

Spatial Adaptation of the Cortical Visual Evoked Potential of the Cat

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Adaptation that is spatially specific for the adapting pattern has been seen psychophysically in humans. This is indirect evidence for independent analyzers (putatively single units) that are specific for orientation and spatial frequency in the human visual system, but it is unclear how global adaptation characteristics may be related to single unit performance. Spatially specific adaptation was sought in the cat visual evoked potential (VEP), with a view towards relating this phenomenon with what we know of cat single units. Adaptation to sine-wave gratings results in a temporary loss of cat VEP amplitude, with induction and recovery similar to that seen in human psychophysical experiments. The amplitude loss was specific for both the spatial frequency and orientation of the adapting pattern. The bandwidth of adaptation was not unlike the average selectivity of a population of cat single units. Invest Ophthalmol Vis Sci 25:640-646, 1984

Steady viewing of a high contrast, periodic pattern such as a sine-wave grating results in a transient reduction of contrast sensitivity that is specific to certain spatial parameters of the viewed pattern. Sensitivity to gratings with a spatial frequency or orientation that is significantly different from that of the adapting pattern is reduced much less than for gratings that match the adapting pattern.^{1,2} The specificity of pattern adaptation has been used as evidence for the existence of discrete channels in the visual pathways that are selective for spatial frequency and orientation.^{2,3} The common assumption has been that these channels are physiologically realized by cells in the striate cortex, which have the requisite stimulus specificity⁴⁻⁶ and that pattern adaptation simply reduces the contributions from cells most strongly driven by the adapting pattern.^{1,7} The channel characteristics revealed by adaptation are believed by some (eg, references 2 and 8) to reflect the spatial properties of neurons in the human visual system.

Recently, however, it has been shown that, at least in the cat, pattern adaptation of striate cortical cells alters the spatial selectivity of the cells themselves.⁹ If the cat is a valid model of pattern adaptation in the human, this complicates the interpretation of the channels that are inferred psychophysically. Since single-unit selectivity is changed by adaptation, channel

characteristics demonstrated by adaptation may resemble neither the characteristics of single cells nor unadapted excitatory channels as revealed, for example, by subthreshold summation.¹⁰

This study has two goals, the first being to test the adequacy of the cat as a model for pattern adaptation in the human. The cortical visually evoked potential (VEP) is used as an indicator of global cortical performance under conditions of stimulation similar to those used in psychophysical pattern adaptation experiments. Results show that, both qualitatively and quantitatively, the cat is similar to humans in the degree of adaptation, rate of recovery, and spatial specificity of adaptation for both spatial frequency and orientation. As is also seen in single units,⁹ adaptation of the VEP results in changes of both the slope of the response versus log contrast function as well as sensitivity.

The second goal is a comparison of the spatial bandwidth of the adapted spatial frequency and orientation channels with known behavior of cat single units to estimate the degree to which channels measured by adaptation are adequate predictors of single unit characteristics. Despite the changes in single unit selectivity caused by adaptation, adaptive channel bandwidths for both orientation and spatial frequency are not unlike the *average* selectivity of single units.

Materials and Methods

Preparation and Recording

All procedures described herein conform to the ARVO Resolution on the Use of Animals in Research. Sixteen adult cats (2.5-4.2 kg) initially were anesthetized with Fluothane (Ayerst Labs, NY) and cannulated

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in a forelimb vein. Surgical anesthesia subsequently was maintained with 2.5% Surital (thiamylal sodium). After cannulation of the trachea, the animal was mounted in a stereotaxic headholder. The scalp was reflected on the midline and stainless steel screws were inserted in the skull at bregma (indifferent electrode) and at H-C coordinates L0, P4 (recording electrode) which is centered between the Area Centralis representations in Area 17. Evoked potentials were amplified $\times 10,000$ (band-limited within 1–100 Hz) and sent to the computer for digitization.

Mydriasis and cycloplegia were induced with topical phenylephrine HCl (10%) and atropine sulfate (1%). Contact lenses with 4 mm artificial pupils were fit to the nearest 0.25 mm base curve. Spectacle lenses rendered the retinae conjugate with the stimulus plane as dictated by direct ophthalmoscopy. Areae centrales were aligned on the center of the stimulus field with a reversible ophthalmoscope. Stimulation was always monocular. Every 4 hr, the contact lenses were removed and cleaned and the eyes were irrigated with 3% saline.

For recording, the cats were paralyzed with gallamine triethiodide (10 mg/kg-hr) in a solution containing lactose and a small amount of Surital (1 mg/kg-hr) to help stabilize anesthesia.¹¹ A breathing mixture of nitrous oxide (75%), oxygen (23.5%), and carbon dioxide (1.5%) was delivered at 30 strokes/min in a volume sufficient to maintain the peak expired CO₂ at 4.2%, which is normal for the resting cat.¹² Rectal temperature was held at 37.5°C, and heart activity was monitored as an indicator of adequate anesthesia.

Stimulation and Data Processing

Sine-wave gratings were generated digitally on one of two displays, a Tektronix (mean luminance 100 cd/m², P31 phosphor) or a Joyce Electronics (m.1. 280 cd/m², P4 phosphor). Both displays had linear luminance modulation for contrasts of at least 0.8. Viewing distance was either 57 or 114 cm, and displays were masked to a circular field subtending at least 10 deg.

Responses were digitized with 12 bits of resolution and loaded into histograms at 128 bins/sec. Following the method of Shapley and Snyder,¹³ the gratings phase-reversed (square-wave) at 1 Hz, yielding a response waveform every 500 msec. When Fourier transformed, the response energy is contained at harmonics of 2 Hz. Root mean square (RMS) summation of the amplitudes of the first 15 harmonics (2, 4, 6 . . . 30 Hz) yields a figure for signal plus noise. The first 15 odd harmonics (1, 3, 5 . . . 29 Hz) are not correlated with the stimulus and yield a figure for noise alone. Stimuli were presented in blocks lasting 4 or 10 sec in random order to minimize the effects of endogenous cortical response variability¹⁴ or adaptation by the test stimuli.

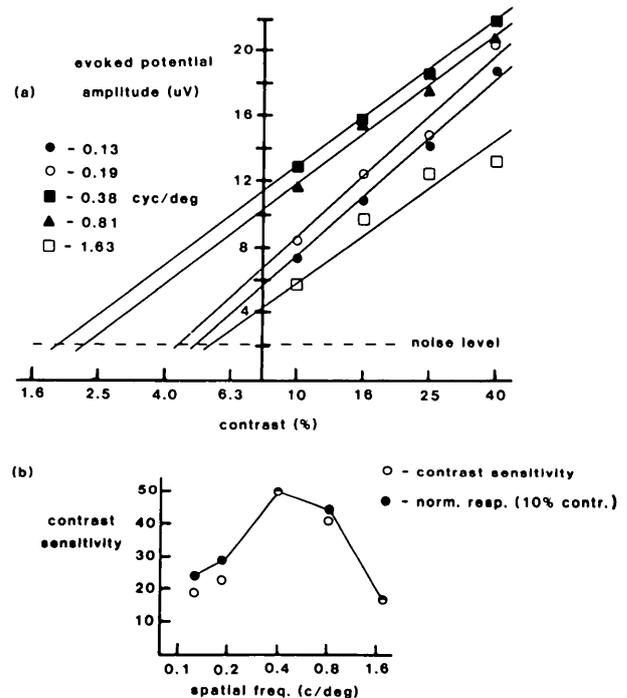


Fig. 1. The normal cat VEP. **a**, Contrast-response functions for five different spatial frequencies. Linear extrapolations to the noise level (mean of all measurements, see text) provide an indicator of "threshold".^{3,13} **b**, The inverse of the contrast "threshold" is plotted as contrast sensitivity (open circles). The shape of the contrast sensitivity curve is not unlike the response function at 10% contrast (filled circles), which has been normalized so that the peak values (at 0.38 cycle/deg) coincide.

A total of 200 sec of averaging per datum resulted in a best signal to noise ratio of about 14:1.

Results

Normal VEP

The overall visual performance of each animal was screened by presenting a series of spatial frequencies spanning the cat's range of resolution. Each spatial frequency was presented at several contrasts. In healthy animals, the response amplitude was found to be linear with the logarithm of the contrast¹⁵ over a very wide range (Fig. 1a). A least-squares linear fit was used to define threshold (intercept with the noise level) and the slope of the response versus log contrast function (a correlate of the gain) for each spatial condition. VEP threshold derived in this way is reasonably closely related with the psychophysical threshold in both the human³ and the cat.¹⁵ In these measurements, contrast sensitivity ranged from about 40–100 at the optimum spatial frequency, which was usually 0.4–0.5 cycles/deg. The highest effective spatial frequency averaged about 3 cycles/deg and once exceeded 4.5 cycles/deg. Comparable figures for the behaving cat are a contrast sensitivity of about 100 at peak and a cutoff of 5 cycles/

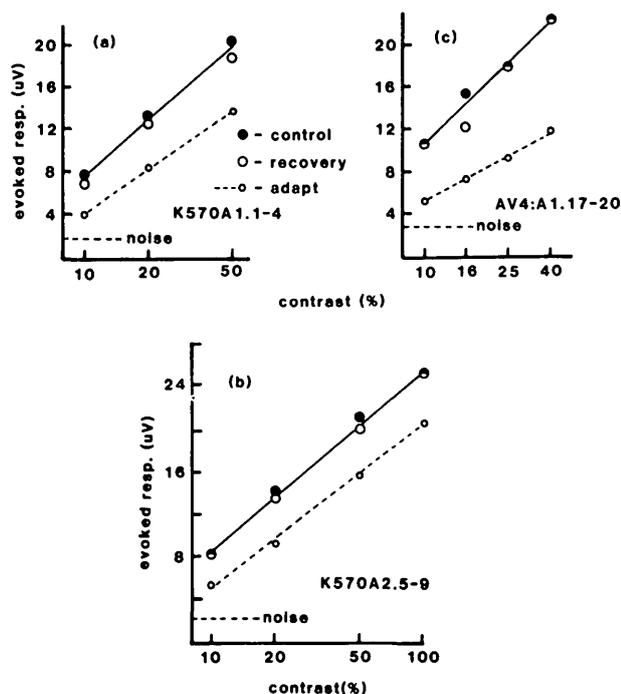


Fig. 2. Three examples of the degree and nature of adaptation. The large filled and open circles represent control measurements made immediately before and at least 40 min after adaptation, respectively. The solid lines are fitted to the mean of the point pairs. The small open circles and dotted lines show the contrast-response function during adaptation to a spatially identical 80% contrast grating. All gratings were 0.4 cycle/deg and horizontal.

deg.¹⁶ While there are differences in the behaving cat and the VEP at the limits of performance, the VEP nonetheless seems to provide a reasonable estimate of global visual function.

Nonoptimal spatial frequencies, which resulted in higher thresholds, generally yielded linear fits with reduced slopes so that the fitted lines did not cross each other above threshold (eg, Fig. 1a), although this was not always the case. When the lines did cross, usually well above threshold, line pairs did not share the same intersection. The shape of the response versus spatial frequency function thus changed somewhat with increasing contrast, but for low contrasts (eg, 20% or less) the functions bore a close resemblance to the contrast sensitivity functions calculated from the VEP thresholds (Fig. 1b). For this reason, data resulting from low-contrast stimuli will be used for comparison with psychophysical results, which are all based on threshold measurements.

Degree of adaptation

Every adaptation sequence began with a control measurement to assess responsiveness in the unadapted condition. Each test consisted of a 10-sec exposure of a stimulus condition selected at random from a list. Each list entry was presented 20 times altogether. After

control measurements, the adapting pattern was shown for a primary exposure of 30 sec. Data measurements that followed were 4 sec long, and each was followed by a 4-second "topping up" exposure of the adapting stimulus. After every stimulus condition in the list (eg, all spatial frequencies at all contrasts) had been presented once, the primary exposure was repeated and followed by more data collection. The entire sequence was repeated 50 times. Finally, after at least 30 min to allow recovery from adaptation, a second control measurement was made.

The intrinsic variability of cortical responsiveness is a very real and troublesome phenomenon (eg, references 17 and 18), especially when measurement sequences require several hours as was the case here. Increases or decreases of responsiveness on the order of 30% were not uncommon, so the interpretation of adaptation results had to be approached with some caution. Ideally, cases were considered valid when the amplitudes resulting from both the pre- and postadaptation control measurements agreed reasonably well. Since adaptation results in a *decrease* in responsiveness, cases also were accepted if either the preadapt control had to be scaled *up* or the postadapt control had to be scaled *down* to match the other control. In either instance, such scaling indicates a net *increase* in responsiveness over the long term, which is not confused easily with the response decrease caused by adaptation.

Three examples of the impact of adaptation are shown in Figures 2a-c. These examples all had good agreement between pre- and postadaptation controls and were considered most representative. In all of these cases, test and adapting gratings shared the same spatial configuration, horizontal and 0.4 cycle/deg, which is near the optimum for the cat. Adaptation contrast was 80%.

Adaptation clearly results in decreases of both sensitivity and the slope of the response versus log contrast curve, although there appears to be no set rule relating these changes. In Figure 2a, the slope is reduced by 25% and sensitivity (ie, threshold is elevated) by 0.15 log unit. Similar figures for 2b and c are 8% and 0.2 log unit and 45% and 0.15 log units, respectively. Note that the results of Figures 2a and 2b, which show markedly different losses in slope, come from the left and right eyes of the same cat.

The impact of pattern adaptation on the cat VEP threshold is, thus, reasonably robust, although less than the effect seen psychophysically in humans, which can show shifts of up to 0.5 log unit.^{2,19} Either the cat is inherently less susceptible to adaptation or some aspect of the recording situation reduces the apparent effectiveness of adaptation. Since the slope of the supra-threshold response function also decreases with adaptation, responsiveness (as gauged by the stimulus contrast required to produce a criterion response level)

decreases even more for suprathreshold stimuli. This is at odds with one report on the effectiveness of adaptation on suprathreshold observations in the human. By contrast matching in adapted and unadapted regions of the visual field, Blakemore, Muncey, and Ridley¹⁹ found that adaptation reduced perceived contrast *less* for higher contrast test stimuli. This is consistent with an increase in threshold, but also implies an increase in gain. The author has no explanation for this discrepancy.

Time Constant for Recovery

Pattern adaptation is a transient phenomenon. In the original studies, a "topping up" exposure of the adapting grating between test presentations was found to be necessary to maintain adaptation. Recovery of psychophysical threshold after adaptation, followed in time by a method of tracking, appeared to be exponential with a time constant of about 20 sec.² This has not been confirmed in the human VEP.

The multiple histogram approach allows observation of the recovery of the VEP after adaptation despite the requirement for long averaging times for each datum. In these experiments, both the adapting and test gratings were again horizontal and 0.4 cycle/degree. The experiments began with a 30-sec exposure to the adapting pattern (80% contrast) similar to the primary adapting exposure of the previous experiment. The adapting exposure was followed by a 3-sec foreperiod during which the screen was illuminated uniformly at the mean level, then a test pattern was shown for 2 sec. The test pattern was low contrast (20% or less) to minimize the adaptive effects of the test itself. The 3-sec foreperiod/2-sec test procedure was repeated 12 times, for a total interval after adaptation of 60 sec. Evoked potentials from each of the 12 tests were directed, in order, to separate histograms. After testing, a uniform screen was displayed for another 60 sec to allow for further recovery, and the entire process was repeated beginning with the primary adapting exposure. Fifty repetitions of this sequence provided only 100 sec of averaging per datum, so the signal/noise ratio was not so good as in other experiments, but further averaging made the experiments far too lengthy.

Changes in the response amplitude resulting from this procedure are normalized to the last four points taken during the test interval, ie, 45–60 sec after adaptation stops. This test, therefore, does not address long-term components of adaptation. While a comparison with the totally unadapted condition would have been more desirable, in two of the four cases showing short-term adaptation recovery, the control measurements made before this procedure produced amplitudes lower than the last points in the test interval, most likely a result of response variability.

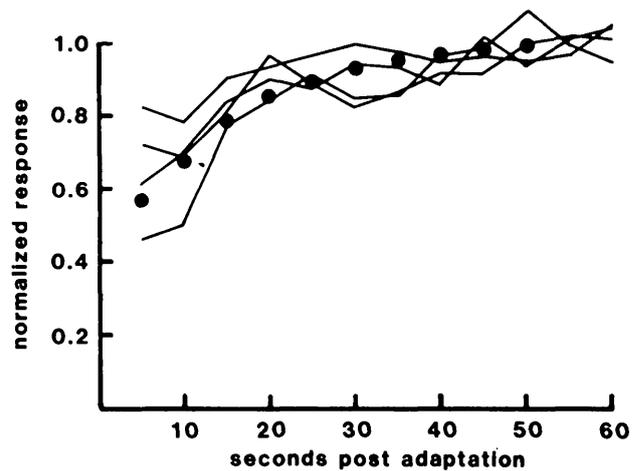


Fig. 3. Rate of recovery from adaptation. The solid lines are four examples of response recovery after adaptation to an 80% contrast 0.4 cycle/deg horizontal grating for 30 sec. The test gratings, presented at 5-sec intervals (see text), were spatially identical to the adapting grating and had a contrast of 20%. Responses were normalized to the last four points in the test interval. The filled circles represent an exponential rise with a time constant of 13 sec.

The initial response after adaptation (Fig. 3) ranged from 0.45 to 0.82 times the control value in the four cats tested this way. Recovery is generally monotonic, but is not sufficiently well-organized to suggest any particular time function. An exponential function with a time constant of 13 sec (filled circles) is at least helpful in describing the trend, and is similar to the human time constant of 20 sec.

Spatial Specificity of Adaptation

The primary feature distinguishing spatial adaptation is its specificity, which is seen in the degree to which adaptation fails to alter responses to stimuli that are spatially dissimilar to the adapting stimulus. Here spatial specificity is reflected by a characteristic change, during adaptation, of the shape of the function relating response amplitude with some spatial parameter. The first series of experiments tested the impact of adaptation on responses to spatial frequencies that were different from the adapting frequency. Control measurements were made both before and after adaptation. In eight cases, the shapes of both control measurements were consistent; three additional cases showed some changes in the preparation during the measuring process and were discarded.

In five of the eight consistent cases, the response loss was greatest at the spatial frequency of adaptation; adaptation was thus judged to be pattern-specific. Examples are shown in Figure 4, where all responses are from a test contrast of 20%. Adaptation at 0.4 cycle/deg results in a response attenuation of 0.60 (Fig. 4a) and 0.61 (Fig. 4c) at 0.4 cycle/deg. The average attenuation one octave away in either direction is 0.80, that

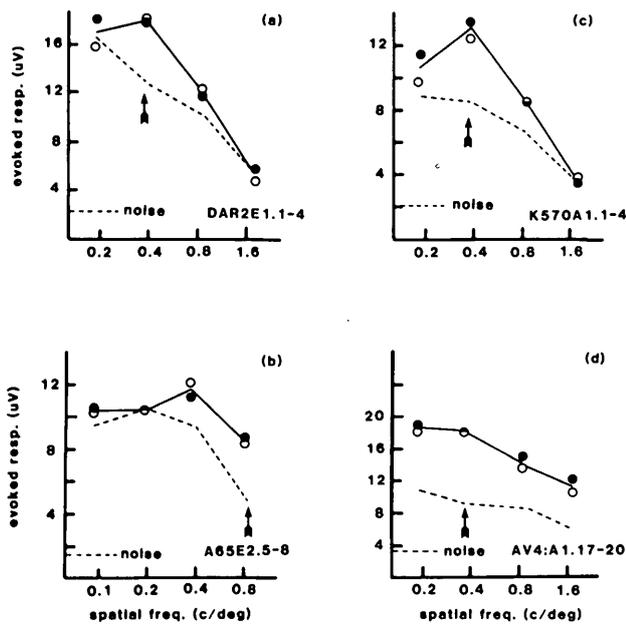


Fig. 4. Four examples of spatial frequency specificity of adaptation. The display scheme is as in Figure 2, except that the curves intersect explicit data points or point pair averages instead of representing a mathematical fit. Adapting contrast was 80% and the test contrast was 20%. a, c, and d, Adaptation at 0.4 cycle/deg; b, adaptation at 0.8 cycle/deg.

is, the effect of adaptation is reduced by one-half. Similarly, adaptation at 0.8 cycle/deg (Fig. 4b) yields attenuation of 0.50 at that same frequency, 0.81 one octave away and virtually no change two or more octaves away.

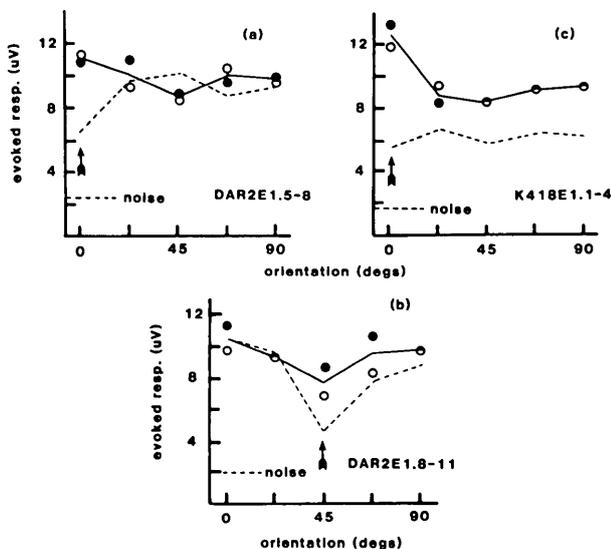


Fig. 5. Three examples of orientation specificity of adaptation. The display scheme is the same as in Figure 4. a, b, Complementary adaptation in the same animal; in a, adaptation and a selective loss is at 0 deg (horizontal), and in b, adaptation and a selective loss is at 45 deg (right oblique). c, A local component of loss at 0 deg is accompanied by a global loss at all orientations.

In the human, enhancement of contrast sensitivity has been found for test spatial frequencies at least three octaves removed from the adapting frequency.²⁰ This kind of reciprocity is not seen here (eg, Fig. 4b), but the failure may be due to the limited spatial bandwidth of the cat. A usable three-octave spread required low-frequency stimuli of 0.2 cycle/deg or less; such stimuli barely qualify as periodic, since at best only three cycles could be displayed on the screen.

Three of the eight cases used to study spatial frequency specificity showed that response losses due to adaptation were uniform over the spatial frequency spectrum tested. The result may be spurious in two of these instances. Both had postadaptation control measurements that were uniformly lower in amplitude than the measurements made during adaptation, probably indicating a long-term deterioration of the response. One case, however, (Fig. 4d) showed identical pre- and postadapt control amplitudes, yet adaptation clearly resulted in significant losses at all spatial frequencies tested. Global adaptation also was seen in the orientation domain, as discussed below.

The orientation-selective channels in the human visual system revealed by spatial adaptation are often viewed as indirect indicators of the behavior of orientation-selective cortical cells found in cat and monkey. The next experiments explored the extent to which spatial adaptation in the cat VEP is orientation-specific, with a view towards relating the known orientation characteristics of cat cortical cells with this more indirect indicator of orientation selectivity.

Control measurements were made with gratings oriented at several meridians spanning at least 90 deg. Spatial frequency was fixed at 0.4 cycle/degree and, at each orientation, gratings were presented at several contrasts. Response amplitude varied with orientation, usually systematically, with the largest responses resulting from presentation of horizontal and vertical gratings. This "oblique effect" was seen in 13 of the 16 cats studied.²¹ At the obliques, amplitudes were smaller than those for gratings presented at the principal meridians by an average of 0.77. The oblique effect could be enhanced markedly or eliminated by adaptation, depending on the adapting conditions.

The procedure for adaptation was the same as that described in the previous section except that testing was parametric on orientation instead of spatial frequency. Response losses were usually greatest at the orientation of the adapting grating. In 9 of the 12 acceptable experiments, adaptation was confined to the adapted orientation, with little or no loss of response at orientations as close as 22.5 deg. Figures 5a and b demonstrate that the response loss was correlated with the adapting grating. In the first example, the adapting grating was presented at an orientation of 0 deg (horizontal). The response for that orientation was reduced

by almost one-half, but little systematic change is seen in responses from the other orientations. In Figure 5b, the experiment was repeated in the same cat with the adapting grating oriented at 45 deg. Again, response losses were concentrated at the adapted orientation; only a small decrease is seen at 67.5 deg.

Not all of the results were so clear-cut. In an additional three cases, adaptation was found to have a global component in addition to the local effect. Figure 5c shows an example in which adaptation at 0 deg resulted in a very large loss at that same orientation, with more moderate reductions at all of the other orientations tested. This global loss could have been due to a general decrease in responsiveness from natural variability rather than from the adaptation process. In this and one other example, however, the control measurements taken after adaptation had to be scaled down to get good agreement with the control taken before adaptation, arguing against a general loss of responsiveness due to variability. While spatial adaptation measured psychophysically in the human does not usually have a global component, unselective losses have been seen when the effects of adaptation are measured with the VEP. One study²² reported that, while the primary loss was at the spatial frequency of adaptation (4 cycle/deg), responses also were attenuated somewhat over the range of 0.6–20 cycle/deg. Smith and Jeffreys²³ showed that substantial global losses (with local components) over both spatial frequency and orientation were the rule rather than the exception.

Discussion

This study demonstrates clearly that in the cat the amplitude and sensitivity of the evoked response can be modified selectively by adaptation to high contrast patterns. Such a modification addresses the origins of the evoked response itself. While there are no substantiated theories on the generation of the visual evoked potential, current ideas suggest that the surface potential is a reflection of the summation of slow PSP changes within neurons near the recording electrode, as well as possible fiber activity.^{24,25} One must then consider the possibility that some component of the signal that is measured over area 17 originates in LGN afferent fibers and their terminations rather than from cortical neurons. Since LGN neurons are not susceptible to pattern adaptation,²⁶ much of the VEP measured here must come from cortical activity. The selectivity of adaptation in the orientation domain supports this view, since the responses of LGN neurons are not greatly dependent on stimulus orientation. On the other hand, LGN contributions to the signal may account for the smaller amount of adaptation seen in the cat VEP as compared with human psychophysics.

Additional evidence for the causal relationship between cortical activity and the VEP comes from the

marked similarity between the adaptive behavior of area 17 single units and the VEP. In two studies,^{9,27} all cortical units that had a vigorous and organized response showed a decrease in response amplitude when exposed to a strongly effective stimulus. Adaptation was induced in less than 30 sec and reduced suprathreshold responses 0.3–0.5 log units. Recovery was exponential, with time constants ranging between 5 and 35 sec for different cells (cf, Fig. 3). These figures also compare favorably with psychophysical studies in the human,^{2,19} although, as pointed out earlier, adaptation in the human is more profound. On the whole, it is reasonable to conclude that the processes governing pattern adaptation are similar in cats and humans.

It has been suggested that the selectivity of spatial adaptation is direct evidence for the existence of channels in the human visual system that are selective for spatial frequency and orientation [eg, reference 2]. While I find no argument with this idea, the implication that the bandwidth of adaptation in either the spatial frequency or orientation domain is a direct indicator of the channel (putatively realized by single units in cortex) bandwidth^{2,8} is rather harder to confirm. No clear resolution to this question presents itself. In the human, there is already some dispute based on the finding that channel bandwidths revealed by sub-threshold summation are consistently narrower than those realized by adaptation.¹⁰ On the other hand, single units in the cat do not adapt globally but in a way that is selective for the spatial configuration of the adapting stimulus, arguing for adaptive mechanisms that are more narrowly selective than are single units. The data reported here are, unfortunately, supportive of both ideas. The adapted bandwidth for spatial frequency spans on the order of one octave in each direction. A study of 156 cells, both simple and complex, located within 5 deg of area centralis reports an average one-half amplitude bandwidth of 1.3 octaves, with a range of 0.7–3.2 octaves.⁶ The bandwidth for VEP adaptation is consistent with these figures and does not, in fact, show the narrowness that might be predicted from the adaptive selectivity of the single units. On the other hand, the VEP adapted bandwidth is narrower than the broadest single-unit bandwidths. A similar comparison can be made in the orientation domain. Eighty-eight single units showed an average orientation bandwidth (one-half amplitude) of ± 18.3 deg,⁵ comparable to the ± 22.5 deg bandwidths found here. Again, while the average values agree, the existence of single units with far broader selectivity than the average would predict a broader adapted bandwidth. What can be said with some assurance is that the adapted bandwidths in the cat agree fairly well with the *average* bandwidths of cat single units, so it is reasonable to suspect the same in humans despite the complication of the adaptive selectivity of single units.

The nature of the changes wrought by adaptation and the possible underlying physiologic substrates are a final consideration. Adaptation results in both reductions in slope (gain) and sensitivity (right shift) of the response-versus-log contrast curves. Similar changes are seen in single units.⁹ A reduction in sensitivity is, of course, required to account for the elevation of psychophysical thresholds. The effect is not attributable to a simple mechanism such as fatigue, since the responses of single units can remain normal at test spatial frequencies removed from the adapting frequency.⁹ This latter finding suggests that adaptation is involved in some way with inhibitory mechanisms that may enhance cortical selectivity.²⁸ Prolonged inhibition has been implicated as a factor in spatial adaptation as measured psychophysically,⁸ but whether and how this comes about remains unclear.²⁹ At the cellular level, models of inhibition generally involve an increase in membrane conductance, which serves to shunt PSP activity to the outside media resulting in reductions in gain.³⁰ This mechanism does not, however, account for changes in sensitivity. One attractive alternative is to assume that the visual cortex has an independent gain control mechanism that adjusts its operating point as a function of stimulus contrast, analogous to the luminance gain control found in the retina. Preliminary evidence for such a control has been reported recently.³¹ Spatial adaptation, as measured here, may then simply reflect the slow recovery of this system after having adjusted to the high contrast of the adapting stimulus.

Key words: spatial frequency, orientation, cat, visual cortex, visual evoked potential

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