT neurons showed direction-specific adaptation to moving bar while non-direction-selective neurons did not show significant adaptation, which are distinct from our findings (see above). Since the lack of more neurophysiological data, especially the ones obtained in MT using complex optic flow stimuli, it is unclear whether these discrepancies should be due to the different stimulation. Further experiments are necessary to confirm, if any, differences between PMLS and MT concerning their involvement in vision motion adaptation.

The time constants (τ) shown in Fig. 1 were obtained from the mean response decrement curves, in the way also taken by Giaschi *et al.* [10]. If the analysis was performed on individual cells, most τ values ranged from 1 to 10 s, with an average of ~ 3 –4 s for adaptation in preferred direction (excluding the curves could not be fairly fitted). It should be noted that, since the goodness of fitting varied with cell and became quite poor for some curves, the mean values are not really reliable and the data range for the majority of samples may make more sense. Taken all these into consideration, we still found that the time constants were generally lower than those previously reported for the cat striate cortex [4,9,10], implying that the response decay is relatively faster for PMLS neurons during adapta-

tion to optic flow fields. It remains unclear whether the faster change is determined upon the stimulation or it is an inherent feature of PMLS cells.

CONCLUSION

The present study is the first to report different adaptation effects induced by simple translation and complex optic flow fields (radiation and rotation) at the neuronal level. We found that PMLS cells displayed pronounced response reduction during and after prolonged radiation/rotation stimuli and the adaptation was direction-specific. Most neurons became less direction-sensitive after adaptation in preferred direction and some cells even reversed their preferred directions. In contrast, adaptation in non-preferred direction enhanced the overall direction selectivity though producing a smaller extent of response changes. When the stimulus mode was changed to translation, the decrement of neuronal responsiveness was significantly less and the adaptation was independent of the direction of test stimulus. These results suggest that PMLS may play an important role in the perception of motion after-effects to complex optic flow fields, while the adaptation to simple translation might be generated at a relatively earlier level of the visual system, presumably the primary visual cortex. Moreover, our findings may add support to the hypothesis

about multiple stages of motion processing for optic flow fields.

REFERENCES

1. Sutherland NS. *Q J Exp Psychol* **13**, 222–228 (1961).
2. Levinson E and Sekuler R. *Vis Res* **16**, 779–781 (1976).
3. Mather G. *Perception* **9**, 379–392 (1980).
4. Vautin RG and Berkley MA. *J Neurophysiol* **40**, 1051–1065 (1977).
5. von der Heydt R, Hanny P and Adorjani C. *Arch Ital Biol* **116**, 248–254 (1978).
6. Saul AB and Cynader MS. *Vis Neurosci* **2**, 609–620 (1989).
7. Hammond P, Mouat GSV and Smith AT. *Exp Brain Res* **60**, 411–416 (1985).
8. Hammond P, Mouat GSV and Smith AT. *Vis Res* **26**, 1055–1060 (1986).
9. Marlin SG, Hasan SJ and Cynader MS. *J Neurophysiol* **59**, 1314–1330 (1988).
10. Giaschi D, Douglas R, Marlin S *et al.* *J Neurophysiol* **70**, 2024–2034 (1993).
11. Petersen SE, Baker JF and Allman JM. *Brain Res* **346**, 146–150 (1985).
12. Wenderoth P, Bray R and Johnstone S. *Perception* **17**, 81–91 (1988).
13. Steiner V, Blake R and Rose D. *Perception* **23**, 1197–1202 (1994).
14. Tootell RBH, Reppas JB, Dale AM *et al.* *Nature* **375**, 139–141 (1995).
15. He S, Cohen ER and Hu XP. *Curr Biol* **8**, 1215–1218 (1998).
16. Bex PJ, Metha AB and Makous W. *Vis Res* **39**, 2229–2238 (1999).
17. Payne BR. *Cerebr Cortex* **3**, 1–25 (1993).
18. Dreher B, Wang C, Turlejski KJ *et al.* *Cerebr Cortex* **6**, 585–599 (1996).
19. Wang Y, Wang L, Li B *et al.* *Neuroreport* **6**, 1969–1974 (1995).
20. Li B, Li B-W, Chen Y *et al.* *Eur J Neurosci* **12**, 1534–1544 (2000).
21. Morrone MC, Burr DC and Vaina LM. *Nature* **376**, 507–509 (1995).
22. Gurney K and Wright ML. *Perception* **25**, 5–26 (1996).

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