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The Dependence of Response Amplitude and Variance of Cat Visual Cortical Neurones on Stimulus Contrast

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Summary. For neurones in the cat's striate cortex, we examined the dependence of response on the contrast of moving sinusoidal gratings. Most neurones showed a clear threshold contrast below which no response was elicited. Such thresholds presumably contribute to the animal's behavioural threshold, which should not be accounted for solely in terms of the detection of a signal in the presence of spontaneous "noise". Above threshold, the response amplitude usually increased linearly with contrast until it began to saturate at the highest contrasts. The variance of the response increased with its amplitude; this finding perhaps underlies the Weber-Fechner relation for psychophysical contrast discrimination.

Key words: Visual cortex – Response linearity – Response variance

The manner in which a neurone's response depends on the contrast or intensity of a stimulus is of interest for several reasons.

First, the way it responds must partly determine the properties of neurones which it drives. If a neurone receives several signals which are not linearly related to contrast, it is unlikely to exhibit linear spatial summation (Enroth-Cugell and Robson 1966). Simple cells in the cat's striate cortex do linearly summate inputs from different parts of their receptive fields, implying that the inputs are from neurones whose response amplitude is directly proportional to stimulus contrast (Movshon et al. 1978a). Complex cells, however, show profound non-linearities of spatial summation (Movshon et al. 1978b) but this need not imply that their response amplitude is non-linearly related to contrast. For instance, the complex cell might rectify and add its inputs.

Second, many psychophysical experiments use contrast as the dependent variable. Contrast is adjusted until the stimulus is no longer visible. It is generally assumed in psychophysical literature that neurones do not have a threshold contrast below which they will not respond; rather, the psychophysical threshold arises because a small response may not be sufficiently distinguishable from the inherently variable spontaneous activity (Green and Swets 1966). It is therefore of interest to ascertain whether or not cortical neurones do exhibit strict contrast thresholds.

Third, the just noticeable difference in contrast between two otherwise identical stimuli increases as the contrast of the comparison stimulus increases (Campbell and Kulikowski 1966; Nachmias and Sansbury 1974; Tolhurst and Barfield 1978). This observation might suggest that the response amplitude is some compressive function of contrast. Indeed, Maffei and Fiorentini (1973) and Ikeda and Wright (1974) claim to have demonstrated such a relationship for neurones in the cat's striate cortex. Is the Weber-Fechner relation in the contrast domain explicable only in these terms?

This paper attempts to answer these questions by describing how response amplitude and variability change with stimulus contrast. Some of these results have been reported briefly (Movshon and Tolhurst 1975).

Methods

These have been described in detail (Movshon et al. 1978a). Activity of single neurones was recorded in adult cats weighing 2–3.5 kg. Anaesthesia was induced with halothane and, after

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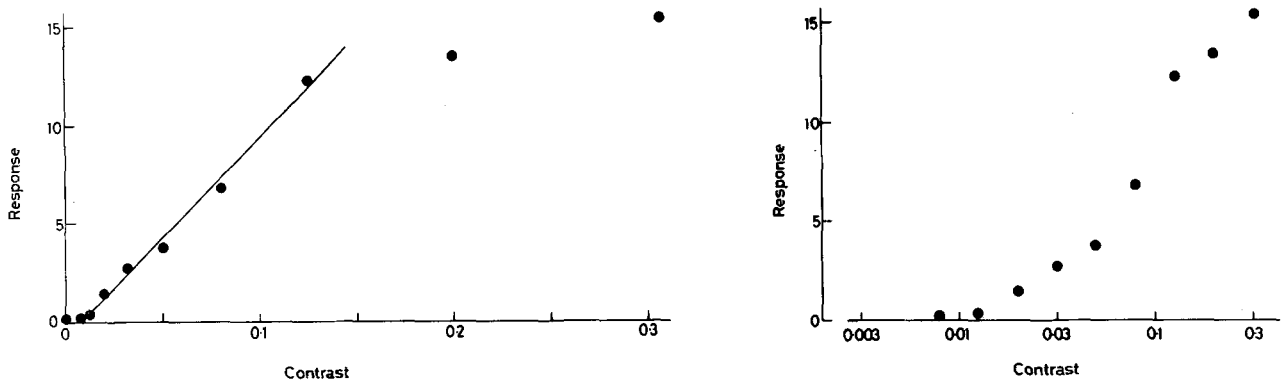

Fig. 1. The dependence of response amplitude on stimulus contrast for a simple cell. In both parts of the figure, the abscissa represents the grating's contrast. The scale is linear on the left, logarithmic on the right. The response amplitude is the mean of 100 measurements of the number of action potentials elicited by the movement of one cycle of the grating past an arbitrary point on the display; movement of one cycle took 0.5 s. The line drawn through the points in the left-hand part was fitted by eye. At a contrast of 0.5 the response was 13.7, and at a contrast of 0.79 was 11.7

cannulation of the radial vein, was maintained during surgery by injection of methohexitone. During recording, the cats were anaesthetised by artificially hyperventilating with a mixture of 75% N_2O: 23% O_2: 1.5% CO_2. The anaesthesia was sometimes supplemented with 0.5% halothane added to this mixture or with small injections of sodium brietal. The depth of anaesthesia was monitored by examination of the waveform of the electroencephalogram. The cats were paralysed with an i.v. infusion of Flaxedil (gallamine triethiodide) at 10 mg/kg/h. The pupils were dilated by topical application of homatropine and the corneas were protected with neutral contact lenses, opaque except for a central 3 mm diameter clear aperture. Spectacle lenses were used to focus the eyes on the stimulus display, at a distance of 114 cm.

A hole (2–3 mm diameter) was drilled over the representation of the *area centralis* in area 17 (4–7 mm posterior, 0–2 mm lateral). The dura was removed. The recording micro-electrodes were electrolytically sharpened tungsten housed in glass pipettes (Levick 1972). Neuronal activity (extracellular recording) was monitored by a PDP-11/20 digital computer.

The visual stimuli, generated by the computer, were sinusoidal gratings displayed on the face of a cathode ray tube by modulating the luminance of a raster. The screen was rectangular, subtending 12.5 by 10 deg at the cat's eye. The display had a space-averaged mean luminance of 150 cd/m^2, which was unaffected by any experimental procedure. The contrast of the gratings was defined as

$$\frac{L_{max} - L_{min}}{L_{max} + L_{min}}$$

where L is the luminance of a point on the screen. Contrast can, thus, vary between 0 and 1.

The grating, whose extent was much greater than that of the neurone's receptive field, was chosen to be at the optimal orientation and spatial frequency. Orientation was adjusted until the response seemed subjectively to be largest; the optimal spatial frequency was determined objectively (Movshon et al. 1978c). The grating moved steadily in the neurone's preferred direction at 2 cycles/s. In a typical experiment, this grating would be presented at 10–15 contrasts, including zero to give the spontaneous level of activity. The highest contrast used was usually 0.7 or 0.8. The stimuli were presented in random order for 5 s each, so that the responses as 10 cycles of the grating moved through a point in the receptive field could be determined. When each contrast had been presented once, the order of presentation was re-randomised and the process was repeated. In all, the responses to 50 or 100 cycles at each contrast were determined.

Results

The dependence of response on contrast was determined for 39 neurones (19 simple, 20 complex). The neurones were classified as simple or complex following the criteria of Hubel and Wiesel (1962).

Response Amplitude

Figure 1 shows how the response amplitude of a simple cell depended on the contrast of moving sinusoidal gratings. The response measure plotted is the average number of action potentials elicited in 0.5 s. In simple cells (whose responses to moving gratings contain pronounced modulation in synchrony with the movement of the grating) the depth of modulation of response is also a useful measure. In general, the mean activity and the depth of modulation depended in the same way on stimulus contrast (Movshon et al. 1978c). In the left-hand part of Fig. 1, the abscissa has contrast on a linear scale. At contrasts below about 0.01, the neurone did not respond: the firing rate was little different from the very low spontaneous level. Between contrasts of 0.01 and 0.13, the amplitude of response was approximately linearly dependent on contrast. At higher contrasts, the response did not increase as rapidly: it began to saturate. In this neurone, the responses to contrasts higher than those illustrated were very

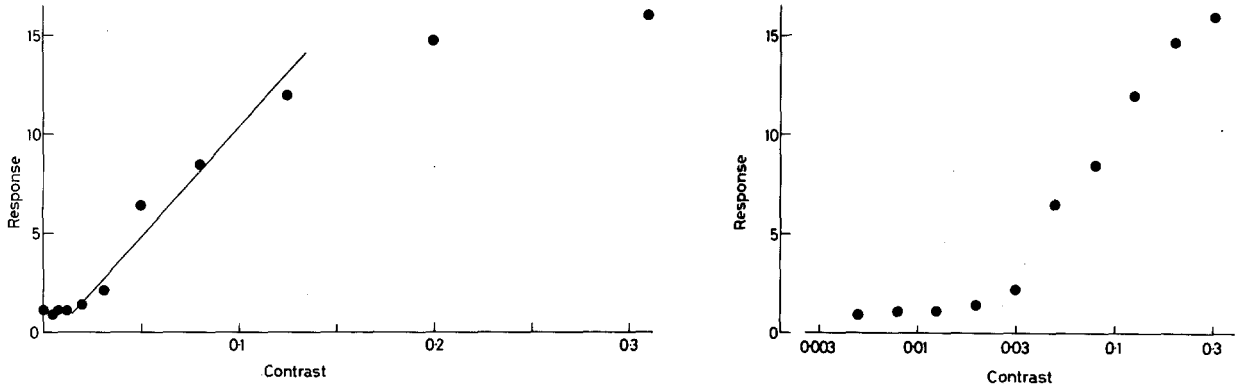

Fig. 2. The dependence of response amplitude on contrast for a complex cell. Conventions as for Fig. 1. The response at a contrast of 0.5 was 19.5, and at a contrast of 0.79 was 20.7

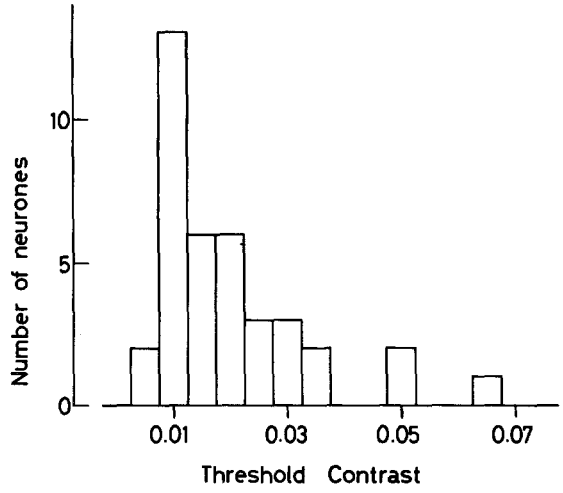

Fig. 3. The distribution of thresholds for 38 neurones. The measurements were made at the neurones' optimal spatial frequency and orientation

similar to those at a contrast of 0.3 (see legend). In some neurones, complete saturation was not evident: response amplitude continued to creep up slowly at contrasts as high as 0.8.

For comparison, the right-hand part of Fig. 1 plots the same data against the logarithm of contrast. The threshold is still apparent, but the saturation appears less extreme. There is sufficient curvature on the graph at low contrasts to suggest that response amplitude is not appropriately described as proportional to the logarithm of contrast. At low contrasts, the response appears to increase linearly with contrast, although a logarithmic formulation might provide a better description at higher contrasts. However, saturation would still be apparent at very high contrasts even with a logarithmic relation (see legend).

Figure 2 illustrates similar data for a second cell (a complex cell), which had significant spontaneous activity. In most respects, the behaviour of this neurone was similar to that of the simple cell illustrated in Fig. 1. There was an obvious threshold contrast (at about 0.015) and the response began to saturate at the higher contrasts. However, it is not clear what relation describes the response in the contrast range between threshold and saturation: on neither linear nor logarithmic plot is a straight line a convincing description of the lower contrast data. Deviation from a straight line on either plot could be due to an aberrant response at only one contrast.

About two thirds of our data suggested a linear relation between response amplitude and contrast over the lower contrast range (as in Fig. 1). The remaining data included presumably erratic responses which made a linear relation less convincing; the data illustrated in Fig. 2 were those which most convincingly suggested a logarithmic relation. In all 39 neurones, a threshold was evident, even when the neurone exhibited considerable spontaneous activity. The range of threshold contrasts is illustrated in Fig. 3. Most neurones showed some sign of response saturation at high contrasts, beginning 0.8–1.5 log units of contrast above threshold. Simple and complex cells behaved similarly except that saturation usually occurred more suddenly in complex cells.

Response Variance

For 20 neurones we examined the variance as well as the amplitude of the response. The variance only of the *mean* response to each cycle of the grating was examined.

Figure 4 plots the variance against the mean number of action potentials elicited by each cycle of the grating for two neurones. Each point represents one contrast of grating. Variance increased with increasing firing rate, as has been found in neurones at other sites in the nervous system (Werner and

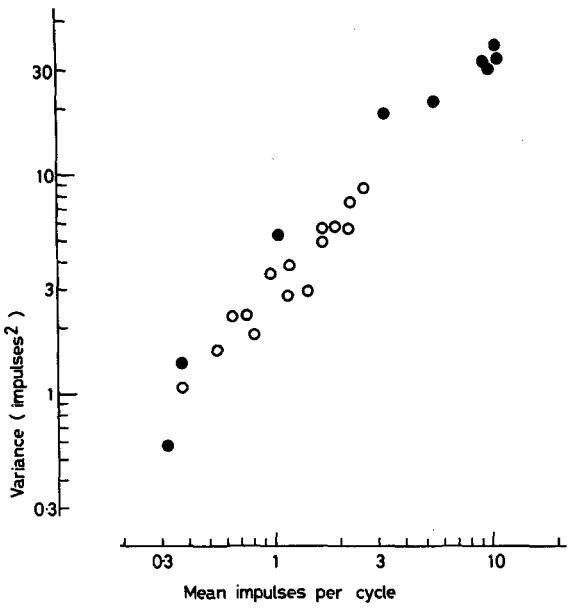

Fig. 4. Relationship between amplitude and variance of response for two neurones, a simple cell (○) and a complex cell (●). The mean and variance of the number of action potentials elicited by each of 100 stimulus cycles are compared. Each point represents a different contrast

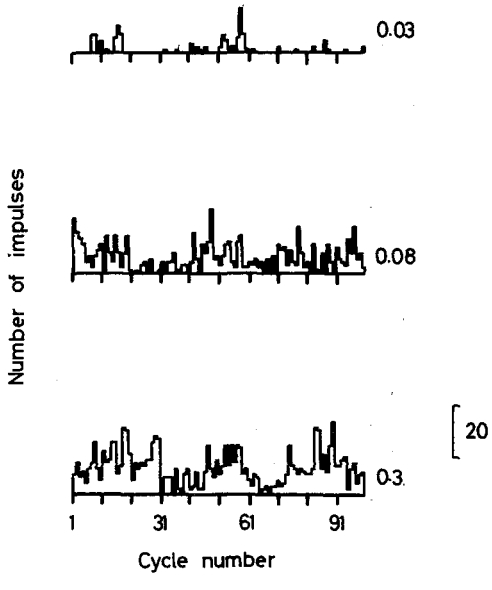

Fig. 5. The number of action potentials generated by a complex cell for each cycle of a grating at three contrasts. The contrast is indicated to the right of each histogram. The stimuli were presented in blocks of ten cycles at a time. When every contrast had been presented for one block, the order of presentation was re-randomised and the stimuli were each presented for another block of ten cycles. The abscissa is, therefore, approximately equivalent to time, the total duration being about 20 min

Mountcastle 1965; Jansen et al. 1967; Matthews and Stein 1969; Barlow et al. 1971). On a double logarithmic plot, our data were approximately described by straight lines having slopes in the range 1.0–1.4.

A surprising feature of our data was that the variance was three to five times greater than the response. The ratio of mean to variance has been used to speculate on the process underlying the variability of activity (Barlow and Levick 1969). At first sight, our results might suggest that, if a cortical neurone fires at all, it is likely to produce a burst of three to five action potentials. But behaviour of that kind has not been reported when cortical neurones respond to single electrical stimuli in the peripheral visual pathway (Stone and Dreher 1973; Singer et al. 1975). A single input trigger does not usually produce a burst of activity. What, then, is the origin of the high variance obtained in our experiments?

A major contributor to the high variance seems to have been a pronounced non-stationarity of responsiveness. This is illustrated by Fig. 5 which shows the number of action potentials generated by a complex cell in response to each of the 100 cycles of the moving grating. Responses to three contracts are shown. The abscissa can be regarded as being roughly equivalent to time with the three data sets being approximately synchronous (see legend). The experiment lasted about 20 min, during which time the responsiveness of the neurone clearly changed cyclically. For parts of the experiment the neurone responded well at all three contrasts; at other times, it responded poorly. To demonstrate the non-stationarity, an analysis of variance was performed: for each neurone for each contrast, the variance within each block of ten cycles was compared with the variance between the means of the five or ten blocks. In over 75% of the data sets, the response could not be considered to be uniform through the course of the experiment ($p < 0.05$). The apparently uniform responses were usually elicited by very low contrasts, when the response was close to zero *all* the time.

Such changes in responsiveness with a period of a few minutes were common in our sample of cortical neurones. These changes contributed markedly to the high ratio of overall variance to overall mean firing rate. If variance was estimated only during phases when responsiveness was relatively constant, it was still proportional to the mean but was now less than twice the mean.

Discussion

Below a certain stimulus contrast, the activity of a cortical neurone is little different from its spontane-

ous level of activity. A threshold contrast is apparent even in neurones possessing a significant level of spontaneous activity. The neurones showed contrast thresholds in the range 0.005–0.065. The lowest thresholds shown by cats in behavioural experiments are of the same order (Berkley and Watkins 1973; Bisti and Maffei 1974). The thresholds of neurones could, therefore, contribute to the behavioural threshold. But, as spontaneous activity and response are variable, some kind of statistical decision would be required for the instantaneous activity of a neurone to be regarded as being due to the presence of a stimulus. If the cat's behavioural response relied upon the activity of only one neurone, its behavioural threshold would be higher than that of the neurone. We can be confident that a neurone responded to a stimulus whose contrast slightly exceeded threshold only because we averaged the responses to many repetitions of the stimulus. To have low behavioural thresholds for a single stimulus presentation, the cat must presumably base its decisions upon the activity of several neurones.

For about 1 log unit of contrast above threshold, response amplitude seems to increase linearly with contrast. Linearity of response at these lower contrasts is evident also in the data of Dean (1980). The saturation at higher contrasts introduces the temptation to describe the whole relation as being logarithmic (Maffei and Fiorentini 1973; Ikeda and Wright 1974), but this does not seem to be a correct generalisation at low contrasts. Robson (1975) suggested a formulation which might have been appropriate to describe our data:

$$\text{response} \propto \log\left(1 + \frac{C}{k}\right)$$

where C is the contrast and k a constant. The relation is linear at low contrasts but exhibits logarithmic saturation at high contrasts. However, this formulation was a disappointing fit to our data: the response saturation exhibited by the neurones was usually too sudden and complete to be described by the more gradual logarithmic formulation.

The variance of the response increases with response amplitude, a finding which has interesting implications for the interpretation of one kind of psychophysical experiment. The discriminability of two gratings of different contrast will presumably depend on any differences in neuronal responses to the two gratings. One should expect that differences in response amplitude would be an important factor, but the discriminability should also depend upon any differences in response variance or, more exactly, response standard deviation (Green and Swets 1966). If response standard deviation did not change with contrast, the discriminability of two gratings would depend upon differences only in response amplitude. That the just noticeable difference in contrast increases with the contrast in psychophysical experiments would then imply that response amplitude is a compressive, perhaps logarithmic, function of contrast. However, we have shown that response standard deviation *does* increase with response amplitude, to the power 0.5–0.7 (variance increases to the power 1.0–1.4). The just noticeable difference in contrast increases with contrast to the power 0.8 (Nachmias and Sansbury 1974; Tolhurst and Barfield 1978; Kulikowski and Gorea 1978). Thus, the change in variability of response rather than a compressive response non-linearity could be a considerable factor determining the dependence of the just-noticeable difference on contrast.

This interpretation should perhaps be tempered by our observation that responsiveness was not stationary (Tomko and Crapper 1974). The non-stationarity would at least increase the measured variance of response, and we can only assume how variance and response amplitude are related when neurones are behaving in a stationary manner, if that is their normal behaviour. We do not know whether non-stationarity is a pathological result of paralysis and anaesthesia or whether it is a reflection of a normal physiological process, such as selective attention (Tomko and Crapper 1974). It would be interesting to have data from alert animals.

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References

Barlow HB, Levick WR (1969) Changes in the maintained discharge with adaptation level in the cat retina. J Physiol (Lond) 202: 699–718

Barlow HB, Levick WR, Yoon M (1971) Responses to single quanta of light in retinal ganglion cells of the cat. Vision Res [Suppl] 3: 87–102

Berkley M, Watkins D (1973) Grating resolution and refraction in the cat estimated from evoked cerebral potentials. Vision Res 13: 403–416

Bisti S, Maffei L (1974) Behavioural contrast sensitivity of the cat in various visual meridians. J Physiol (Lond) 241: 201–210

Campbell FW, Kulikowski JJ (1966) Orientation selectivity of the human visual system. J Physiol (Lond) 187: 437–445

Dean AF (1980) The contrast dependence of direction selectivity. J Physiol (Lond) 303: 38–39P

Enroth-Cugell C, Robson JG (1966) The contrast sensitivity of retinal ganglion cells of the cat. J Physiol (Lond) 187: 517–552

Green DM, Swets JA (1966) Signal detection theory and psychophysics. Wiley, New York

Hubel DH, Wiesel TN (1962) Receptive fields, binocular interactions, and functional architecture in the cat's visual cortex. J Physiol (Lond) 160: 106–154

Ikeda H, Wright MJ (1974) Sensitivity of neurones in visual cortex (area 17) under different levels of anaesthesia. Exp Brain Res 20: 471–484

Jansen JKS, Nicolaysen K, Rudjord T (1967) On the firing pattern of spinal neurones activated from the secondary endings of muscle spindles. Acta Physiol Scand 70: 188–193

Kulikowski JJ, Gorea A (1978) Complete adaptation to patterned stimuli. A necessary and sufficient condition for Weber's Law for contrast. Vision Res 18: 1223–1227

Levick WR (1972) Another tungsten microelectrode. Med Biol Engin Comput 10: 510–515

Maffei L, Fiorentini A (1973) The visual cortex as a spatial frequency analyzer. Vision Res 13: 1255–1268

Matthews PBC, Stein RB (1969) The regularity of primary and secondary muscle spindle afferent discharges. J Physiol (Lond) 202: 59–77

Movshon JA, Thompson ID, Tolhurst DJ (1978a) Spatial summation in the receptive fields of simple cells in the cat's striate cortex. J Physiol (Lond) 283: 53–77

Movshon JA, Thompson ID, Tolhurst DJ (1978b) Receptive field organization of complex cells in the cat's striate cortex. J Physiol (Lond) 283: 79–99

Movshon JA, Tompson ID, Tolhurst DJ (1978c) Spatial and temporal contrast sensitivity of neurones in areas 17 and 18 of the cat's visual cortex. J Physiol (Lond) 283: 101–120

Movshon JA, Tolhurst DJ (1975) On the response linearity of neurones in cat visual cortex. J Physiol (Lond) 249: 56–57P

Nachmias J, Sansbury R (1974) Grating contrast discrimination may be better than detection. Vision Res 14: 1039–1042

Robson JG (1975) Receptive fields: spatial and intensive representation of the visual image. In: Carterette D, Friedman W (eds) Handbook of perception, vol V. Academic Press, New York

Singer W, Tretter F, Cynader M (1975) Organization of cat striate cortex. A correlation of receptive field properties with afferent and efferent connections. J Neurophysiol 38: 1080–1098

Stone J, Dreher B (1973) Projection of X- and Y-cells of the cat's lateral geniculate nucleus to areas 17 and 18 of the visual cortex. J Neurophysiol 36: 551–567

Tolhurst DJ, Barfield L (1978) Interactions between spatial frequency channels. Vision Res 18: 951–958

Tomko GJ, Crapper DR (1974) Neuronal variability: non-stationary responses to identical visual stimuli. Brain Res 79: 405–418

Werner G, Mountcastle VB (1965) Neural activity in mechanoreceptive cutaneous afferents: stimulus-response relations, Weber functions and information transmission. J Neurophysiol 28: 359–397

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