

Direction-specific adaptation in area MT of the owl monkey

STEVEN E. PETERSEN*, JAMES F. BAKER and JOHN M. ALLMAN

Division of Biology, California Institute of Technology, Pasadena, CA 91125 (U.S.A.)

(Accepted May 29th, 1985)

Key words: motion aftereffect — middle temporal area — owl monkey — extrastriate cortex

NOTICE: This material may be protected by copyright law (title 17 U.S.C. 1009)

Single neurons were recorded in owl monkey middle temporal visual cortex (MT). Directional neurons showed direction-selective adaptation to pattern motion: responses to motion in the preferred direction were reduced by adaptation to motion in the preferred direction and enhanced by adaptation in the opposite direction. Non-directional neurons did not show significant adaptation.

After prolonged exposure to motion in a certain direction, such as staring at a waterfall, stationary objects appear to move in the opposite direction (see ref. 20). This motion aftereffect, or 'waterfall illusion', may reflect short-term changes in neural populations. It has been suggested that the visual cortex area MT (middle temporal area) is involved in motion perception⁵, because it contains a high percentage of cells that are selective for the direction of stimulus motion. In this paper we report on neurons in MT which exhibit changes in responsiveness following prolonged exposure to moving visual stimuli. When MT neurons are adapted to movement in their preferred direction, responses to bars moving in the preferred direction are reduced; when adapted opposite to the preferred direction, responses to identical bar motion are enhanced.

The middle temporal area (MT) of the owl monkey is a heavily myelinated striate-receptive region which is coextensive with an orderly map of the visual hemifield². Homologies of MT have been documented in several primate species^{5,16}, and the directionality of MT cells has been studied in the owl monkey^{5,8,22} and the macaque^{1,7,11,14,17,21}. The directional cells in MT respond well to movement of a visual stimulus in a preferred direction, and poorly to stimuli moving in other directions, with stimuli moving in the direction

180° opposite least effective or inhibitory.

Neurons from MT and surrounding cortex were recorded in 4 chronically prepared owl monkeys. Techniques were similar to those used by Baker et al.⁵, except that the stimuli were presented on a TV screen by computer-controlled hardware rather than projected on a tangent screen⁴. The TV screen was placed either 28.5 or 57 cm away from the animal so that the 40 mm by 30 mm screen subtended either 40° by 30° or 80° by 60° of the visual field.

A neuron's preferred direction of movement was determined using a series of bar stimuli swept through the receptive field in 12 different directions. The directions were pseudorandomly interleaved and presented 5 times each. The bar was usually oriented orthogonally to the direction of movement, and was of a length, width, and velocity qualitatively determined to elicit a good response from the neuron.

The cell was then tested for direction-specific adaptation as shown in Fig. 1A. A 20-s adaptation period of random visual noise (dot size = 2 mm, 50% density) was presented moving in the preferred direction, 180° opposite to the preferred direction, or as a stationary field. Each adaptation period was followed, after a 5-s delay, by a bar sweeping through the receptive field in the best or opposite direction.

* Present address: Laboratory of Sensorimotor Research, National Eye Institute, Bethesda, MD 21205 U.S.A.

Correspondence: J. F. Baker, Northwestern University Medical School, Physiology Department Ward 5, 303 E Chicago Avenue, Chicago, IL 60611, U.S.A.

Fig. 1. The best random after adaptation in the opposite direction while the animal is at rest.

The test paired adaptation presented sequence.

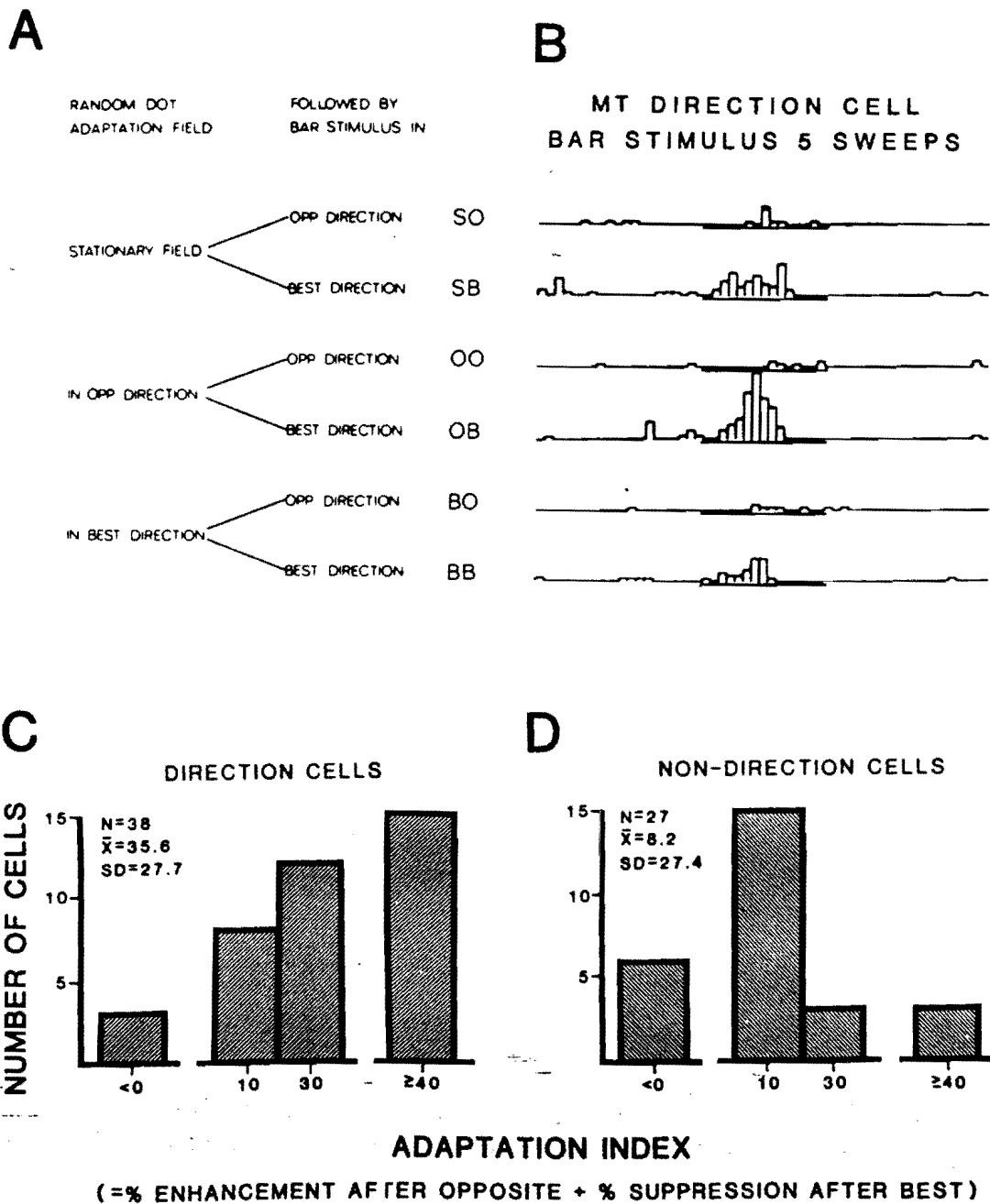


Fig. 1. A: diagrammatic representation of an adaptation series. A period of adaptation to stationary noise, or noise moving in either the best or opposite direction was followed by a bar stimulus moving in the best or opposite direction. These 6 conditions were pseudorandomly interleaved, and presented 5 times each. B: shows an example of an adaptation series. Notice that the response is strongest after adaptation in the opposite direction, and weakest after adaptation in the best direction. C and D: show the distributions of adaptation indices (AIs) for directional and non-directional cells. The AI was calculated by adding the % enhancement after adaptation in the opposite direction to the % suppression after adaptation in the best direction. The AIs for directional cells are generally high, while those for the non-directional cells tend to congregate near zero. The difference between these distributions is statistically significant at the 0.001 level.

The test consisted of 6 conditions: 3 adaptation fields paired with either of 2 bar stimulus conditions. In an adaptation test series, each of the 6 conditions was presented 5 times in a pseudorandomly interleaved sequence. The stationary noise conditions (SB,SO)

were used as control conditions to compare changes in responsiveness following adaptation in the best and opposite directions.

We completed quantitative testing on 65 neurons. We saw strong adaptation effects in most of the direc-

tional cells in MT. An online display of an adaptation series is shown in Fig. 1B. In 3 of the test conditions, SB, OB and BB, identical bars were moved through the receptive field in the same direction, but the response of the neuron to the bars was affected in a systematic way by the preceding adaptation period. Adaptation in the preferred direction of movement suppressed the response to the bar in the best direction, while adaptation in the opposite direction enhanced the response to the bar in the best direction. The responses to bars in the opposite direction (SO, OO, BO) were generally much weaker, and there was no significant change in their responsiveness following adaptation.

To compare populations of cells, an adaptation index (AI) was computed using the formula:

$$\begin{aligned} \text{AI} &= \% \text{ enhancement after adaptation in the opposite direction } (\text{OB}/\text{SB}-1) \\ &+ \% \text{ suppression after adaptation in the best direction } (1-\text{BB}/\text{SB}) \\ &= (\text{OB}/\text{BB})/\text{SB} \end{aligned}$$

The distribution of AIs for 38 directional cells is shown in Fig. 1C. A cell was considered directional if it fired 3 times more to a stimulus in the preferred direction than to stimuli in directions 120°, 150° or 180° opposite. Sixty-one percent of the cells studied were directional by this stringent criterion. In a previous study⁵, 66% of MT cells were found to meet this criterion, and the result is in keeping with other reports (see ref. 8, Table 1). Seventy percent of directional cells had AIs higher than 20, 38% higher than 40. The mean AI for directional cells was 36.5 with approximately equal contributions from enhancement (mean = 18.7) and suppression (mean = 17.9) effects. A distribution of the much weaker adaptation effects for non-directional cells from MT and surrounding cortex is shown in Fig. 1D. Eighty percent of the non-directional cells' AIs were lower than 20, and the mean AI of 8.2 was not significantly different from zero ($t = 1.56$, n.s.). The difference between directional and non-directional cell populations was significant ($t = 3.95$, $P < 0.001$).

Directional cells which exhibited direction-specific adaptation effects were intermixed with non-directional cells that did not show the effect. An example of an oblique penetration is shown in Fig. 2. In this

penetration, complete direction preference and adaptation information was collected for 8 cells. Five of these cells were clearly directional and had clear adaptation effects. The 3 non-directional cells showed little systematic change following the adaptation stimuli.

Although most MT cells respond well to visual texture within the classically mapped receptive field⁵, the adaptation field produced by the TV system typically extended into a surrounding inhibitory region^{3,4} and so rarely (5/38 cells) evoked strong responses from directional neurons, and in only one case was this response comparable to the best response to a moving bar. Most often the neurons responded weakly to movement of noise in the best direction, with very weak or no response to either the stationary noise field or the field moving in the opposite direction. A strong response to the adaptation field was not necessary to produce a strong adaptation effect. In the example in Fig. 1B, no response above spontaneous was observed to any of the adaptation stimuli.

Barlow⁶ reported directional cells in the retina of the rabbit which, after prolonged stimulation, showed a suppression of spontaneous firing for a period of time appropriate to the waterfall illusion. Vautin and Berkley¹⁸ and Von der Heydt et al.¹⁹ have shown that cat striate cortex cells exhibit habituation effects which are consistent with the decay of motion aftereffects. These cells showed some direction specificity, and gave considerably reduced responses to their preferred direction of movement following adaptation in that direction. Movshon et al.¹³ demonstrated that adaptation effects for contrast sensitivity were present at the level of the striate cortex but were absent at the level of the lateral geniculate nucleus (LGN). In cat striate cortex, the directional cells were more affected by adaptation. Fatigable cells such as these could provide input to the adaptable MT neurons.

None of these experimenters showed statistically significant enhancement of responses following adaptation. The enhancement of MT cell responses following adaptation opposite their preferred direction could be the result of the habituation of an inhibitory input tuned to the direction opposite the preferred direction of movement. However, the adaptation effects of MT neurons probably cannot be explained by

DIREC

BAXX21A

BAXX21C

BAXX21E

BAXX21F

BAXX21G

BAXX21H

BAXX21I

BAXX21J

Fig. 2. A hand column with strong directional preference for those cells

fatiguing stimulus. Some explain adaptation specific movement directional neurons consist

- 1 Allbright organ: MT of
- 2 Allman: al field: the o (1971)
- 3 Allman: specif

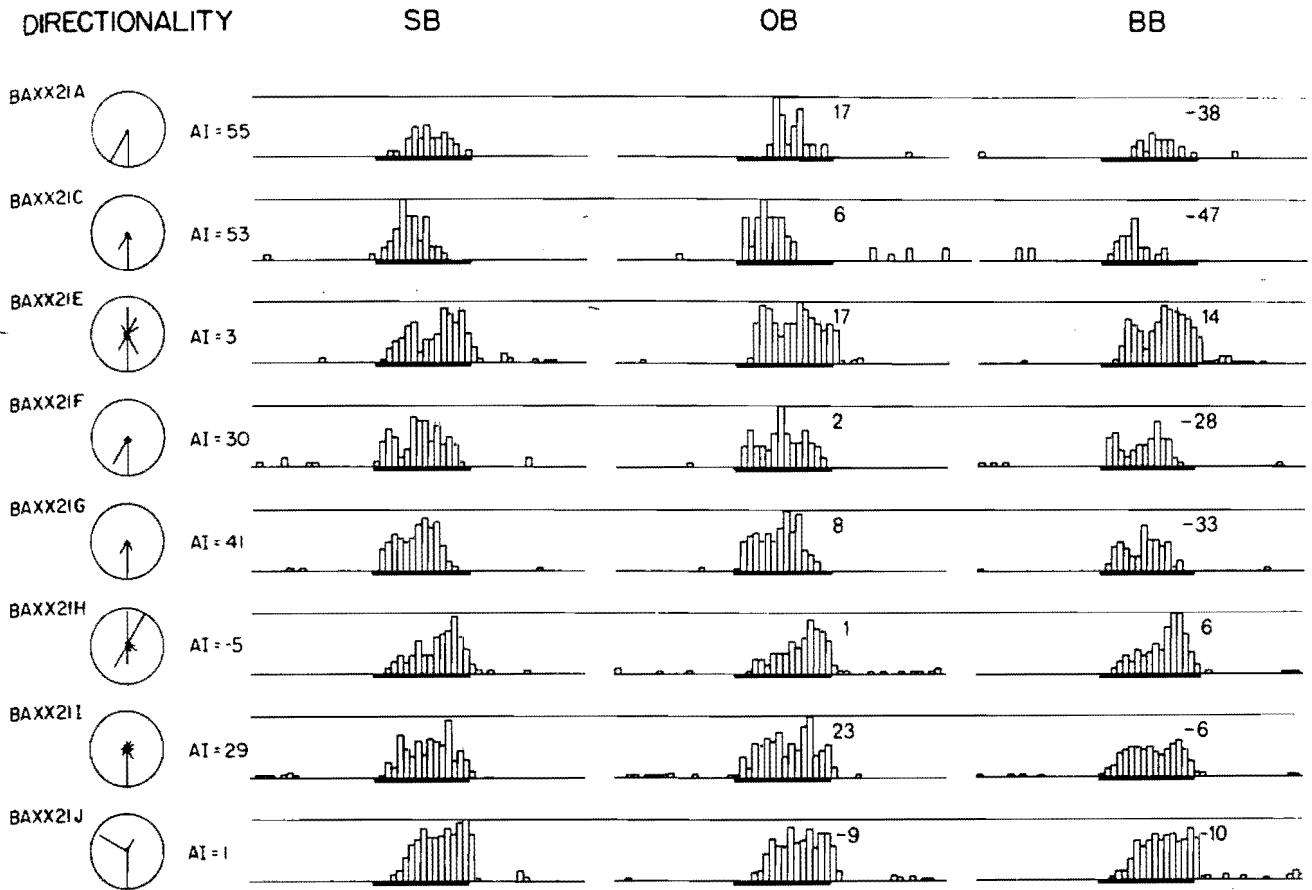


Fig. 2. A display of adaptation effects for 8 cells from the same penetration. The polar plot of a cell's directionality is shown in the left hand column, the adaptation index (AI) next to the polar plot and the appropriate histograms in the succeeding 3 columns. For cells with strong directional preferences, such as BAXX21A, C, F, G and I, the AIs are high, and the histograms reflect this effect. For those cells which are without directional preference, E, H and J, the AIs are uniformly low.

fatiguing at the level of MT, since the adaptation stimulus rarely fired an MT cell at a high rate.

Some models put forward by psychophysicists to explain the motion aftereffect and direction-specific adaptation include comparisons between direction-specific channels tuned for opposing directions of movement^{12,15}, or distributions of activity of several direction-specific channels^{9,10}. The juxtaposition of neurons with opposite preferred directions in MT is consistent with these models¹⁻⁵. The model described

by Moulden and Mather¹² predicts responses similar to the enhancement effect we report here in MT cells.

We thank Leslie Wolcott for drawing Fig. 2. This research was supported by NIH Grants NS-00178, EYNS-03851 and GM-07737; NSF Grant BNS-77-15605, and the Pew Memorial Trust. Preparation of this report was also supported by NIH Grant EY-05289.

- 1 Albright, T.D., Desimone, R. and Gross, C.G., Columnar organization of directionally selective cells in visual area MT of the macaque, *J. Neurophysiol.*, 51 (1984) 16-31.
- 2 Allman, J.M. and Kaas, J.H., A representation of the visual field in the caudal third of the middle temporal gyrus of the owl monkey (*Aotus trivirgatus*), *Brain Research*, 31 (1971) 84-105.
- 3 Allman, J.M., Miezin, F. and McGuinness, E., Stimulus specific responses from beyond the classical receptive field:

neurophysiological mechanisms for local-global comparisons in visual neurons, *Annu. Rev. Neurosci.*, 8 (1985) 407-430.

- 4 Allman, J.M., Miezin, F. and McGuinness, E., Direction and velocity specific responses from beyond the classical receptive field in cortical visual area MT, *Perception*, in press.
- 5 Baker, J.F., Petersen, S.E., Newsome, W.T. and Allman, J.M., Visual response properties of neurons in four extrastriate visual areas of the owl monkey (*Aotus trivirgatus*): a

- quantitative comparison of medial, dorsomedial, dorsolateral and middle temporal areas, *J. Neurophysiol.*, 45 (1981) 397-416.
- 6 Barlow, H.B. and Hill, R.M., Evidence for a physiological explanation of the waterfall phenomenon and figural aftereffects, *Nature, (London)* 200 (1963) 1345-1347.
 - 7 Dubner, R. and Zeki, S.M., Response properties and receptive fields of cells in an anatomically defined region of the superior temporal sulcus in the monkey, *Brain Research*, 35 (1971) 528-532.
 - 8 Felleman, D.J. and Kaas, J.H., Receptive-field properties of neurons in middle temporal visual area (MT) of owl monkeys, *J. Neurophysiol.*, 52 (1984) 488-513.
 - 9 Levinson, E. and Sekuler, R., Adaptation alters perceived direction of motion, *Vision Res.*, 16 (1976) 779-781.
 - 10 Mather, G., The movement aftereffect and a distribution-shift model for coding the direction of visual movement, *Perception*, 9 (1980) 379-392.
 - 11 Maunsell, J.H.R. and Van Essen, D.C., Single unit responses in the middle temporal area of the macaque. I. Direction, speed, and orientation, *J. Neurophysiol.*, 49 (1983) 1127-1147.
 - 12 Moulden, B. and Mather, G., In defense of a ratio model for movement detection at threshold, *Q. J. Exp. Psychol.*, 30 (1978) 505-520.
 - 13 Movshon, J.A., Bonds, A.B. and Lennie, P., Pattern adaptation in striate cortical neurons, *ARVO* (abstr.) (1980) 193.
 - 14 Newsome, W.T., Mikami, A. and Wurtz, R.H., Direction selective responses to sequentially flashed stimuli in extrastriate area MT in the awake macaque monkey, *Soc. Neurosci. Abstr.* 8 (1982) 812.
 - 15 Sutherland, N.S., Figural aftereffects and apparent size, *Q. J. Exp. Psychol.*, 13 (1961) 222-228.
 - 16 Van Essen, D.C., Visual areas of the mammalian cerebral cortex. In W.M. Cowan (Ed.), *Annu. Rev. Neurosci.*, Vol. 2, Annual Reviews, Palo Alto, CA, 1979, pp. 227-263.
 - 17 Van Essen, D.C., Maunsell, J.H.R. and Bixby, J.L., The middle temporal visual area in the macaque: myeloarchitecture, connections, functional properties, and topographic organization, *J. Comp. Neurol.*, 199 (1981) 293-326.
 - 18 Vautin, R.G. and Berkley, M.A., Responses of single cells in cat visual cortex to prolonged stimulus movement: neural correlates of visual aftereffects, *J. Neurophysiol.*, 40 (1977) 1051-1065.
 - 19 Von der Heydt, R., Hanny, P. and Adorjani, C., Movement aftereffects in the visual cortex, *Arch. Ital. Biol.*, 116 (1978) 248-254.
 - 20 Wohlgenuth, A., On the aftereffect of seen movement, *Br. J. Psychol. (Mongr. Suppl.)*, 1 (1911).
 - 21 Zeki, S.M., Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey, *J. Physiol. (London)*, 236 (1974) 549-573.
 - 22 Zeki, S.M., The response properties of cells in the middle temporal area (area MT) of owl monkey visual cortex, *Proc. R. Soc. London Ser. B*, 207 (1980) 239-248.

Seven
cleus (P
(AII) an
tagonist
effect of
AII- an

The
lar stru
by an
(ACh
sponse
releas
in the
avent
hypot
these
and ce

In
nous
ing to
SFO
rons i
al stu
ACh-
be de
to the
recep
fect o
on th
ally i
and t

Corres

0006-*

