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Deep tectal cells in pigeons respond to kinematograms

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Summary. Deep tectal neurons in pigeons respond selectively to moving visual stimuli, and are inhibited by large background patterns moved in-phase with these stimuli. In this investigation we demonstrate that these same deep tectal neurons respond equally well to kinematograms as they do to traditional luminance contrast stimuli typically employed in visual experiments.

Computer generated kinematograms, the motion domain equivalents of random dot stereograms, were used as stimuli in these experiments. These kinematograms, where a small centrally located set of random dots is moved coherently in one direction while the remaining dots are moved in a different direction, thus constitute a pure motion stimulus where the stimulus form is only visible in the dynamic pattern, but does not exist on any single frame. Both 'object' configured and 'hole' configured kinematograms were employed; the former appearing as regions of texture moving over, or in front of, the background texture, while the latter appear as windows through which a more distant textured surface is revealed.

Extracellular recordings from isolated deep tectal cells showed that all units responded in a very similar manner whether the stimulus was an 'object' configured kinematogram or the more traditional luminance contrast variety. This similarity included directional selectivity, the in-phase inhibition anti-phase facilitation effect, and sensitivity to opposed motion independent of direction. However, when the kinematograms were configured as 'holes' none of the units tested responded to these stimuli. The significance of these observations for tectal functioning, image segmentation through motion and animal camouflage is discussed.

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Introduction

It has long been recognized that one of the fundamental processes that must occur in a visual system is to segregate or parcellate different regions of an image appropriately into the separate objects and surfaces that constitute the scene. This process was termed 'figure-ground' segregation by early Gestalt psychologists (Wertheimer 1923) who listed several rules (such as spatial and temporal proximity, similarity, continuity, closure, uniform density and common orientation [Uttal 1981]) by which elements in an image might be grouped into various figural regions. While each of these rules has obvious utility in some controlled situations, especially static 2D pictorial representations, few are effective when used alone in the real world for parsing a scene into the 'objects' which compose it. An indication of the problems inherent in the application of a set of simple rules to appropriately parse an image into 'objects' is provided by the difficulty this has presented to computer scientists working on machine recognition (Besl and Jain 1985).

In natural scenes, 'objects' or 'surfaces' seldom have the uniform color, brightness, and texture that make these rules effective. Yet even simple organisms appear to have evolved visual mechanisms to accomplish appropriate parsing and recognition of significant 'objects' from these cluttered environments (Srinivasan and Dvorak 1980; Reichardt et al. 1983; Egelhaaf 1985). Furthermore, protective coloration and camouflage have co-evolved to thwart the operation of these mechanisms and prevent detection by predators (Cott 1940; Portmann 1959; Edmunds 1974; Fleishman 1986).

The two factors that have the most utility in

specifying an 'object', even when it is composed of various different parts, are stereopsis and motion (or common fate). In the case of stereopsis, different features will be seen as a unit if all have a common, similar or systematically varying disparity distribution of their elements which differs from other areas in the image. In fact, much has been made in the literature of the utility and evolutionary significance of stereopsis in breaking camouflage (Cott 1940; Portmann 1959; Edmunds 1974). Thus in random dot stereograms (Julesz 1971), connected regions of common retinal disparity emerge as 'objects' or figures, even when there is no other variable specifying object boundaries. Similarly, in the case of motion, different features will also be seen as a single unit or 'object' if they all have common, similar or systematically varying motion vectors which differ from other adjacent areas in an image. So powerful is motion in organizing the optic array, that protective coloration and camouflage in animals is almost invariably associated with the behavioral response of 'freezing' to achieve its effectiveness. Some animals, such as walking stick insects and Australian horned toads even produce motion patterns that simulate the common motion of wind-blown grasses and branches surrounding them to blend into the background and become inanimate objects to their predators. Regions of common disparity in random dot stereograms when viewed binocularly are organized into 'figure and ground'. In a similar manner regions of common motion in random dot fields lead to the vivid emergence of figures from these *kinematograms* (Julesz 1971; Regan 1986). These compelling visual phenomena are consistent with several mathematical and theoretical analyses which show that information about the 'figure-ground' boundaries, object rigidity, object motion and self-motion through the environment are all available from an animal's dynamic optic array (Nakayama and Loomis 1974; Longuet-Higgins and Prazdny 1980; Reichardt et al. 1983).

In previous work (Frost 1978; Frost et al. 1981; Frost and Nakayama 1983) we have shown by a series of experiments on relative motion, that most neurons in the deeper laminae of the pigeon's tectum are specialized to respond to the motion of 'objects' and are inhibited by translation of the whole retinal image. This type of processing, which is remarkably congruent with tectal participation in 'orienting' behavior (Stein 1984; Knudsen 1982; Hess et al. 1946) is accomplished by a double opponent-process directional receptive field mechanism (von Grunau and Frost 1983; Bender and Davidson 1986). In a recent paper, Frost and Nakayama (1983) showed these same deep tectal neurons were responding to the *relative* directions of motion between test stimuli and backgrounds rather than the absolute directions, and it was suggested that this generalized response might indicate their involvement in 'figure-ground' segregation through motion.

Consequently, the present study was undertaken to see if these deep tectal cells of pigeons respond to computer-generated kinematograms, where moving 'objects' or 'apertures' are specified by different patterns of coherent motion in random dot arrays.

Materials and methods

Experiments were performed on 27 white Carneaux pigeons (Palmetto Pigeon plant, Sumter, S.C.) which were anesthetized with a 5–7 ml i.p. injection of 20% urethane, placed in a modified Stoelting stereotaxic instrument, and the meso-lateral region of their right optic tectum exposed. Other preparation procedures were essentially similar to those reported in detail previously (Frost and DiFranco 1976; Frost 1978; Frost et al. 1981). Although no refractive correction or paralysing agents were used, we are satisfied resolution is near optimal since cells would often respond to motion of a single pixel human observers had difficulty seeing, and that eye movements were not occurring. Single cell responses were recorded from the stratum griseum et fibrosum superficiale (approximately 400 μm) through to the underlying ventricle using tungsten-in-glass microelectrodes (exposed tip 10–15 μm). A stepping motorized hydraulic microdrive system with digital readout was used to advance electrodes radially through the tectum. By zeroing the micron counter on contact with the surface and noting the depth the electrode emerged into the ventricle it was possible to localize electrode position reasonably precisely within the major subdivisions of the tectum. Conventional methods were used to isolate responses of a single cell, and standardized pulses, each representing a spike, were stored in a Tracor Northern NS-570 Signal Averager to produce peri-stimulus-time histograms (PSTHs).

Upon isolation of a cell, the excitatory receptive field (RF) boundary was mapped using a light spot from a hand-held ophthalmoscope projected onto tracing paper attached to a large tangent screen located 1 m from the bird's eye. Visual landmarks such as the pecten, fovea and ora terminalis were also plotted on the screen by the reversing ophthalmoscope technique (Cooper and Pettigrew 1979). Details concerning electrode depth, directional and velocity tuning characteristics, preferred stimulus size, etc. were recorded before the more formal quantitative procedures were used to assess a unit's responsiveness to different types of kinematograms.

Kinematogram stimuli were generated by a Grinnell 270 Image processing computer hosted by a PDP 11–23, and displayed either on a high resolution Hitachi VM-173C monitor or back projected onto a tangent screen through an Electrohome EDP57 projection monitor. Both are interlaced monitors with a refresh rate of 30 H, and the phosphors for the two video systems were P22 and P4, respectively. Both systems yielded essentially similar results. The image characteristics consisted of a 512 × 512 pixel × 256 grey level display format. Kinematograms were produced by 2 different regions of random, black or white elements ($p = 0.5$) which could be independently

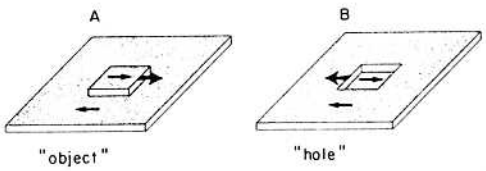

Fig. 1 A, B. Kinematograms produced by moving a central region of elements in a random dot display in one direction, while the surrounding region of dots is moved in a different direction (small arrows). If movement characteristics of 'figure' and 'ground' are identical, complete camouflage occurs. **A** When the boundary (large arrow) between centre and surround is moved with the same motion characteristics as the *central region* an 'object' is seen moving over or in front of the background. **B** When the boundary (large arrow) moves with the same motion characteristics as the *surround* then a 'hole' is perceived sliding over a more distant background

moved in any direction and at any velocity. The display was programmed so that one region of coherently moving elements occupied most of the display area while a typically smaller target region of similar elements was coherently moved in a different direction in a central region as shown in Fig. 1 A. If the boundary between the two regions of moving elements is moved coherently with the target or *central region* then one perceives an 'object' moving in front of a textured background as shown in Fig. 1 A. If, however, the boundary between the two motion regions coherently moves with the *surrounding region* as illustrated in Fig. 1 B, then one perceives an aperture or 'hole' or window through which a continuous field of elements is visible. These two classes of stimuli, called here 'objects' and 'holes', are conceptually (and perceptually) equivalent to the 'crossed' and 'uncrossed' disparity cases, respectively, in random dot stereograms. In most of the experiments reported below the 'object' configured kinematogram was employed. Variables such as the contrast, brightness, size of elements, speed of direction of background and figure regions, size of 'object' and length of its trajectory, plus interstimulus delay could all be varied by a menu-driven display on the computer terminal.

After the RF of a unit had been plotted, kinematograms were presented either on the Hitachi monitor or back-projected onto the target screen via the EDP-57. Care was taken to choose an 'object' size, stimulus direction and velocity that matched the qualitatively determined characteristics of the cell. Then one or other of the stimulus variables were manipulated to produce a tuning curve.

Results

Quantitative observations were made on a total of 75 cells recorded from 27 pigeons. In the first instance it was immediately apparent that all deep tectal cells responded in a very similar fashion to moving kinematograms and to moving luminance spots and squares. Typical results from these experiments are illustrated in Fig. 2 where it can be seen that this unit, recorded at a depth of 737 μm from the tectal surface, responded quite reliably when a white 2.3° square was swept forward (preferred direction) through the ERF. The null direction responses produced by stimuli moving in the opposite direction, have not been presented here

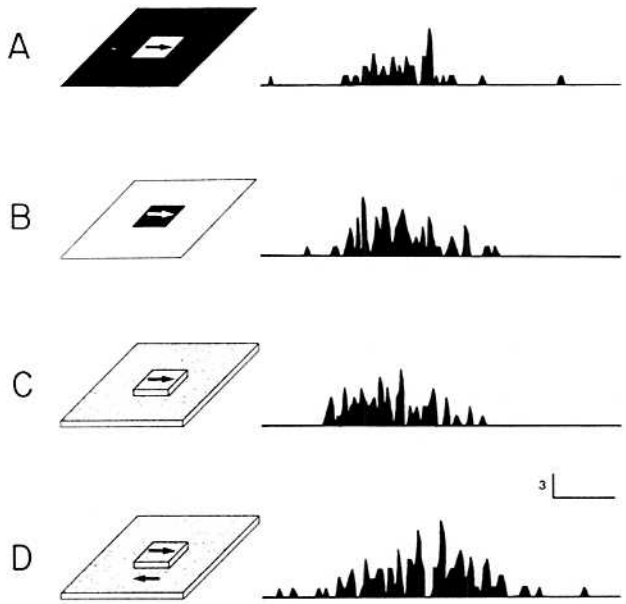

Fig. 2. Responses of a tectal cell to conventional stimuli consisting of a light square on a dark ground (**A**), and a dark square on a light ground (**B**). This cell responded well to both forms of luminance contrast stimuli moved in its preferred direction. The cell responded equally well to the 'object' kinematogram moved over a stationary background (**C**). The cell's response was facilitated (55%) when presented with the 'object' kinematogram where 'object' and background moved in 'anti-phase' (**D**). The cell produced no response to motion in the null direction. The size of each texture element in the kinematogram was 0.37°, the square stimuli subtended 2.3° and were moved at 25°/s with an I.S.I. of 5.0 s. PSTHs represent the sum of spikes for 8 sweeps. Calibration mark: 3 spikes and 1 s

because no responses occurred. The PSTH in Fig. 2 B shows an increased response when contrast was reversed and a black square was swept along the same path. When the kinematogram illustrated in Fig. 1 C, where the surrounding elements were stationary and the central zone and boundary were moving to produce the square 'object' (or crossed disparity equivalent), was swept along an identical trajectory, the cell responded almost identically to the moving dark square. It should be remembered that on any single frame of a kinematogram there is nothing but a homogeneous pattern of random dots presented, but over successive frames the coherent motion or displacement of a spatially contiguous cluster of elements results in the vivid impression of an 'object' moving over, or in front of, a continuous background surface.

In our previous studies (Frost 1978; Frost et al. 1981; Frost and Nakayama 1983) most deep tectal neurons were *facilitated* when background textured patterns were moved in anti-phase to luminance spots moving in the preferred direction of

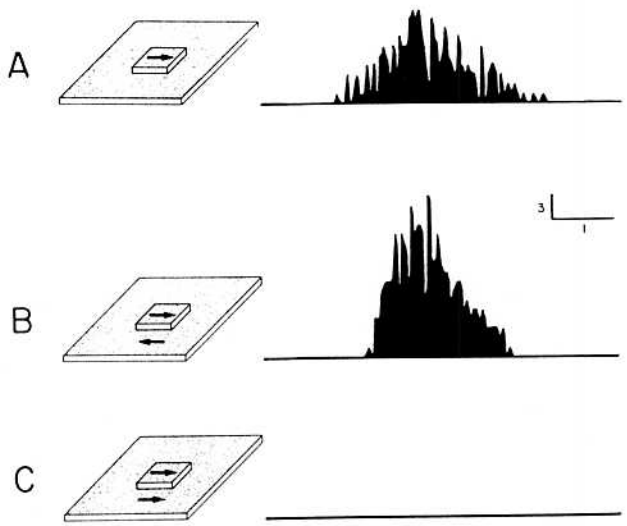

Fig. 3. Responses of a tectal cell presented with the 'object' kinematogram where **A**: the 'object' moved over a stationary background or **B**: over a background moved in the opposite direction (anti-phase) or **C**: where the 'object' moved in the same direction and with the same motion characteristics as the background. Note the facilitated (46%) response in **B** and the complete absence of response in **C** where the object is completely camouflaged by the surround. Stimulus parameters are similar to those in Fig. 2

the cell. Figure 2D shows a similar effect was obtained for this unit when kinematograms were employed. The same effect is shown in Fig. 3A and B for another unit recorded from a depth of 681 μm in the tectum. Here 46% facilitation compared to the response in 3A, was obtained for the 'anti-phase' condition shown in Fig. 3B, and complete inhibition was found (Fig. 3C) when the background was moved 'in-phase' with the stimulus 'object'. Of course, under this 'in-phase' condition, where the 'object' and background move in the same direction and at the same velocity, there is complete camouflage of the 'object' except for the instant (frame) when it is first presented, and again when it is removed at the end of its sweep. Human observers notice these events; the replacement of the texture elements at the beginning and end of the sweep, but in these experiments these events took place outside of the ERF so were not registered by the cells under study.

In a recent paper, Frost and Nakayama (1983) showed that deep tectal cells of pigeons responded best to opposed motion between a test stimulus and a large background pattern, largely independent of the direction of the test stimulus. A similar set of experiments were carried out here but employing kinematograms in the 'object' configuration. The results were similar in essential details to those reported previously using luminance stimuli, and the responses of a typical unit located at 335 μm from the tectal surface are illustrated in Fig. 4. To obtain these results an 'object' kinematogram was presented moving either forwards (180°), upwards (90°) or downwards (270°) through the ERF of the cell. Each of these directions produced an excitatory response when the background was stationary, but there was no response when the stimulus was moved backwards (null direction). Then the background directions were swept in random order in 8 different directions for each direction of movement of the 'object' and the response rate of the unit recorded. When the background was moved in a direction opposite to the test stimulus, maximal responding occurred, and when it was moved in the same direction (or had a vector in the same direction) sub-

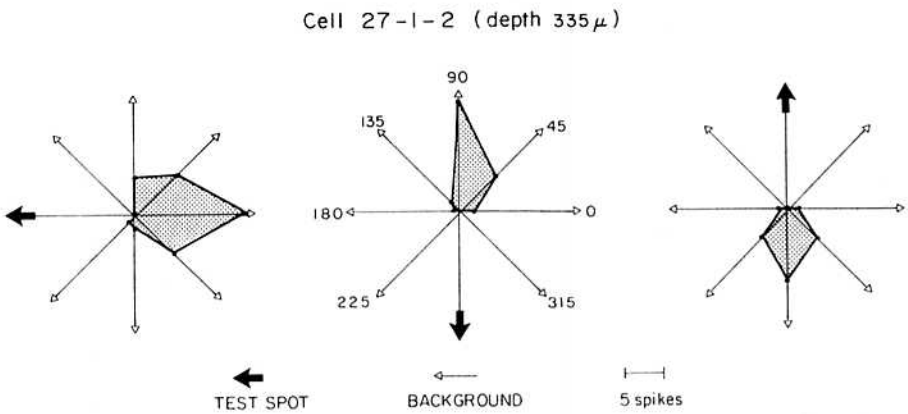

Fig. 4. Polar plots of responses from a single tectal cell showing mean number of impulses as a function of background direction. Each plot was obtained using kinematograms, and choosing a fixed test 'object' direction and varying surround (open arrows) direction. Despite changes in 'object' direction, the cell responded best when surround motion was *opposite* 'object' motion in all three cases, implying that it is the *relationship* between different motion directions of 'object' and surround that produce these responses, rather than sensitivity to absolute directions

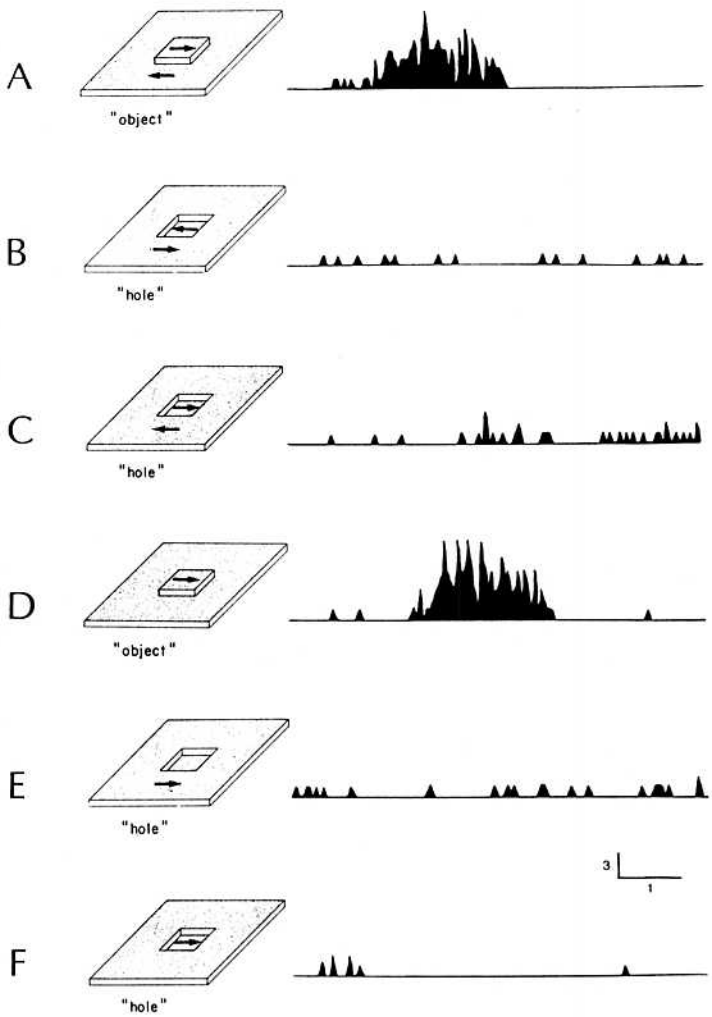

Fig. 5A–F. Responses of a single tectal cell to kinematograms in the 'object' and 'hole' configuration. **A** 'Object' and surround move in anti-phase, where 'object' moves in the cell's preferred direction. **B** 'Hole' moves in the cell's preferred direction, while texture seen through the 'window' moves in null direction. **C** Identical motion characteristics of central and surrounding regions to **A**, except in 'hole' configuration. **D** 'Object' moves over stationary surround. **E** 'Hole' moves in cell's preferred direction with the background stationary. **F** Stationary 'hole' with central background motion in cell's preferred direction. Note that the cell responds to the 'object' configuration only (**A** and **D**) and does not respond to any 'hole' configuration. It can be seen from this Fig. that no responses occur when the 'hole' boundary moves in the cell's preferred direction (**B** and **E**), or when the motion characteristics of central and surrounding regions are identical to the 'object' mode, *except* for the motion characteristics of the boundary (**C**). Stimulus parameters are similar to those in Fig. 2

stantial inhibition was produced. This pattern of responses held for *all excitatory directions* of the cell, again illustrating the importance of the *relative* directions of motion. Opposed directions of motion between figure and ground thus yield the largest response while the same or similar directions of motion between figure and ground show maximal inhibition.

As illustrated in Fig. 1 there are two primary configurations of kinematograms that yield quite different percepts for human observers. These two classes of kinematograms, called respectively 'objects' and 'holes' for convenience, were presented to a number of deep tectal cells. The results were clearcut on all cells tested (57), and indicate that deep tectal cells respond optimally to the 'object' configuration and do not respond to the 'hole' configuration.

A typical set of results is shown in Fig. 5 for a cell located at a depth of 582 μm from the tectal surface. Figure 5A shows the response produced by an 'object' kinematogram when the 'object' moved in the preferred direction of the cell, and the background was moved in anti-phase. This produced a vigorous response similar to those described above. However, when the kinematogram was in the 'hole' or aperture mode, and the 'hole' moved across the receptive field, in the identical path taken by the 'object' in Fig. 5A, then *no* response was produced as illustrated in Fig. 5B. In this case, however, the local motion of the texture elements was in the null direction for both the centre and surrounding areas of the receptive field (double opponent-process directional organization, Frost et al. 1981) while only the global pattern of the 'hole' was in the preferred direction. Consequently, several additional controls were run. Figure 5C illustrates the lack of response generated when a 'hole' configured kinematogram was moved in the null direction of the same cell. In this case the *local* motion of the texture elements *is* in the directions preferred by both its centre and

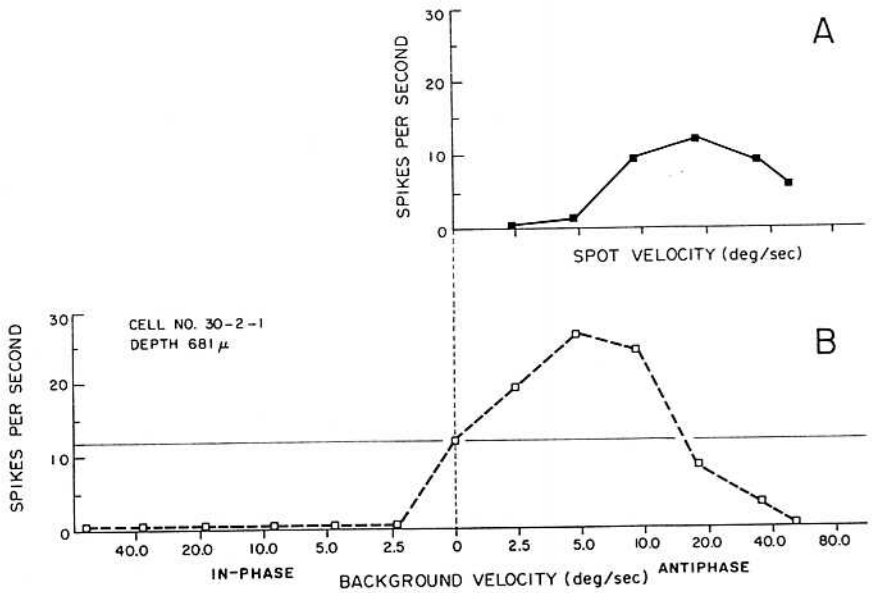

Fig. 6. **A** Velocity tuning curve obtained for an 'object' kinematogram on a stationary background. **B** Velocity tuning curve obtained for different velocities of background motion when the 'object' is moved at optimal velocity as determined in **A**. Responses to the left of zero are to in-phase motion, to the right are to anti-phase motion. All in-phase velocities produced substantial inhibition while some slower velocities of anti-phase motion of the background produced a acilitated response

surrounding regions of the receptive field, while the *global* direction of the 'hole' is in the null direction.

Figure 5D illustrates that an 'object' kinematogram, where the background is stationary, produces a response very similar to that shown in Fig. 5A for the same cell. When a 'hole' is moved across a stationary background in the preferred direction of this cell as shown in Fig. 5E, again no response is produced. Finally, when a stationary kinematographic 'hole' is placed over the centre of the receptive field and the background internal texture moved in the preferred direction of the cell, no response is produced. Thus it would appear that these deeper tectal cells respond well to object motion when both the 'objectness' and its motion emerge from relative displacement of elements. These characteristics should enable cells like this to detect the presence of a camouflaged animal whenever it moves relative to its backdrop.

To investigate the facilitatory and inhibitory effects of the moving 'ground' further, we presented 'object' kinematograms and first of all obtained a velocity tuning curve by moving the stimulus over a stationary background at different velocities. An example of a velocity tuning curve for a cell located at a depth of 681 μm from the tectal surface, derived from this procedure can be seen in Fig. 6A. Then the optimal 'object' velocity was chosen, in this example 18°/s and the velocity (and direction) of the 'ground' varied to yield the tuning curve shown in Fig. 6B. Here it can be seen that anti-phase motion of the background that was the same velocity or faster than the stimulus or 'object' velocity reduced the response rate of the cell, while slower velocities of anti-phase motion produced a substantial facilitation. In contrast, all velocities of in-phase motion produced profound inhibition, even velocities substantially slower than the 'object' motion which, for human observers, result in a clear segregation of 'figure' and 'ground'.

In a recent paper by Mandl (1984) it was reported that some cells in the superior colliculus of the cat seem to respond to the relative velocity between a test stimulus and its background rather than to the retinal velocity of the test stimulus. Consequently, for 6 cells that all responded robustly to kinematograms in the manner illustrated in Figs. 2 and 3, we derived velocity tuning curves for (a) the 'object' kinematogram swept over a stationary background, (b) the 'object' kinematogram swept over a background moving in the opposite direction to the test stimulus at $^1/_2$ the velocity of the test stimulus, (c) 'object' kinematogram swept over a background moving in the opposite direction at $^1/_4$ the velocity of the test stimulus, and in two cells (d) the 'object' kinematogram swept over a background moving in the opposite direction at $^1/_8$ the velocity of the test stimulus. Although there were some slight changes in the shape of the tuning curves for these different ratios of velocities between test stimulus and background, they did not show a systematic shift along the x-axis that would be predicted if they were responsive to relative velocity. Representative results for one cell is shown in Fig. 7 where it can be seen that this cell showed some variability in the peak of the velocity tuning curves but not the systematic x-axis shift.

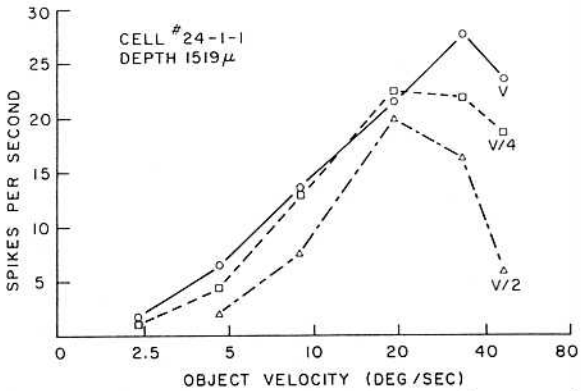

Fig. 7. Velocity tuning curves for a deep tectal neuron stimulated with 'object' kinematograms where background texture was moved at different relative velocities. Circles (*V*) represent the responses obtained when the kinematogram was moved at the velocities indicated on the abscissa while the background was stationary. Triangles (*V/2*) represent the velocity tuning curve obtained when the background was moved at $^1/_2$ the velocity of the 'object' but in the anti-phase direction. Squares (*V/4*) represent the unit's response to object kinematograms where the background was moved in anti-phase at $^1/_4$ the velocity of the object

Discussion

The results of the present experiments indicate that the neurons studied here in detail have very similar response characteristics to those we have investigated previously in the deeper layers of the pigeon tectum (Frost 1978; Frost et al. 1981; Frost 1985). In particular they all exhibited in-phase inhibition and anti-phase facilitation when large, moving, textured background patterns were added to luminance test spots moved through their excitatory receptive fields. These cells were also characterized by broad directional tuning curves with a prominent null direction to stimuli moved horizontally backward (anterior to posterior) through the visual field as reported previously (Frost and DiFranco 1976).

When these same neurons were presented with either luminance spots or kinematograms in the 'object' mode moving in the preferred direction through their RF they responded nearly identically. This would seem to imply that the correspondence problem (Movshon et al. 1984) has been computed at, or prior to, this level of processing in the visual system, because on any single frame there is only a global pattern of random elements, and the 'figure' only emerges from the coherent and different displacement of one spatially contiguous set of elements relative to the others. Moreover, when the same manipulations of the 'ground' were made with kinematographic stimuli as made in our previous studies, very similar results were obtained. Specifically, the anti-phase motion of the background produced a facilitated response while the in-phase motion of the background produced complete inhibition of the response. Further, when different directions of the 'object' kinematogram were used it was found that opposed motion between figure and ground always yielded the largest response and the same or similar motion inhibited or substantially reduced the response. These results are in agreement with those of Frost and Nakayama (1983) for luminance stimuli, and again demonstrate that it is the relative directions of figure and ground that are important for these neurons rather than the absolute directions.

Like random dot stereograms, simple kinematograms can be configured in two classes equivalent to crossed and uncrossed disparity cases. Kinematograms configured as either 'objects' or 'holes' were presented to deep tectal neurons and while vigorous responses were obtained to the former, no responses were obtained to the latter. This lack of response to kinematographic windows or 'holes' occurred under a variety of different stimulus conditions where both the surround and central regions of the display were moving, where only the surround was moving or only the central region of the figure was moving, as illustrated in Fig. 5.

Since all deep tectal neurons sampled in these experiments responded well to 'object' kinematograms, various observations were made on the velocity tuning of both the test spot ('object') and the background texture. Most cells responded best to target velocities between 10° and 40°/s when moved in the preferred direction over stationary backgrounds. When the test spot velocity was held constant at the optimal velocity for a cell and the background velocities were varied over a range of values in the same (in-phase) and opposite (anti-phase) directions, rather striking differences in responsivity were found. Beside the usual in-phase inhibition and anti-phase facilitation that was found, maximum facilitation was produced by relatively slow velocities of opposite background motion, as illustrated in Fig. 6.

The receptive field response characteristics reported here and in our previous studies (Frost 1978, 1982, 1985; Frost et al. 1981) appear to be quite consistent with the view that the optic tectum or superior colliculus plays a central role in integrating spatial position information from several modalities which is required to initiate a shift in gaze or orientation response (Stein 1984; Knudsen 1982; Hess et al. 1946). The natural stimuli that are most likely to initiate such a gaze shift, which presumably involves alignment of the fovea on an

appropriate part of the visual array, are moving objects. The very large inhibitory surrounds and double opponent-process directionally specific receptive field organisation (Frost et al. 1981; von Grunau and Frost 1983; Allman et al. 1985) are particularly well-suited to respond to local (object) motion and to ignore or veto global (self-induced) motion. The observations made here indicate that the receptive field structure may be substantially more complex than previously thought because even when the local motion is in directions shown to be preferred by the centre and surround regions of the RF, these cells will not fire if the overall configuration specifies 'hole' rather than 'object'. Clearly further research is required to elucidate these mechanisms.

Relative motion, produced by parallactic shear, can play a critical role in determining figure/ground boundaries and in the appropriate parsing of the image into its constituent parts; object form and their complex motions in 3-dimensional space (Nakayama and Loomis 1974; Koenderink and van Doorn 1976; Longuet-Higgins and Prazdny 1980; Regan 1986; Frost and Nakayama 1983; Nakayama 1985; Allman et al. 1985). The fact that kinematograms are apparently as effective stimuli for deep tectal cells as luminance stimuli, indicates that part of this complex motion processing takes place in this structure. In addition to processing information about moving objects, the tectum or superior colliculus may well be involved in preprocessing complex motion information for subsequent use by higher levels of 'the second visual system'.

In birds there is a heavy projection from the tectum to the nucleus rotundus which in turn projects to the ectostriatum in the telencephalon. This pathway bears many close resemblances to the mammalian pathway from superior colliculus to pulvinar to lateral suprasylvian area (or middle temporal (MT) area in monkeys) (Allman et al. 1985; Maunsell and van Essen 1983; Newsome et al. 1985; Tanaka et al. 1986). There is a growing body of evidence that indicates that this pathway may be specialized for processing complex dynamic transformations in the visual image. For example, Tanaka et al. (1986) and Saito et al. (1986) have shown that MT neurons in monkey respond optimally to either expansion or contraction, rotation or tilt of images, while Newsome et al. (1985) have shown that small ibotenic acid lesions of monkey MT produce localized deficits in velocity compensation in pursuit eye movements. In pilot studies conducted in this laboratory we have shown that the neurons in nucleus rotundus and ectostriatum of pigeons behave in a similar fashion to those reported here but have very much larger receptive fields (Frost et al. 1983). It remains to be determined whether more complex forms of dynamic transformations are being processed in these structures that receive connections from the tectum.

The use of kinematograms as stimuli in visual experiments has significance for the field of animal camouflage. For example, because the parameters of brightness, contrast and size of texture elements were identical between the figure and ground, motion provided the only information by which the two regions could be differentiated. This is very similar to the cases where animals possess protective coloration or crypsis which allows them to blend with their surroundings. It is probably significant that in the large majority of species that are afforded protection by color and patterning, remaining immobile is an integral part of this strategy. Others such as the vine snake, *Oxybelis aeneus*, superimpose oscillations simulating wind-blown vegetation movement on their forward locomotion to escape detection by its prey (Fleishman 1985). Likewise, it may be supposed that during stalking, animals may place their motion characteristics below the threshold of mechanisms such as those described above, which their potential prey may have evolved to segment the image through motion.

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