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Figuring Space by Time

Review

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Sensory information is encoded both in space and in time. Spatial encoding is based on the identity of activated receptors, while temporal encoding is based on the timing of activation. In order to generate accurate internal representations of the external world, the brain must decode both types of encoded information, even when processing stationary stimuli. We review here evidence in support of a parallel processing scheme for spatially and temporally encoded information in the tactile system and discuss the advantages and limitations of sensory-derived temporal coding in both the tactile and visual systems. Based on a large body of data, we propose a dynamic theory for vision, which avoids the impediments of previous dynamic theories.

Visual and tactile systems share two major strategies: both employ two-dimensional arrays of receptors to capture the spatial variations of the external stimuli, and both employ movements of the sensory organs during active sensing epochs. These movements prevent receptor adaptation when the stimulus is stationary, which allows the sensation of a stationary environment and thus provides a significant evolutionary advantage over species that can sense only external movements or changes. The movements of the sensory organs induce encoding of spatial details in time, in addition to the straightforward encoding in space. However, most of the research on the encoding of stationary stimuli has focused so far on the spatial dimension alone. Temporal encoding of stationary stimuli has been largely ignored, in particular with tactile and visual sensations. We will first review the experimental data describing the sensor movement-based temporal coding scheme in the somatosensory system, focusing on object localization in the rat vibrissal system. Then, we will describe the evidence supporting a similar scheme in the visual system. Finally, we will outline the framework of a new dynamic theory for vision that emerges from these data.

Temporal Encoding-Decoding in the Tactile System

Tactile sensation depends on changes. To perceive stationary objects, the sensory organ has to move. Thus, primates move their fingers across surfaces they try to identify, and rodents, such as rats, move their whiskers in order to localize and identify objects.

Temporal Encoding of Vibrissal Touch and Possible Decoding Schemes

The rat vibrissal system provides a clear example of a dissociated spatiotemporal coding scheme. The mystacial pad of the rat contains about 35 large whiskers, which are arranged in five rows and about seven arcs (columns) (Figure 1). To obtain sensory information, such as the location and texture of external objects (Gustafson and Felbain-Keramidas, 1977; Simons, 1995), the whiskers move back and forth with a rhythmic motion ("whisking") at 4–10 Hz (Carvell and Simons, 1990; Fanselow and Nicolelis, 1999; Kleinfeld et al., 1999; Welker, 1964), covering several cubic centimeters near the snout (Brecht et al., 1997; Wineski, 1983). Each whisker along the same arc scans a different trajectory, while all the whiskers of the same row scan roughly the same trajectory (Brecht et al., 1997). The vertical location of a punctuate object can be extracted from the identity of activated whiskers along each arc. We use the term "spatial coding" to refer to this kind of coding, which is based on the spatial profile of whisker activation. The radial location (i.e., the distance from the face) might also be encoded by whisker identity, due to the gradient of whisker lengths along the rows (Brecht et al., 1997). In contrast, the identity of active whiskers would provide no information about the horizontal location of the object (i.e., its location along the anterior-posterior axis, parallel to the whisker rows). This is because the whiskers are moving along this axis. However, information about the horizontal location of the object can be extracted from the timing of whisker activation: the temporal interval between whisker activation at protraction onset and at the moment of touch is proportional to the spatial distance between whisker retracted position and object position (Ahissar and Zacksenhouse, 2001). This is a form of *temporal encoding*: the horizontal location of the object (in relative coordinates) is *encoded* by this temporal interval.

Existing data and simple reasoning suggest that temporal encoding of object location along the horizontal axis, i.e., along the whisking path, should probably work as follows (Figure 2A): during free-air whisking, each whisker induces spike bursts in the brainstem, whose duration is determined by the duration of the protraction phase (i.e., forward movement, Figure 2A; see Ahissar et al., 2000; Nicolelis et al., 1995; Shipley, 1974). When an object is introduced into the whisking field (Figure 2A, black circle), an additional burst will be generated during protraction (Zucker and Welker, 1969). The onset of the additional burst will be at the time of touch. If the object is located more anteriorly (gray circle), the onset of the additional burst will be delayed. Thus, the horizontal location of the object is encoded by the temporal interval between the two afferent bursts. We ignore here the events occurring during the retraction phase, which is considered to be a resetting phase (Kleinfeld et al., 1999).

The horizontal location of objects could, in principle, be represented by this temporal code throughout its processing in the brain. However, in order to establish a complete representation of the location of the object, this information must ultimately integrate with other sensory information—in particular, with that of the vertical and radial location components, which seem to be coded

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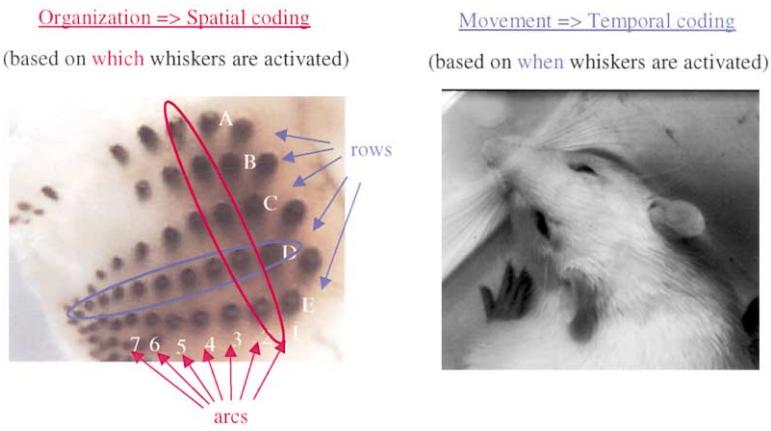

Figure 1. Organization of the Rat Mystacial Pad

(Right) Top view of the rat's head and whiskers. (Left) Spatial organization of the mystacial vibrissae of the rat. Blood sinuses surrounding whiskers' roots were visualized using xylene (see Haidarliu and Ahissar, 1997, for methods). Spatial coding is valid along the arcs (red ellipse), whereas temporal coding is valid along the rows (blue ellipse).

differently. Furthermore, in order to eventually control motor activity, the sensory-derived representations should probably be coded by some form of coding which is not based on accurate sensory timing, most likely a rate population code (Fetz, 1993; Georgopoulos, 1986; Kleinfeld et al., 1999; Salinas et al., 2000; Shadlen and Newsome, 1994; Wise, 1993; Zhang and Barash, 2000). Thus, the temporally encoded information is probably translated into a different coding scheme. We call this translation here "decoding" or "recoding" (Perkel and Bullock, 1968), meaning that the sensory encoding is translated into another code, which is used for internal representations.

The temporally encoded information could be decoded by feedforward bottom-up transformations, without any reference to internally generated expectations (Figure 3A, "passive decoding"). For example, temporal intervals can be converted to spatial representations utilizing neuronal delay lines (Carr, 1993; Jeffress, 1948) or other time-dependent properties (Buonomano and Merzenich, 1995) and only feedforward connections. Alternatively, temporal decoding could be achieved by

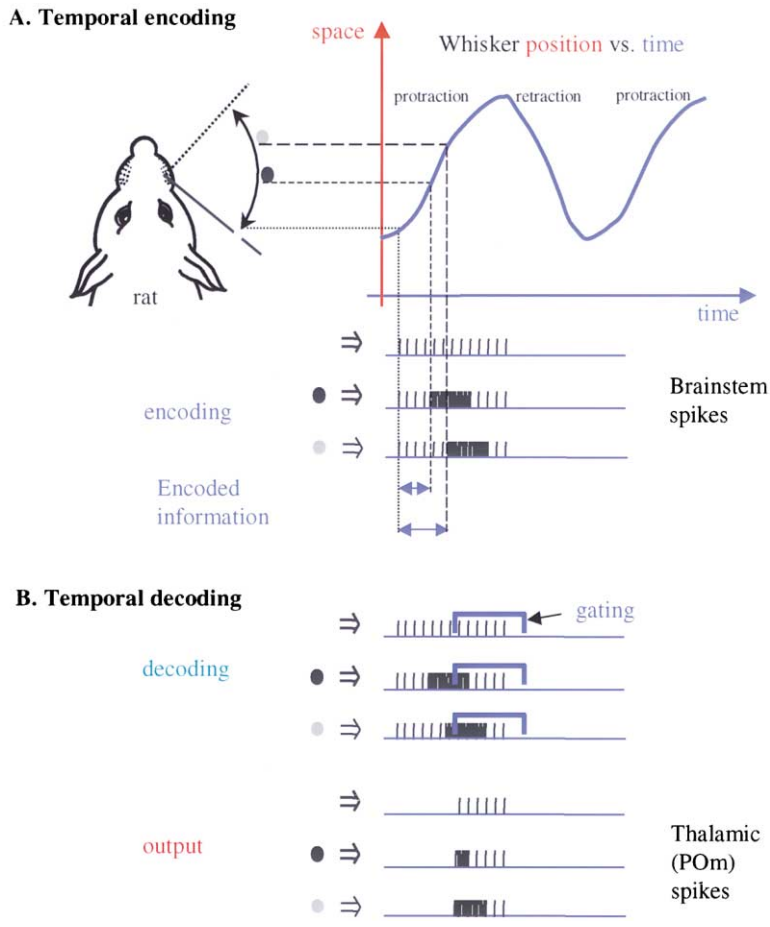

Figure 2. Our Working Hypothesis for Temporal Encoding-Decoding in the Rat Vibrissal System

(A) Encoding. Single-whisker trajectory during whisking is shown: protraction, moving forward; retraction, backward. Black and gray objects are depicted. Horizontal position of an object is encoded by the interval between the onset of the burst generated by protraction onset and the onset of the burst generated by touch. Activation is shown only for the first protraction phase.

(B) Decoding. Decoding of the temporal information is obtained by gating. The delay between protraction onset and gating onset is determined by the thalamocortical closed loop according to the whisking frequency (Ahissar, 1998). For each given frequency, more anterior object positions will generate more delayed touch bursts, and, thus, more spikes will pass the thalamic gate. Thus, higher spike counts represent more anterior positions.

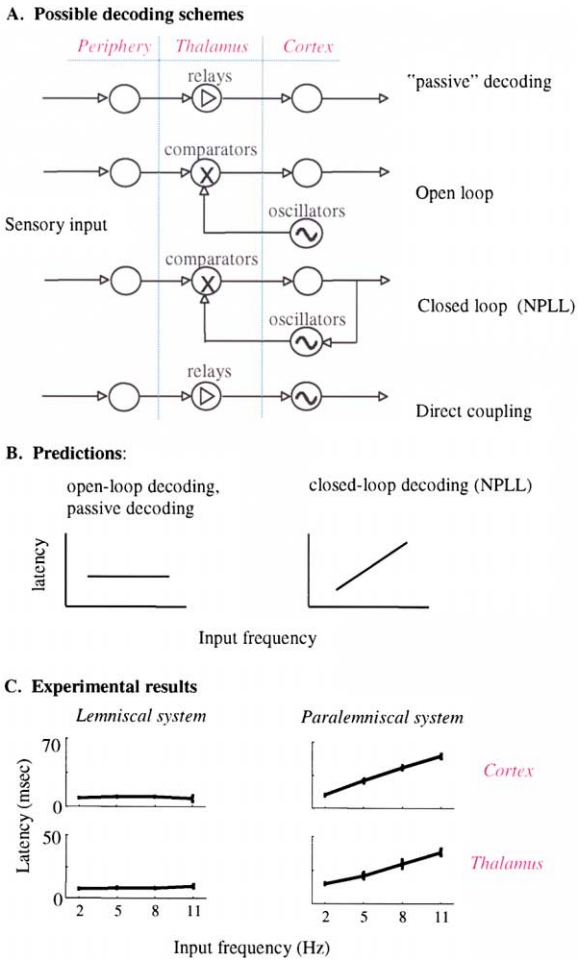

Figure 3. Possible Schemes for Temporal Decoding

(A) Passive decoding is assumed to flow through feedforward connections where the activity at each level depends on the activity at a lower (more peripheral) level. Arrows represent feedforward elements, including simple axons, delay lines, and synapses. Active decoding involves an independent cortical source of information—local oscillators. Information flows both ways and is compared, in this example, in the thalamus. The circuits can be open or closed loops. Open-loop decoding requires a set of oscillators (only one depicted in the figure), each tuned to a specific frequency and phase. Closed-loop decoding can, in principle, be based on a single oscillator (see Ahissar, 1995, 1998). Direct coupling is the case where the input oscillations drive internal oscillators directly or via relays, without intermediate transformations. Adapted from Ahissar et al., 1997.

(B) Predicted dependencies of thalamic and cortical latencies on the input frequency. With closed-loop decoding, such as the NPLL, the latency of the response should increase with the frequency (right). Open-loop and passive decoding (left) predict no effect of the input frequency on the latency.

(C) Average response latencies in the somatosensory system of the anesthetized rat (from Ahissar et al., 2001; Sosnik et al., 2001). Latencies of all local populations whose recording sites were clearly situated within the specific nucleus or layer and for which all stimulus conditions were applied were averaged (n = 7, 12, 7, and 8 recording sites in layer 4, layer 5a, VPM, and POm, respectively). A local population included all single and multiunits recorded from one site (typically about five neurons). Error bars are standard errors.

means of comparisons with internal expectations (Figure 3A). We term such a decoding process, in which the transformation is not determined a priori but rather is dynamically controlled by autonomous neuronal agents, an "active decoding." This decoding scheme requires the existence of independent internal "temporal rulers" which are compared with and thus provide a measure of the temporal intervals of the input (Ahissar, 1998; Ahissar and Vaadia, 1990; see also Talbot et al., 1968). Evidence collected from cortical and thalamic neurons in anesthetized (Ahissar et al., 1997, 2000) and freely moving (Nicolelis et al., 1995) rats indicate that in the rat temporal decoding is probably achieved actively (Ahissar and Zacksenhouse, 2001), using a scheme previously suggested for temporal decoding in primates (Ahissar and Vaadia, 1990). According to this scheme, intrinsic cortical oscillators constitute the internal "temporal rulers" (Ahissar, 1998; Ahissar and Vaadia, 1990). This decoding scheme requires the existence of independent oscillators in the somatosensory cortex, oscillators that can lock their firing phases to periodic inputs and track changes of the instantaneous input frequency (Ahissar, 1998; Ahissar and Vaadia, 1990).

Spontaneous single-cell oscillations were described in the somatosensory cortices of both primates (Ahissar and Vaadia, 1990; Lebedev and Nelson, 1995) and rodents (Ahissar et al., 1997). These neurons tend to oscillate at a given frequency in the absence of any sensory stimulus, but, once a stimulus is applied, they lock to the input frequency, provided that the input frequency is not too far from their spontaneous oscillating frequency. In the rodents (rats and guinea pigs), the oscillation frequencies center around 10 Hz, whereas those of the primates (macaque monkeys) center around 30 Hz. If these oscillators participate in the decoding of temporal sensory information, then this difference should be paralleled by differences in the two sensory systems. Indeed, temporal encoding in the primate tactile system mainly involves rapidly adapting receptors, which are most sensitive around 30 Hz (Talbot et al., 1968), whereas the rat vibrissal system employs a sampling process ("whisking") at around 10 Hz (see Ahissar, 1998).

Elimination of Implausible Active Decoding Schemes

As far as we can see, decoding by local oscillators could take one of three forms: open loop, closed loop, or direct coupling (Figure 3A). All these models utilize local oscillators in different ways and thus yield different predictions (Ahissar, 1995, 1998; Ahissar et al., 1997; Ermentrout and Kleinfeld, 2001; Kleinfeld et al., 1999). We tested these predictions experimentally, beginning at the cortex of anesthetized rats and guinea pigs (these two species demonstrate similar relevant anatomical structures and physiological characteristics, despite their different whisking behavior [Haidarliu and Ahissar, 1997]).

Based on the results obtained from the barrel cortex (Ahissar et al., 1997), both the direct coupling and open-loop models for decoding were rejected, while a specific closed-loop model, named the Neuronal Phase-Locked Loop (NPLL, Figure 3A), was supported. The NPLL is based on a closed-loop circuit in which thalamic neurons function as comparators; they compare the timing of the ascending whisker input with the timing of the descending signal (which is driven by the cortical oscillators). The difference between the two signals, which is the output of the circuit, changes the cortical oscillating

frequency. Decoding by NPLLs is supported by the following findings: (1) cortical oscillators track input frequencies, (2) cortical delays increase with increasing input frequencies, and (3) spike counts of cortical populations decrease with increasing frequencies (Ahissar et al., 1997). Moreover, the specific polarity of these dependencies supports a specific subclass of NPLLs, the one termed "inhibitory PLL" or iPLL (Ahissar, 1998). However, not all cortical neurons behave according to the NPLL predictions; about 25% of the neurons we tested did not display latency shifts with increasing frequencies (ibid.). Thus, if NPLLs are implemented in this system, they are probably implemented by a subgroup of somatosensory neurons. One possibility is that NPLLs are implemented by only one of the two thalamocortical systems of the vibrissal system: the lemniscal or paralemniscal.

Parallel Afferent Pathways

Vibrissal information is conveyed to the barrel cortex via two parallel pathways: the lemniscal and paralemniscal (Woolsey, 1997). The lemniscal pathway ascends via the ventral posterior medial nucleus (VPM) of the thalamus, and the paralemniscal pathway ascends via the medial division of the posterior nucleus (POm). The VPM projects to the barrels in layer 4 and to layers 5b and 6a and receives feedback from layers 5b and 6a (Bourassa et al., 1995; Chmielowska et al., 1989; Lu and Lin, 1993). The POm projects to layers 1 and 5a and to the septa separating the barrels in layer 4 and receives feedback from layers 5 and 6b (Bourassa et al., 1995; Diamond, 1995; Koralek et al., 1988; Lu and Lin, 1993). Thus, the thalamocortical loops formed by the two pathways are, to a large extent, separated. The main differences between the responses to whisker stimulations in the two systems are that paralemniscal latencies are more variable, the responses are weaker, and the RF cores are larger (Ahissar et al., 2000; Armstrong-James and Fox, 1987; Armstrong-James et al., 1992; Brumberg et al., 1999; Diamond et al., 1992b; Friedberg et al., 1999; Nicolelis and Chapin, 1994; Simons, 1978). Furthermore, the cortico-POm connections are exceptionally strong (Diamond et al., 1992a; Hoogland et al., 1988).

The existence of two nearly parallel pathways to the cortex has been puzzling. One possibility is that the POm does not process vibrissal information directly but rather processes the output of the lemniscal pathway in series to lemniscal processing (Diamond et al., 1992a; Hoogland et al., 1988). This scheme views nonlemniscal thalamic nuclei as higher order nuclei, which process the output of primary cortical areas and on which the ascending sensory connections exert only a modulatory action (Kaas and Ebner, 1998). Another possibility, however, is that the paralemniscal pathway directly processes sensory information, in parallel to the lemniscal pathway. Under this hypothesis, the paralemniscal pathway processes sensory information that is different from the information processed by the lemniscal pathway and whose processing requires spatial integration, strong cortical feedback, and variable delays.

Evidence for Parallel Afferent Processing

To probe the type of processing performed in each pathway, we examined the development of the neuronal representations of a basic sensory variable—the temporal frequency of whisker movement. Recordings from all major stations along the two afferent pathways, from brainstem to cortex, in anesthetized rats (see Haidarliu et al., 1999, for methods) showed that the temporal frequency of whisker movement is represented differently in the two pathways: primarily by response amplitude (i.e., instantaneous firing rate) in the lemniscal and primarily by latency in the paralemniscal pathways (Ahissar et al., 2000, 2001; Sosnik et al., 2001). These internal representations are first expressed in the thalamus and are preserved in the corresponding cortical domains of each pathway. Both amplitude and latency representations result in spike count representation (i.e., total number of spikes per stimulus cycle). The paralemniscal latency code and the translation of the latency code to a spike count code are essential features of the NPLL model (Ahissar, 1998). In fact, the increased latency as a function of input frequency, found in thalamic and cortical paralemniscal neurons (Figure 3C), are predicted by the NPLL model, whereas constant or decreasing latencies are predicted by the open loop, passive, or direct coupling models (Figure 3B). Thus, the results of this study are consistent with temporal decoding performed by the paralemniscal system, using an NPLL-like algorithm (Ahissar et al., 2000).

An additional finding of this study was that neuronal representations of the whisker frequency varied among layers of the same cortical columns according to their thalamic affiliation. This was evident during vertical penetrations into the cortex of anesthetized rats while moving the whiskers with air puffs (Ahissar et al., 2001). When recording from barrel neurons in layer 4, the response latency was usually constant for stimulation frequencies between 2 and 11 Hz. However, upon moving from the barrels in layer 4 to layer 5a, a robust latency representation of the whisker frequency emerged. Upon moving further down, to layer 5b, a response pattern similar to that of layer 4 barrels was revealed. Thus, although the two different thalamocortical systems (lemniscal and paralemniscal) share the same cortical columns, they utilize different coding schemes to represent the whisker frequency. Interestingly, neurons in layer 2/3 displayed an integration of these two coding schemes: with increasing frequencies, both latency increments and amplitude reductions were evident. These latter observations are consistent with the anatomical organization of the cortex, where layer 2/3 integrates neuronal data from both granular and infragranular layers (Kim and Ebner, 1999; Staiger et al., 2000) and outputs the results of local computations to higher order cortical areas (Felleman and Van Essen, 1991). In addition, layer 2/3 neurons project also to the infragranular layers (Bernardo et al., 1990; Gottlieb and Keller, 1997; Keller, 1995; Kim and Ebner, 1999; Staiger et al., 2000). The function of these projections is not yet clear.

Neural Representations and Code Transformation

We use the term "neuronal representation" here to refer to a neuronal variable that changes as a function of a stimulus quantity in such a manner that the quantity can be reconstructed from the variable. (We thank our colleague Shabtai Barash for this definition.) Obviously, not every neuronal variable that fulfills the above definition necessarily fulfills the definition of an "internal representation" (Dudai, 1989). Our recordings from the brainstem, thalamus, and cortex revealed several such neuronal

variables that represent the whisker temporal frequency. These were, in different stations, firing rate, latency, and spike count. All these representations appeared first at the thalamus (firing rate and spike count at the VPM and latency and spike count at the POm) and were preserved at the cortex (Ahissar et al., 2000). The cortical spike count representation can be modified by experience in a state-dependent manner (Shulz et al., 2000).

Several transformations were thus observed along the processing pathways from the whiskers to the cortex. The first was the transformation from a simple repetition code at the brainstem to more abstract representations at the thalamus. At the brainstem, burst onset times simply followed stimulus onset times, whereas other neuronal variables remained constant. Thus, the only representation of the stimulus frequency at the brainstem was by interbursts intervals. At the thalamus, this information was translated to two response variables: amplitude (firing rate) at the VPM and latency at the POm. These two representation codes were further transformed into a third, common code—spike count; since response offset timing was constant, both amplitude reduction and latency increments induced spike count reductions. These results demonstrate that, contrary to the classical view, both VPM and POm do not merely relay the sensory information to the cortex but rather actively participate in its processing. These results are in line with recent findings of spatial transformations at the VPM (Ghazanfar and Nicolelis, 1997; Nicolelis and Chapin, 1994).

Temporal (Latency) Coding

Temporal coding is often associated with fixed response latencies (for a review of several examples, see Carr, 1993). However, it is important to note that while *fixed* response latencies are crucial for *relaying* temporal cues, latencies are not required to be fixed during the *processing* of these cues. In contrast, fixed response latencies are crucial for the processing of *spatial cues* obtained by moving sensory organs, such as the whiskers. This is because, during whisking, computations of spatial details must consider the time of activation of the activated whiskers, which are in constant motion. Unreliable latencies will distort the perceived image. Imagine, for example, two whiskers of the same arc moving across a vertical edge. If latencies are not reliable, the two signals (single spikes or bursts) arriving to the thalamus might be delayed from each other and thus interpreted as representing a spatial offset that does not exist. Thus, the fixed latencies observed in the lemniscal system, taken together with the superior spatial resolution in this system, is consistent with the processing of spatial cues, probably those encoded along individual whiskers' arcs.

Unlike the lemniscal system, latencies of the paralemniscal neurons varied with the input frequency. This variation was not random but rather consistent and monotonous, such that response latencies were directly related to the input frequency. As such, paralemniscal latencies could serve as internal representations of the whisker frequency, representations that are used for further computations downstream. Alternatively, paralemniscal latencies could be an intermediate variable that is used locally for temporal processing.

Temporal Decoding

The decoding scheme suggested by the results presented above is demonstrated in Figure 2B. The decoding of horizontal object location is based on thalamic gating (McCormick and von Krosigk, 1992; Sherman and Guillery, 1996). The gating signal is mediated by the strong cortical feedback connections to the POm (Diamond et al., 1992a; Hoogland et al., 1987). If the gating onset occurs at a constant delay from protraction onset, the decoding is simple: the amount (number) of spikes "passing" the gate will be proportional to the delay between protraction onset and touch (Figure 2B). Thus, output spike counts now code horizontal object location. Note that the spike count coding will be a monotonous function of the location of the object only if the gating signal appears at the "appropriate" delay from whisking onset. This delay is determined by the negative closed loop established by the NPLL, which, for each stimulus frequency, keeps a specific constant delay between the cortical oscillators and the input (Ahissar, 1998; Ahissar et al., 1997). This constant delay and the associated spike count (at free-air whisking) establish the set point of the loop.

According to the NPLL model, the latency variations do not establish a solid representation of the input frequency but rather are intermediary to obtaining a robust spike count representation. This mechanism provides a strong prediction: if a temporal input parameter other than the frequency will change, the spike count coding should remain intact, and this should be obtained by adjusting the latency. Alternatively, if the latency coding is a solid one, it should not change by this manipulation. To test this prediction, we varied the input pulse width. Instead of a natural-like pulse width of 50 ms, we applied the same stimuli as before with a pulse width of 20 ms. This manipulation almost abolished the paralemniscal latency coding. In contrast, the spike count coding remained unchanged. Moreover, the spike count coding remained unchanged *because* the latency variations were strongly reduced; had the latency coding been less affected, the spike count coding would be forced to change (Ahissar et al., 2001; Sosnik et al., 2001). This finding strongly suggests that the response latency is an intermediary for obtaining the spike count code and is thus adaptively adjusted to match variations in the stimulus parameters.

Working Model for Object Localization by Whisking

The data collected in our experiments, together with data collected by others, led us to suggest a novel encoding-decoding scheme for the rat vibrissal system (Ahissar and Zacksenhouse, 2001). According to our scheme, the vertical component of the location of an object is encoded by arcs of whiskers and is decoded by the lemniscal system. The horizontal component of the location is encoded by rows of whiskers and is decoded by the paralemniscal system. With this scheme, constant latencies preserved along the lemniscal pathway enable reliable lateral comparisons along the arc representations in the thalamus and cortex. This computation is probably based on rate, since the identity of an activated whisker is rate coded. Such an arc-based computation in the VPM is supported by recent findings (Ghazanfar and Nicolelis, 1997; Ghazanfar et al., 2000).

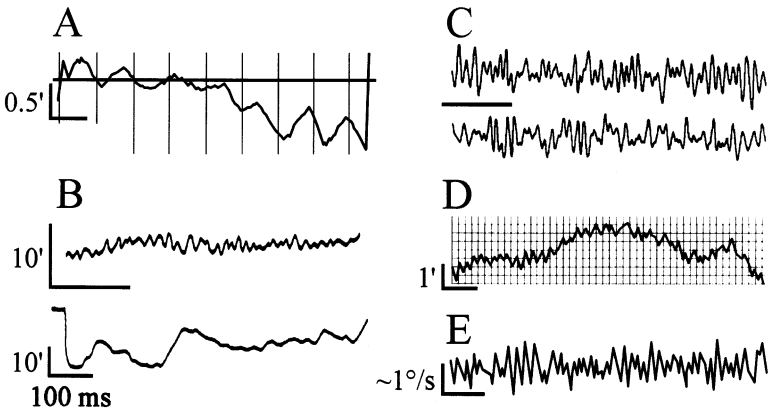

Figure 4. Examples of Records of Fixational Eye Movements in Humans as a Function of Time

All horizontal calibration bars are 100 ms. (A) Eye rotation during a steady fixation (Byford and Stuart, 1961). Recorded with a miniature electric lamp attached to a contact lens via an aluminum tube. (B) Eye rotations of two subjects during a fixational pause between saccades (Barlow, 1952). Recorded by photographing a droplet of mercury placed on the cornea. (C) Velocities of the two eyes recorded simultaneously during fixation with piezoelectric strain gauges (Coakley, 1983; vertical scale not provided). (D) Eye rotation during a steady fixation. Recorded with plane mirrors attached to a contact lens (Matin and Pearce, 1964). (E) Eye velocity during a steady fixation (Bengi and Thomas, 1968). Vertical scale was estimated according to the data provided by the authors. Recorded with a piezoelectric strain gauge.

In the paralemniscal system, the temporal-to-rate transformation results in a rate code representation of the horizontal spatial component. This component is encoded in time by the whiskers (see "Temporal Encoding of Vibrissal Touch and Possible Decoding Schemes" above). The rate-coded representations that result from the parallel computations along the two pathways can be integrated in the barrel cortex (probably in layer 2/3, see Ahissar et al., 2001) to generate a two-dimensional (forward-upward) representation of the object location. The encoding-decoding scheme for the third dimension (the radial distance from the snout, see Brecht et al., 1997) as well as the relation between the decoding processes postulated here and the sensory-derived cortical representation of whisker position (Fee et al., 1997) are not yet clear.

Reservations

Two important reservations should be briefly mentioned. First, the above observations have been obtained in anesthetized animals. In anesthetized animals, the physiological conditions of the neurons are affected by the anesthesia (Simons et al., 1992), and the motor-sensory loop is "open." That is, sensory acquisition does not depend on the motor system, as it does during whisking (Kleinfeld et al., 1999). While anesthesia is unlikely to account for the marked latency shifts observed in the paralemniscal system, natural whisking might induce specific computational constraints that are not expressed in the anesthetized animal. Thus, the working hypothesis we developed should be tested in freely moving animals while they are localizing or identifying objects.

A second reservation is that our theoretical analysis deals so far only with simple tasks: localization of a single punctuate object. What if the whiskers scan a large object with a complex texture? What would temporal and spatial encoding mean, and how would the information be decoded in this case? Although this topic deserves a separate investigation, it is worth mentioning that the principles of sensory coding remain similar. Here again, temporal encoding occurs along the rows: the spatial intervals (between texture edges) along the movement trajectory of each whisker are translated to temporal intervals. Along the arcs, however, a spatio-temporal coding occurs: the spatial offsets along the arcs are encoded by temporal delays between the firing of adjacent whiskers. Note also that edge orientations are encoded by temporal delays along the arcs. The temporally encoded information generated by the interaction of whisker movement and textures contains high frequencies. These frequencies depend on the whisker velocity and the texture's spatial frequencies and are usually well above 10 Hz (Carvell and Simons, 1995). Since the decoding range of the paralemniscal system is limited to the whisking frequencies, i.e., $<$10 Hz, this information must be processed by the lemniscal system. Whether NPLLs of frequencies $>$10 Hz exist in the lemniscal system has to be tested by investigating the latency and spike count coding of stimulus frequencies between 10 and 100 Hz or even higher.

Temporal Encoding-Decoding in the Visual System

The eye is often referred to as a still camera, which captures sequences of frozen snapshots of the visual scene. According to this view, the signals transmitted from the retina are encoded spatially; that is, the image can be reconstructed from the identities of those ganglion cells that were active during a given fixational pause, similar to the encoding of the image by a photographic film. However, an inspection of the characteristics of the fixational eye movements and of the retina shows that this could not be the case.

Saccades, Fixational Pauses, and Fixational Eye Movements

During natural viewing, the eyes are never still. The eyes move from one target to another, using saccadic jumps, and dwell on each target for a fixational pause of a few hundred milliseconds. In some cases, as during the performance of a psychophysical task or during careful observation, the eyes fixate on a single target for a few seconds. But even during fixation or fixational pauses, the eyes are not still. They usually drift and tremble across several arcminutes with amplitudes that fall off with the frequency (Eizenman et al., 1985; Findlay, 1971) (Figures 4, 5A, and 5C). These fixational miniature eye

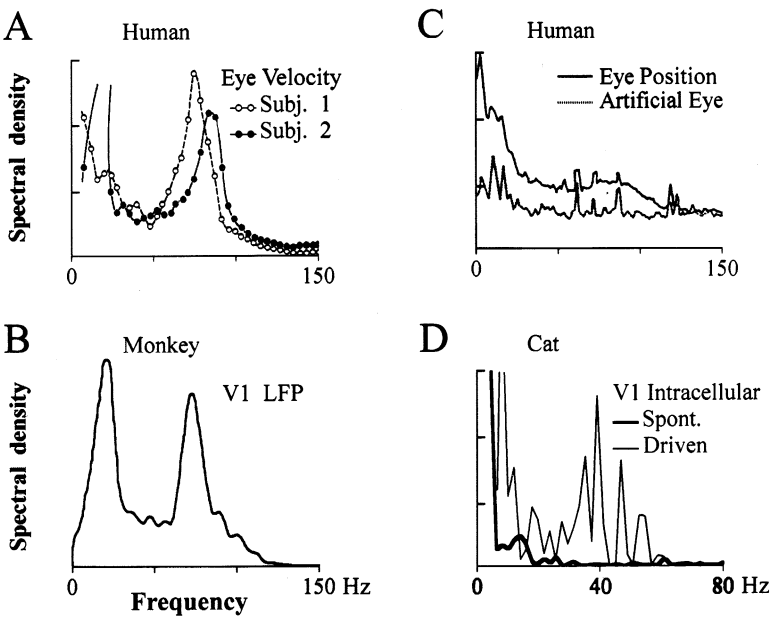

Figure 5. Similarity of Power Spectra of FeyeM and Cortical Oscillations

(A) Velocity spectral density of horizontal FeyeM of two human subjects (Bengi and Thomas, 1972).

(B) Average power spectra of local field potentials recorded from the primary visual cortex of an awake monkey during visual stimulation (Eckhorn et al., 1993).

(C) Power spectra of horizontal FeyeM of a human subject and artificial eye (Eizenman et al., 1985). Recorded with a noncontacting infrared system.

(D) Average power spectra of the membrane potential of a single "chattering" cell (Gray and McCormick, 1996) from the primary visual cortex of an anesthetized and paralyzed cat before (Spont) and during (Driven) visual stimulations.

movements (FeyeM) cover the entire spectrum between 1 to more than 100 Hz (Figures 5A and 5C), with an increased tendency to oscillate within two main frequency ranges: one between 1 and 20 Hz ("drifts") with amplitudes of up to about 10 arcminutes (′) and another between 40 and 100 Hz ("tremor") with amplitudes between a few arcseconds (″) and a few arcminutes (Barlow, 1952; Bengi and Thomas, 1972; Coakley, 1983; Eizenman et al., 1985; Ratliff and Riggs, 1950; Shakhnovich, 1977; Spauschus et al., 1999; Yarbus, 1967). These movements can be interrupted by "microsaccades"—brief movements of a few arcminutes. One can estimate the low-frequency components of his own FeyeM by observing the movements of afterimages, i.e., images that are temporarily imprinted on the retina following endured fixation, while fixating the eyes (Verheijen, 1961). Another way to estimate these movements is by looking at a patch of static random noise after adaptation to a smaller patch of dynamic noise (Murakami and Cavanagh, 1998).

What Are the FeyeM for?

The eyes are fast responding devices whose muscles are in a constant tonus. Thus, one possibility is that the FeyeM are an unavoidable "noise" caused by unbalanced tonus between antagonist muscles (Carpenter, 1988). Even if this was the case, this noise is a fortunate noise, since it keeps stationary images from fading away (Coppola and Purves, 1996; Ditchburn, 1973; Pritchard, 1961; Riggs et al., 1953; Yarbus, 1967). These images would otherwise disappear because of the insensitivity of the retina to steady states (Hartline, 1938; Hubel, 1988). It would make a lot of sense for the evolution of mammals to maintain this advantage, which allows vision of stationary objects. Moreover, it seems that separate mechanisms evolved to control eye movements specifically during fixation, since, during fixational viewing, the scatter of the eye is usually larger than the minimal possible scatter (Barlow, 1952). There are, in fact, indications that the brainstem oculomotor circuits control the FeyeM (Coakley, 1983; Eizenman et al., 1985; Shakhnovich, 1977; Spauschus et al., 1999). Such a control could evolve to optimize the processing of the retinal output, using a servo-like sensory-motor closed-loop operation, of the type proposed by Wiener's cybernetic theory (Wiener, 1949).

Can the Eye Function as a Still Camera?

Whatever their evolutionary origins are, the existence of the FeyeM does not allow a high-resolution camera-like operation of the eye, much as high-resolution stills cannot be obtained from a camera held by a trembling hand. The amount of smearing depends on hand velocity, the shutter opening time, and the time constant of the decay of the photographic film. Similarly, retinal smearing would depend on eye movement velocity, the duration of the fixational pause, and retinal memory (Barlow, 1952). Luckily enough, the retina has usually only a short memory trace. However, even during periods similar to retinal time constants (30–200 ms; Barlow, 1952; Nirenberg and Meister, 1997; Sakuranaga et al., 1987), the eye would travel a distance of a few to few tens of foveal photoreceptors (Riggs and Ratliff, 1954). Note that, even if the visual system could employ some kind of an "internal shutter" and could capture brief snapshots from the retinal output, smearing should still occur; this is because, at any given moment, activity of retinal ganglion cells contains traces of previous activations (Barlow, 1952). These retinal traces would smear the image if the readout circuits would assume only spatial coding, namely, that the spatial map of retinal activity (at a given moment) represents the external image, regardless of its temporal pattern. The task presented to such a readout circuit is demonstrated in Figure 6. In this figure, the spatial map of retinal activity, sampled at three different brief snapshots, is estimated, assuming retinal time constant of 100 ms and real traces of eye movements.

Although the spatial map of retinal activity is smeared, the perceived visual image is not. Moreover, details of

the visual image can be resolved with hyperacuity, i.e., with a precision that is much better than that offered by the retinal granularity. For example, human subjects can detect spatial offsets which are only a fraction of the diameter of a photoreceptor (Westheimer, 1976). This ability is usually demonstrated by the Vernier stimulus, in which two lines are misaligned by a few arcseconds. Human subjects can detect Vernier offsets of 3″, whereas the smallest photoreceptors have a diameter of about 20″. How can this be achieved with a trembling eye?

The only way in which a camera-like mechanism could obtain high-resolution visual images with a constantly moving eye is with external flashes, similar to stroboscopic illumination. This way, if the interval between flashes is large enough compared with retinal time constants, the internal image would not be smeared (although it would be constantly moving). Unfortunately, the world is usually not flashing, and, thus, the visual system has to work differently. One possibility is that the visual image is acquired at the retina with low resolution using camera-like spatial coding, and a high-resolution perception is obtained by cortical interpolation (Barlow, 1979; Crick et al., 1981; Fahle and Poggio, 1981). However, this hypothesis, which emerged to explain hyperacuity of moving stimuli assuming a still eye, is not consistent with retinal data (Shapley and Victor, 1986) and does not seem to hold for FeyeM (see "Alternative Models" below).

How It Might Work

The continuous movement of the eye puts several constraints on the way that the visual information is encoded. The main constraint is demonstrated by the schematic case depicted in Figure 7A, in which two ganglion cells are excited by a single spatial offset. During a rightward eye movement, the RFs of the two cells move from one location (solid circles) at time t to another location (broken circles) at time $t + \Delta t$. During this movement, a burst of spikes is triggered in each of the ganglion cells at the moment its RF crosses the stimulus edge. The durations of the bursts are determined by the retinal time constants. If the readout circuit relies only on spatial coding and only on the output of these two cells, then the spatial offset will not be sensed. This is because, with spatial coding, the information is assumed to be coded by the *identity* of the activated cells. However, the fact that these two neurons fired would only mean that each of them faced a luminance change; no information about the existence, direction, or magnitude of the spatial offset is contained in the spatial code. Neither is this information encoded by the firing rates of these neurons. The information about the spatial offset is contained solely in the temporal dimension—the onset of one burst is delayed relative to the other. The duration of the delay represents a certain amount of spatial offset. Thus, to represent the spatial offset, the readout system must decode the temporal delay.

Interestingly, the necessity of temporal decoding mechanisms is widely accepted in the case of moving stimuli (Barlow, 1979; Burr and Ross, 1986; Fahle and Poggio, 1981) but not in the case of stationary stimuli. We argue that, in principle, there is no difference between the processing of stationary and moving stimuli—retinal images are always moving (Steinman and Levinson, 1990). Whether movements of the retinal image are

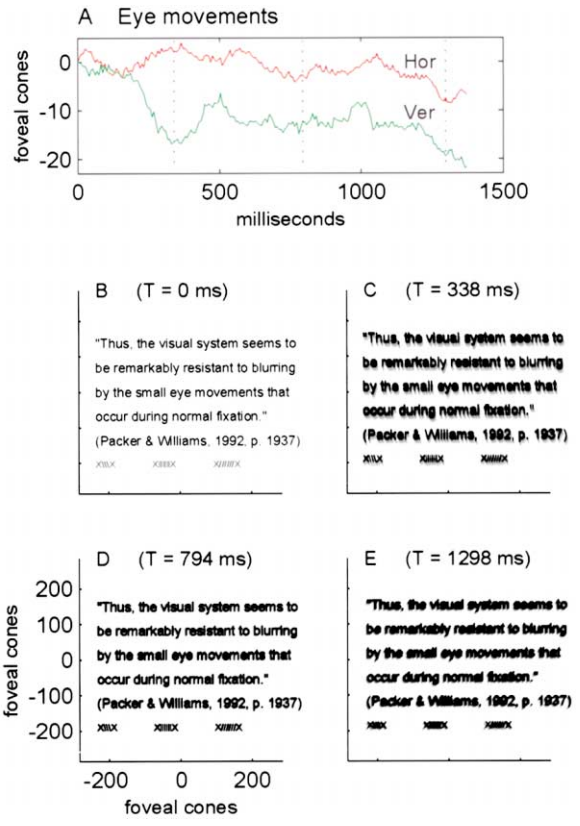

Figure 6. A Demonstration of Smearing of Spatial Snapshots during Fixation

(A) Horizontal (Hor) and vertical (Ver) FeyeM recorded by Matin and Pearce (Matin and Pearce, 1964), expressed as foveal distances in cones. Cone spacing of 20″ is depicted in both directions. (B) A sharp image (a citation from Packer and Williams, 1992, and oriented gratings) that is presented to the eye. (C–E) Illustrations of snapshots of the retinal output at different times during fixation (vertical dotted lines in [A]). Gray levels of text represent probability of firing of ganglion cells. The text in (B) was shifted horizontally and vertically according to the data in (A), scaled for a viewing distance of 50 cm. Gray levels for all positions visited before a given snapshot time (T) were determined as $\exp((t - T)/100)$, $t < T$, where t is time in ms. Optical blurring is not included. Note that the maximal gray level per pixel is the same in (B)–(E). The boldface appearance in (C)–(E) is due to the spatial smear.

imposed by external movements or by eye movements, the basic task introduced to the brain is similar—the extraction of spatial details from moving retinal images. Indeed, in awake behaving monkeys, cortical neurons in V1 respond similarly to a moving stimuli, whether the movement is induced by the external stimulus or by the eye (Snodderly et al., 2001).

While examining the effect of FeyeM on contrast sensitivity, Packer and Williams concluded that the visual system "seems to be remarkably resistant to blurring by the small eye movements that occur during normal fixation" (Packer and Williams, 1992). As you will see below, we propose that vision is not *resistant to* and does not *correct for* but rather *utilizes* the small FeyeM. Previous attempts to assign perceptual roles to fixational eye movements (by so-called "dynamic theories") were not successful (Steinman and Levinson, 1990). As

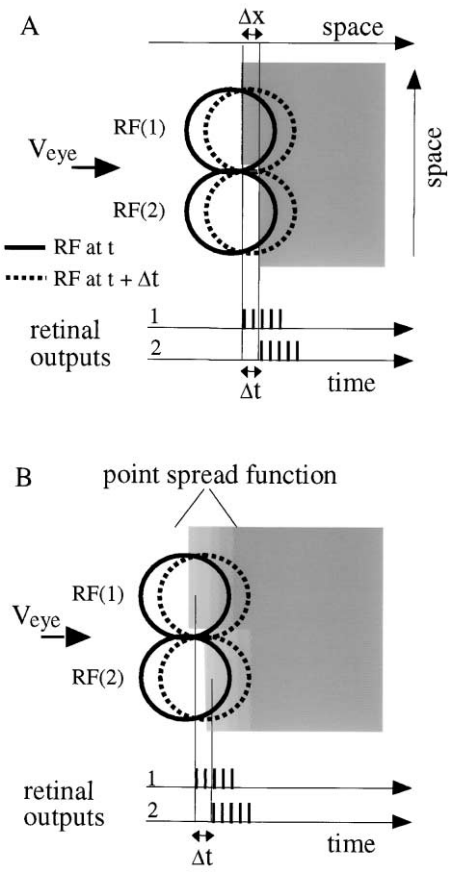

Figure 7. Temporal Encoding at the Retina

(A) Encoding of spatial offsets. The spatial offset Δx is transformed to a temporal delay Δt between the responses of two adjacent ganglion cells. Each ganglion cell responds with a burst whose onset time is the time at which the illumination threshold of the cell is crossed; OFF cells are depicted. For ganglion cells whose RFs (solid circles at t, broken circles at $t + \Delta t$) are aligned perpendicular to the spatial offset and whose thresholds are identical, $\Delta t = \Delta x/V_{eye}$, where V_{eye} is the horizontal eye velocity.

(B) Resistance to point spread. Optical blurring converts the sharp edges to gradual brightness changes (only one-dimensional blurring is shown). However, if the threshold mechanism is sensitive enough, this should only cause a temporal shift of both threshold crossings, preserving Δt.

far as we can judge, the failure of previous dynamic theories was mainly due to two shortcomings. First, most of these models did not assume temporal encoding by the eye movements but, rather, spatial averaging or spatiotemporal filtering, both of which necessarily induce loss of information. Second, these models did not provide a conceivable mechanism to restore the lost information (see "Comparison with Previous Dynamic Models" below). Our proposal continues the line of thought presented by these previous dynamic theories but presents a new view of retinal encoding and central decoding.

A New Dynamic Theory for Vision

Our dynamic theory postulates that a *temporal* encoding-decoding scheme is utilized for processing fine spatial details in *relative* coordinates, while a *spatial* encoding-decoding scheme is utilized for processing coarse spatial details in *absolute* coordinates.

Temporal Encoding

The FeyeM induce a simple spatial-to-temporal transformation, similar to that induced by fingers scanning a surface or rodents' whiskers scanning the environment. The basic encoding scheme, along a single axis, i.e., along the eye movement path, is demonstrated in Figure 7. When the RF of a ganglion cell crosses an illumination contrast, a burst is triggered (Figure 7, retinal output "1"). The onset of the burst will occur at the time in which the illumination level within the RF crosses the cell's firing threshold (upward or downward for ON or OFF cells, respectively). If the illumination contrast is located further along the movement path, the onset of the burst will be delayed (Figure 7, retinal output "2"). Thus, the relative locations of two illumination contrasts, i.e., spatial offsets within the visual field, would be encoded by temporal delays between activation onsets of retinal ganglion cells (see Bryngdahl, 1961; Darian-Smith and Oke, 1980). In Figure 7A, the spatial offset (Δx) is translated, by a rightward eye movement, to a temporal delay [$\Delta t = \Delta x/V(t)$, where $V(t)$ is the eye velocity] between the activation of spatially aligned RFs. The accuracy of this coding is not limited by the spatial receptor granularity, because the intercone gaps are scanned during eye movements. The factors that limit coding accuracy here are the temporal accuracy of spike generation and conduction mechanisms and eye velocity. Since the temporal accuracy of the above mechanisms is usually constant, spatial resolution depends mainly on eye velocity. For example, with eye velocities between 10′ to 100′/s (natural FeyeM velocities) and a spatial offset of 3″, Δt would be between 5 to 0.5 ms, respectively. These temporal intervals are well within the range of intervals that can be reliably detected by a variety of neuronal circuits (Ahissar, 1998; Carr, 1993). Still, if the visual system can control the velocity of FeyeM, it can optimize the temporal delays to meet the limitations of its actual readout circuits and even to enable the detection of very small spatial offsets ($<$1″, see Klein and Levi, 1985).

An additional advantage of this encoding is its resistance to optical blurring. This is because optical blurring affects the absolute location of light distribution across the retina but not the relative distances between image details (Figure 7B). The temporal code is a differential code, since it is based on the difference between activation times of neighboring ganglion cells. Therefore, it is almost not affected by optical blurring. The only effect optical blurring has on this temporal code is increasing the temporal noise by reducing local contrasts. However, if the light-to-firing transfer function is sharp enough, this temporal noise can be very small. In general, this differential temporal code makes the detection of spatial offsets, though not their absolute localization, immune to various types of common-mode noise, that is, noise that affects neighboring receptors similarly. In fact, the retinal temporal encoding proposed here is an implementation of the idea of "differential amplifier" suggested by Westheimer to explain hyperacuity (Westheimer, 1990).

Naturally, the differential nature of temporal encoding entails an inability to resolve absolute location. Interest-

ingly, this is also the case with hyperacuity: it is a differential acuity and not an absolute acuity (Westheimer, 1990). If, for example, the two lines composing a Vernier are presented each to a different eye, the acuity drops to the "normal" acuity levels (McKee and Levi, 1987). The same happens when lines are not presented simultaneously, and, therefore, the comparison is between the location of one of the lines with the memory of the other (McKee et al., 1990). All is consistent with hyperacuity being mediated by the differential temporal encoding and normal acuity, which is associated with absolute localization, mediated mainly by spatial encoding. Another limitation of the temporal encoding is that it takes time. With temporal encoding, hyperacuity can be obtained only after the relevant location has been scanned at the right direction with the proper velocity. Moreover, decoding of this information might even require a few repetitions of this scanning movement (e.g., Ahissar, 1998). This limitation implies that accurate vision should require continuous fixation. Common experience and controlled studies indicate that visual acuity indeed improves with longer fixations (Keesey, 1960; Morgan et al., 1983; Packer and Williams, 1992; Riggs et al., 1953).

Reading the Temporal Code

As demonstrated in Figure 7, the temporal interval (Δt) encoding the spatial offset is defined as the interval between the *onsets* of the two bursts. Thus, to read this code, the visual system has to identify the onset of each burst and measure the interval between them. While there are probably several possible solutions to this task, one seems especially attractive to us. From electronic solutions to similar computational tasks (Gardner, 1979) and from our findings in the vibrissal system (Ahissar et al., 1997, 2000, and see above), we know that such temporal measurements can be achieved via predictive phase locking between the sensory input and local oscillators. The local oscillators would provide an internal source of timing, somewhat like a "processing clock," and the phase locking with the FeyeM would synchronize this processing clock with the input signals. This decoding scheme requires the existence of independent oscillators in the visual cortex, which are tuned to frequencies similar to those of the FeyeM and can lock their firing phases to periodic inputs and track changes of the instantaneous input frequency (Ahissar, 1998).

Interestingly, the visual system is equipped with exactly such oscillators. The intrinsic oscillations in the visual cortex display oscillating frequencies that match those of the FeyeM (Eckhorn, 1994; Gray et al., 1989; Gray and McCormick, 1996). In particular, similar to the FeyeM, cortical oscillations tend to oscillate within the α (around 10 Hz) and γ (40–100 Hz) ranges. Figure 5 demonstrates the matching of frequency ranges. The spectral densities of human eye position (Figure 5C), eye velocity (Figure 5A), and stimulus-driven oscillations of local field potentials in the monkey visual cortex (Figure 5B) are strikingly similar, all emphasizing the α and γ modes. Note that the spectral density of cortical oscillations is more similar to that of eye velocity, which emphasizes high frequencies, than to that of eye position. This might imply that the spectral density of the retinal output is more correlated with that of eye velocity rather than eye position. Single-cell cortical oscillators were characterized so far only in cats. The spectral density of these oscillations, as well as of those of multiunits and local field potentials, preserve the α/γ bimodal distribution, albeit the γ frequency mode in cats appears at a lower frequency than in monkeys, around 40 Hz (Figure 5D). This difference agrees with the observation that cats' eye tremor frequencies are limited to about 40 Hz (Pritchard and Heron, 1960).

The frequencies of the visual cortical oscillations can be locally controlled (Gray and McCormick, 1996) or modulated by external stimuli (Eckhorn et al., 1993; Gray and Viana Di Prisco, 1997), as it is the case in the somatosensory system. This is a basic requirement of a predictive phase-locking mechanism. Such a local control enables phase locking between the local oscillators and the FeyeM. This can be obtained by thalamocortical loops, while they function as neuronal phase-locked loops (NPLLs, see "Temporal Encoding-Decoding in the Tactile System" above). Phase locking is obtained by virtue of a negative feedback loop, and decoding is achieved by comparing the predicted timing, i.e., the timing of the local oscillators, with the actual input timing, i.e., that of retinal output bursts. The decoding of the local details of an image would be based on a population of such NPLLs, whose individual working ranges vary in both spatial and temporal dimensions and together cover the entire visual field and the entire spectrum of FeyeM frequencies (Ahissar, 1998).

Let us now come back to the question of smearing. Retinal smearing due to FeyeM is caused by the fact that each ganglion cell generates a burst of spikes for each activation rather than a single spike (e.g., Figure 7A). The duration of this burst is determined by the retinal time constants relevant for that cell. The temporal coding scheme is able to overcome this smearing only if the readout circuit is able to measure the delay between the *onsets* of these bursts. Thus, to decode this temporal delay, the readout circuits have to identify the beginning of each burst and to treat each burst as a single encoding event. Thalamocortical NPLLs do exactly this—they chunk the afferent information stream according to FeyeM cycles. For each FeyeM cycle, the NPLLs would translate the retinal temporal code (Δt) into a spike count code in which cortical spike counts represent the relative spatial locations of illumination contrasts in the visual image. These spike counts would be the total number of spikes generated within a single "processing cycle" (single FeyeM cycle). Thus, fine spatial details along a scanning trajectory can be extracted by comparing spike counts of adjacent NPLLs at each processing cycle. For example, decoding the Vernier offset of Figure 7 can be accomplished by comparing the spike counts of two NPLLs driven by two adjacent channels. The decoding process is similar to the one suggested for the vibrissal system (see Figure 2) and involves a direct interaction of ongoing ("predictive") cortical activity with the incoming sensory signals (Arieli et al., 1996; Tsodyks et al., 1999).

Dimensional Reduction

One interesting outcome of the active acquisition process induced by the FeyeM can be called dimensional reduction of the effective stimuli for cortical visual neurons. This dimensional reduction is demonstrated in Figure 8. The figure describes the effect of FeyeM on re-

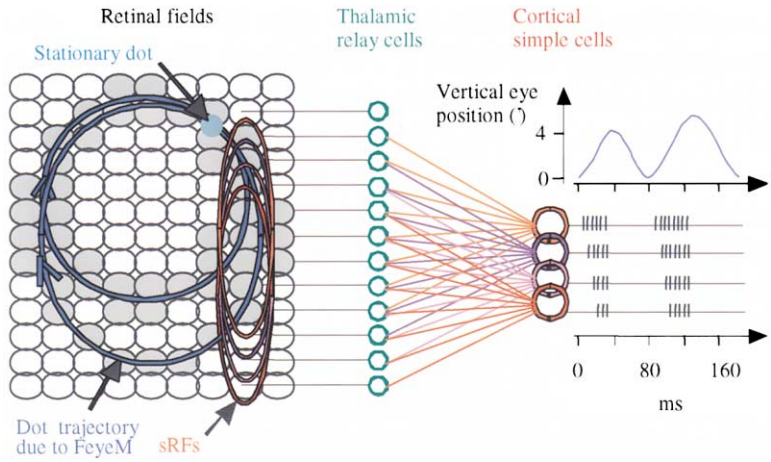

Figure 8. Retinal Trajectories of a Stationary Dot and the Resulting Cortical Activation

A rectangular retinal mosaic (left) scans a stationary dot (light blue). Every circle represents the center of a ganglion RF, 30″ in diameter. Only OFF-center RFs are depicted for simplicity. Two consecutive cycles of FeyeM are depicted, producing two cycles of dot trajectory (blue) on the retina. For simplicity, elliptical trajectories with no slow drift were depicted, and torsional movements were ignored. The four cortical simple cells receive their inputs, via thalamocortical neurons, from elongated retinal fields (Hubel, 1996). Every entrance of the dot to an OFF region of a ganglion cell (gray circles) produces a spike that propagates to the simple cells' output (right). Different sRFs produce bursts with different phases and lengths depending on their intersection with the dot trajectory.

sponses of cortical simple cells, assuming the afferent scheme proposed by Hubel and Wiesel (the scheme and supporting evidence are reviewed in Hubel, 1996). According to this scheme, cortical simple cells receive inputs from elongated arrays of thalamic neurons, and thalamic neurons ensure transmission of retinal signals by conducting them in parallel (Figure 8). Note that excitatory fields of RFs of cortical simple cells (sRFs) at the fovea can be as narrow as a single retinal cone (Dow et al., 1981). In awake fixating animal, external image elements move across the retina along a trajectory which is a mirror image of the FeyeM trajectory. Thus, during fixation, a single external dot passes through a series of oriented sRFs (some of them are plotted in Figure 8, left). According to available data, this should induce responses in cortical simple cells because (1) simple cells usually exhibit an OR-like response fashion, in which any spot flashed within their excitatory zone activates the cell (Gur and Snodderly, 1987; Hirsch et al., 1995; Hubel and Wiesel, 1962), and, (2) in the anesthetized cat, simple cells are effectively activated by illuminated spots that are swept along the long axis of their RF (A. Engel, S. Haidarliu, M. Brecht, and E.A., unpublished data). The retinal location and orientation of each sRF would determine its response pattern for each FeyeM trajectory (Figure 8, right).

Thus, the same anatomy underlies both orientation tuning for moving bars when the eyes are paralyzed and trajectory tuning for stationary dots in the awake fixating animal. We refer to this as "dimensional reduction" that is induced by the FeyeM: a single dot, which is a poor stimulus for cortical simple cells in paralyzed animals, becomes an effective stimulus during FeyeM, when the RF of a simple cell "scans" the stationary dot along the long axis of its RF. Similarly, a stationary bar becomes an effective stimulus when scanned by the RF of a complex cell. Indeed, V1 neurons with large RFs are effectively activated when their RF scans a stationary bar during FeyeM (Martinez-Conde et al., 2000; Snodderly et al., 2001). Thus, we might say that stimuli that are most effective for LGN and simple cells in paralyzed animals are optimal for simple and complex cells, respectively, in freely viewing animals. Consequently, simple and complex cells might function as trajectory and edge detectors, respectively, during free viewing.

Visual Stability

When considering FeyeM, the following puzzle is frequently raised: if the FeyeM move the retinal image across a significant number of photoreceptors, why don't we perceive a drifting and jittering world? This puzzle bears the assumption that visual perception of *absolute* target position is sensitive to changes smaller than the scatter of the FeyeM; otherwise, the FeyeM could not cause a perception of movement. This is because FeyeM induce only *absolute* position changes in the entire visual field; these movements cannot be measured against a reference point. However, the above assumption is probably not correct. Errors in spatial localization without a simultaneously presented visual reference, i.e., errors in *absolute* spatial localization, are larger than the scatter of the eye (a few arcminutes), even in the fovea where cone spacing allows much higher accuracy. In fact, the main reason for foveal mislocalization of absolute position appears to be the FeyeM (Matin et al., 1981; White et al., 1992). Thus, it is very well probable that if the entire world "shifts around" by a few arcminutes we will not be aware of it at all.

Thus, it seems that the drifting world puzzle can be explained by the dual processing scheme proposed here: fine image analysis is based on temporal coding, in relative spatial coordinates, and global image analysis is based on spatial coding, in absolute coordinates. It is not impossible that these different coding schemes underlie, in general, the processing of "*what*" and "*where*" in the visual system (Goodale, 1993; Ungerleider and Haxby, 1994). The visual system could sacrifice absolute coordinates for the sake of high-resolution analysis of features but must work in absolute coordinates when dealing with sensory-motor coordination, such as during reaching. This is consistent with the finding that the accuracy of visual sensory-motor control is worse than the scatter of the eye (van Opstal and van Gisbergen, 1989; White et al., 1992). Overall, this scheme is in line with the notion that the resolution in which retinal inputs are associated with unique "local signs" (Lotze, 1885) is that of the sensory-motor *where* system and is poorer than that employed by the sensory *what* system (see Morgan et al., 1990).

In neuronal terms, the dual processing scheme suggests that the analysis of *what* is based on temporal

coding by small RF cells, whereas that of *where* is based on spatial coding by larger RF cells. The RF distinction is consistent with the traditional association of *what* and *where* processing with the parvo- and magnocellular systems, respectively (Livingstone and Hubel, 1988). However, the coding distinction seems to oppose traditional view. According to the traditional view, since parvocellular neurons exhibit poorer temporal locking to external stimuli, they probably do not process temporally encoded information, a task which is traditionally assigned to the better-locking magnocellular neurons. However, as with the distinction between lemniscal and paralemniscal neurons in the vibrissal system, we believe that fixed temporal locking signals the opposite: the magnocellular neurons, which accurately preserve input timing, probably do not *process* the temporally encoded information but only *relay* this information downstream. This information is likely to be crucial for sensory-motor coordination, such as reaching or orienting, which depends strongly on timing. In contrast, the "unreliable" temporal locking of parvocellular neurons might be an indication for a temporal-to-rate transformation process, a process that is essential for translating the FeyeM-dependent coding into a more "abstract" code, such as the spike count code.

Comparison with Previous Dynamic Theories

Several models have been proposed for the potential role of the FeyeM in vision since their discovery (Adler and Fliegelman, 1934; for review, see Steinman and Levinson, 1990). Most of these models, which focused on the utilization of the γ frequency FeyeM (tremor), assumed integration of the temporally encoded outputs of the retina (e.g., Arend, 1973; Marshal and Talbot, 1942). However, simple integration would loose the fine temporal information, embedded in the retinal output—information that, as we showed here, has a hyperacuity resolution. In contrast, our model (1) relies on the entire spectrum of the FeyeM and (2) does not assume integration. Our model suggests, instead, that the fine temporal structure of the retinal output carries the information about the fine spatial details of the image. Furthermore, we propose that an active process, which is based on internal low-level (automatic) timing expectations, performs the decoding of the fine temporal details. Arend (1973) postulated a mechanism that discriminates between eye and object movement already at early processing stages. We suggest that the only discrimination done at early visual stages is between local and global motion, whatever the global source is.

Aliasing

According to our model, vision is a sampling process in time. Thus, retinal motion is always an apparent motion, whose sampling rate, which is the frequency of FeyeM, is not constant. One of the clear signs of a sampling process is a phenomenon called "aliasing." Any continuous signal can be fully reconstructed after sampling if the sampling frequency is higher than twice the maximal frequency contained in the signal. However, if the sampling frequency is lower, part of the input information is lost, and aliasing occurs: high input frequencies are aliased to a lower frequency range. Some well-known aliasing effects are caused by the constant-frequency sampling process used in movies or that induced by neon light vision at night. For example, car or wagon wheels can be seen rolling in the opposite direction in these conditions. This would happen when the sampling interval (1/frequency) is longer than the time required for one spoke to pass half of the interspoke interval but shorter than the time required for passing the entire interspoke interval. In this case, the brain interprets the apparent motion signals as indicating motion in the opposite direction (Shechter et al., 1988). Under certain conditions, aliasing occurs also with continuous-light vision (Purves et al., 1996). However, in most cases, the visual system succeeds in avoiding aliasing. One of the major factors helping to avoid aliasing is probably the pattern of eye movements: unlike the stereotypic whisker movements in rodents or the constant frequency in movies, eye movements almost never exhibit a repetitive scanning along a fixed linear section and with a constant frequency. While the quasirandomized nature of eye movements makes the decoding process much harder than the one required for a simple periodic scanning, it probably provides an enormous advantage by enabling a reliable and unambiguous reconstruction of external movements.

Alternative Models

If, contrary to our hypothesis, the FeyeM are not utilized for vision, then the visual system should overcome their effect. Only a few studies and theories directly addressed this issue. Packer and Williams (1992) demonstrated that visual acuity is impaired during the first $\sim$200 ms of fixation and gradually improves with longer fixations. One of their conclusions is cited in our Figure 6B. To explain how blurring due to FeyeM is overcome, they suggest that the visual system computes a moving average over its input, detects those periods with high contrasts (corresponding, according to their model, to periods of relatively stable eyes, e.g., Figure 6D), and performs spatial analysis only during those periods. However, if the visual system can ignore low-contrast periods, why does acuity deteriorate following stimulus onset? According to this model, the visual system should always base its processing on the high contrast produced by the stimulus onset and ignore the consequent low-contrast periods when the response is influenced by FeyeM. Furthermore, since the FeyeM are not correlated between the eyes (see, for example, Figure 4C), two separate moving-window processes, one for each eye, would operate in early visual stages and would provide their outputs in uncorrelated times, posing significant computational difficulties for binocular vision. Finally, consider the paradox introduced here: Packer and Williams suggest that visual acuity is best in conditions in which the retinal output is the least informative (since its main driving force, luminance transitions, are largely eliminated). Altogether, this process would be inefficient, since the system would have to wait for those rare periods of complete motionless or compromise for periods with small movements which still cause significant blurring (Figure 6) and ignore all the accurate information that is continuously available during ongoing FeyeM. In fact, as mentioned above, during fixational pauses, the scatter of the eye is usually larger than the minimal possible scatter (Barlow, 1952), which is in favor of an active sampling mechanism rather than a mechanism that relies on stable eyes.

We could not find other models that explicitly ad-

dressed the problem of blurring by FeyeM. However, models that offer general solutions for unblurring could, in principle, apply to FeyeM as well. Anderson and Van-Essen (1987) have suggested a universal error correction neural circuit which they called "shifter circuits." These circuits could correct blurring due to external or retinal motion, by shifting and redirecting the inputs according to some global command that predicts the blurring source. In the case of FeyeM, such circuits could produce a stable cortical image if the direction and speed of the eye were available to the cortex before or at least in parallel to the arrival of the retinal signals. However, neither such a command signal nor shifter circuits has been found so far in the visual system. On the contrary, RFs in the primary visual cortex were found to be locked to the retinal fields during FeyeM (Gur and Snodderly, 1997). In any case, even if they existed in higher stages, shifter circuits could not be sufficient for "unblurring" the image, since even the briefest retinal snapshot is already blurred due to retinal memory (Figure 6). The best such spatial shifter circuits could do is to align the centers of the consecutive blurred images. What is required for unblurring the image is some sort of "temporal shifter circuits," and, in a way, this is what the thalamocortical circuits proposed by us accomplish.

Since retinal images are always moving, visual perception of both stationary and moving objects face similar challenges and thus might utilize similar mechanisms. Based on studies of moving stimuli, Barlow (1979), Burr et al. (1986), Fahle and Poggio (1981), and others have suggested that the visual system achieves hyperacuity by interpolation. Indeed, it has been shown that the visual cortex contains enough neurons to interpolate the retinal input down to a resolution of 3″, provided that the basic representational unit is a single neuron (Crick et al., 1981). However, as mentioned by Wilson (1986), the visual cortex probably does not have enough neurons to support acuity of $<1''$, which is attainable under appropriate conditions (Klein and Levi, 1985). Moreover, such interpolation can work only with constant-speed movements (Crick et al., 1981) and probably only when the direction of movement is known. FeyeM's speed is not constant, and it is not at all clear where in the brain the information about its direction is extracted.

Integration of Models

In principle, even if the visual cortex would be able to perform the proper interpolation, a mechanism that acquires the image at low resolution and then "up-samples" it should be less accurate and much less efficient than a mechanism that acquires the image already with a high resolution. However, it seems that these two mechanisms might be operating in series in the visual system. The visual system contains a large number of spatiotemporal channels suitable for spatiotemporal integration (Burr and Ross, 1986). These spatiotemporal channels exhibit a wide distribution of spatial frequencies but a narrow distribution of temporal frequencies: they are mostly tuned to temporal frequencies within the α frequency range (around 10 Hz; Burr and Ross, 1986). This raises the following interesting hypothesis. Since the visual cortex cannot contain enough hard-wired channels to cover all possible spatial and temporal variations of FeyeM, some of these variations must be treated online. An online adjustment of a temporal tuning of a filter requires retuning of its band-pass range according to the input frequency. This is exactly what is accomplished by NPLLs—by forcing its local oscillator to follow the input frequency, a PLL circuit implements an adaptive band-pass filter that follows the varying input (Gardner, 1979). This process, in which the temporal processing of the current input is based on the temporal properties of the past input cycles, can in principle be regarded as temporal extrapolation, whose existence is implied by several psychophysical studies (e.g., Nijhawan, 1997). On the other hand, the interpolation power of cortical neurons can be used to smooth the spatial representation (coded by spike counts) of the NPLLs' outputs. We thus postulate an integrated model in which early processing of the visual image includes two stages in series: first, the temporal code is decoded and removed, and then the spatial details are processed. This scheme resembles the temporal-then-spatial filtering scheme suggested by Morgan and Watt (1983), only that in our scheme the temporal filter is not a passive filter but an active, retunable one. The processing of spatial details, performed on the output of the temporal decoders, is probably conducted in parallel by a number of spatial mechanisms, each tuned for both orientation and spatial frequency (Wilson, 1986, 1991). Interestingly, the entire temporal encoding-decoding stage (i.e., encoding by FeyeM and decoding by NPLLs) can probably be bypassed, in the laboratory, by using a paralyzed experimental animal or by applying high-intensity brief flashed stimuli, which eliminate FeyeM effects (Hadani et al., 1984). In these conditions, cortical spatial mechanisms can probably restore hyperacuity based on spatial cues alone. (In some conditions, the decoding of the high-intensity flashed stimuli can still be based on a differential temporal code. For example, following a high-intensity brief presentation, the receptors that are "marked" by the afterimage will not respond when the eye, which continues to move due to FeyeM, crosses illumination contrasts that activate their neighbors. The times of "silence" and thus also of the following activity onset will have the same temporal delays that represent the spatial offset imprinted by the brief stimulus.) However, during natural viewing, when images are not flashed onto the retina but rather are continuously scanned, the retinal output should first be decoded, by a mechanism that is temporally locked to the FeyeM, before it can be interpolated. Note that this order is the logical order of processing and does not necessarily entail a clear temporal or spatial separation between the two processes.

Limitations and Predictions

We hope that by now we have convinced the reader that, during normal vision, the constraints imposed by the physiology of the eye, the nature of the visual world, and perceptual limits reveal a need for computation based on temporal coding. The dynamic model outlined here is consistent with a large body of physiological, neurophysiological, and psychophysical data. However, this dynamic process is not the only one of the processes affecting and limiting performance. The spatial mechanisms, which as we suggest process the output of the temporal mechanisms, add additional limitations

of their own (see Crick et al., 1981; Levi, 1999; Swindale and Cynader, 1986; Wilson, 1986).

Still, several clear predictions can be derived from the dynamic model. One is that visual perception should be directly related to the FeyeM. For example, to detect Vernier offsets, FeyeM should have a movement component along the axis of the Vernier offset. FeyeM velocities should also have direct effect on perception. For example, to detect very small offsets (of a few arcseconds), eye velocity should be relatively slow (few to a few tens of arcminutes per second). Moreover, if the visual system indeed employs an active control of eye velocity, then eye velocity should be reduced as the spatial frequency increases. Another set of predictions can be derived from the proposed decoding mechanism. For example, response latencies and magnitudes, in thalamus and cortex, should show inverse dependencies on the temporal frequency of the stimulus, as is the case in the somatosensory paralemniscal system of the rat.

Summary and Conclusions

We propose a novel encoding-decoding scheme for the tactile and visual systems. In this scheme, spatial encoding is induced by the spatial arrangements of the receptors, and temporal encoding is induced by the movements of the sensory organs. The temporal cues provide a higher fidelity; however, their coding is a differential one providing only relative spatial information, whereas the spatial cues provide spatial information in absolute coordinates (relative to head position and gaze). The decoding of the temporal information is slower and requires phase locking to the movements of the sensory organs. In the rat somatosensory system, temporal and spatial coding seem to be used for encoding object location in horizontal and vertical axes, respectively. In addition, temporal and spatial coding are probably used for fine and coarse texture analysis, respectively. In the visual systems, temporal coding might be used for fine feature analysis (*what*) and spatial coding for coarse feature analysis and for absolute localization (*where*).

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