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# NEURAL REPRESENTATION AND THE CORTICAL CODE

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■ **Abstract** The principle function of the central nervous system is to represent and transform information and thereby mediate appropriate decisions and behaviors. The cerebral cortex is one of the primary seats of the internal representations maintained and used in perception, memory, decision making, motor control, and subjective experience, but the basic coding scheme by which this information is carried and transformed by neurons is not yet fully understood. This article defines and reviews how information is represented in the firing rates and temporal patterns of populations of cortical neurons, with a particular emphasis on how this information mediates behavior and experience.

## INTRODUCTION

The concept of neural representation is central to neurophysiology, but what does it actually mean to suggest that a neuronal signal is a representation? Many reviews of neural representation in individual sensory systems can be found in the literature (Andersen et al 1997, Bertenthal 1996, Bisiach 1993, Colby et al 1995, Damasio 1996, Edelman 1998, Edelman & Duvdevani-Bar 1997, Eggermont 1998, Farah & Feinberg 1997, Fregnac et al 1996, Gallistel 1989, Gross 1992, Grossberg 1994, Knudsen & Brainard 1995, Kuhl 1994, Laurent 1996, Logothetis 1998, Margoliash et al 1994, Maunsell 1995, Meister 1996, Nakayama & Shimojo 1990, Olson & Gettner 1996, Perrett et al 1989, Phillips 1993, Pons 1988, Rauschecker 1998, Roland & Gulyas 1994, Rolls 1992, Schacter 1990, Singer 1998). Drawing together a synthesis of views on neural representation requires us to ask how neural structures code signals, how organisms perceive and respond to their environment, and how these two processes are linked together. We begin with a question to which we will return to conclude: How does one determine whether a particular neuronal signal is part of the representation of a perceptual experience? If one could measure the activity of every neuron in the brain, how would one go about decoding cortical signals?

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A neural code is a system of rules and mechanisms by which a signal carries information. Coding involves many different brain structures, but this review seeks general principles of population and temporal coding only within the cerebral cortex. There is a large literature on cortical coding, which has been reviewed in depth from a number of perspectives, including single cortical areas (Andersen 1989, Callaway 1998, Duhamel et al 1992, Fujita et al 1992, Goldman-Rakic et al 1990, Gross & Sergent 1992, Maunsell & Newsome 1987, Miyashita 1993, Tanaka 1996, Zeki 1993), sensory or movement modalities (Schwartz 1994b, Wurtz et al 1990), particular species (Knudsen & Brainard 1995, Konishi 1985, Riquimaroux et al 1991, Suga et al 1987), anatomical studies (Felleman & Van Essen 1991, Gilbert et al 1990, Kaas 1987, Ungerleider & Mishkin 1982, Zola-Morgan & Squire 1993), physiological methodologies (Fox et al 1986, Raichle 1994), unique physiological properties (Llinas 1990, Miyashita 1988, Miyashita & Chang 1988, Sakai & Miyashita 1991, Steriade et al 1993, Fuster 1973, Gross 1992), development (Bertenthal 1996, Katz & Callaway 1992, O'Leary et al 1994), and plasticity (Buonomano & Merzenich 1998, Kaas 1991, Karni & Sagi 1993, Merzenich & deCharms 1996, Recanzone et al 1992a, Weinberger 1995). This review focuses on the principles governing cortical representations across different cortical areas and how these representations are used in cognition and behavior (Creutzfeldt 1977, Deadwyler & Hampson 1997, Edelman 1987, Poggio 1990, Stevens 1994, Tononi & Edelman 1998). The review is comprised of an initial section, which introduces concepts in neural representation, the main body, which focuses on cortical coding mechanisms and the relationship of neural representation to behavior, and a concluding section, which returns to our initially stated question of defining representation.

Although a neural code is a system of rules and mechanisms, a representation is a message that uses these rules to carry information, and thereby it has meaning and performs a function. A recurring theme of this review is that representation is defined by two principal and overlapping characteristics: content and function. Content is the information that a representation carries, for example, what the signal signifies about a sensory input. Function is the effect the signal can have on cognitive processes and resultant behavior, e.g. the function of a neuron's spikes in triggering an eye-blink reflex. The function of a representation is typically studied through perturbation experiments such as ablation, stimulation, or mimicry that disturb a signal in order to observe the resultant effects.

## NEURAL REPRESENTATION

### Examples

To begin, several simple examples illustrate general conundrums in defining neuronal representations. Perhaps the simplest example of a neuronal representation in a model organism is illustrated in Figure 1. Imagine recording from the neuron labeled B1 during different types of stimuli or behaviors and discovering the

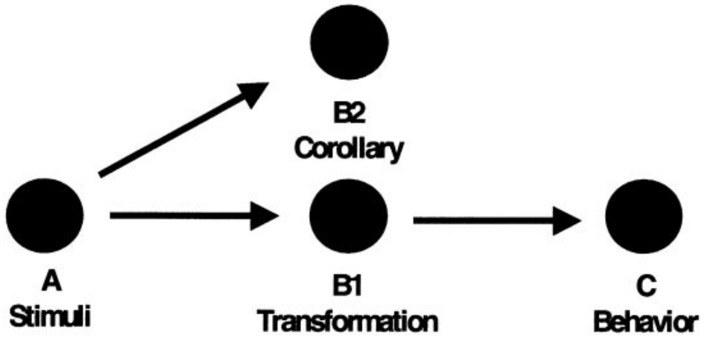

**Figure 1** Example connectivity patterns. (*A*) A set of stimuli; (*B1* and *B2*) populations of neurons (or single neurons) involved in transforming these stimuli; and (*C*) the resultant behaviors from an organism. (Arrows) Transfers and transformations of signals, not necessarily direct or exclusive connections. Therefore, *B1* can be a model of the entire nervous system, or a particular cortical area, or even a single neuron within a given cortical area.

information that this neuron carries about the organism's environment—the content of this neuron's signal. Also imagine recording from the neuron at B2 that receives identical information about stimuli. To give a concrete example for the perceptual discrimination of visual motion, these might be two neurons in the middle temporal cortical area (MT), an area believed to be involved in the representation of visual motion. The response properties of these two neurons to stimuli are identical by construction, yet neuron B2 has no axon and hence serves no functional role whatsoever. Can one say what these two neurons represent?

Although these two neurons respond identically to stimuli and their recorded signals carry the same information, they serve very different representational functions. To the extent that a neuron with no axon represents anything at all, it does so only for the experimentalist because no one else is "listening." From the organism's point of view, only the neuron with an axon is involved in representation. The issue here is not only about neurons without projections, it is that the representational relevance of neuronal signals comes not from content alone, but also from the functions that result from the way in which the content is used.

In a second example, a neuron carries a large amount of information about the auditory environment. It is highly tuned for complex features of sounds. However, only a small fraction of this information is used by the organism in a particular behavioral condition, e.g. sleep. During other circumstances, this neuron's signal may be more fully utilized, but during sleep, the neuron's complex auditory response signal functions only in a startle reflex to any loud noise. This neuron cannot be said to represent large amounts of information about the auditory world in this situation, except perhaps to an experimentalist listening with an electrode and making calculations. For the sleeping organism, the neuron's signal indicates only the onset of a loud noise, so this sets the limit of how the information signal is used and what it can be said to represent. These examples illustrate that neuronal representation is ideally defined with respect to both the content of neuronal signals and their functional relevance to an organism in a particular behavioral context. This is not captured by any measure that reflects only the relationship of a neuronal signal to stimuli being presented, for such measures ignore how (and even if) the neuronal signal is being decoded or used.

## Contents of Representations

The content of a neuronal signal is the message or information that the signal provides when decoded. This can be assessed using the classical approach based upon the tuning curve, or it can be assessed using more recent stimulus reconstruction methods. Studies of tuning in each sensory modality have demonstrated that most cortical neurons carry information content about only a limited range of stimulus features rather than about all possible features. This information is often graded for adjacent feature values. As examples from the tuning-curve methodology, (*a*) the action-potential firing rates of neurons in the primary visual cortex are tuned to the spatial location, orientation, and direction of motion of visual stimuli (Hubel & Wiesel 1962); (*b*) neurons in the primary auditory cortex are tuned to sound frequency and intensity (Schreiner & Read 2000); and (*c*) neurons in the primary motor cortex are tuned to the planned direction of reaching movements (Georgopoulos et al 1986). In each case, the tuning curve assesses how a feature is encoding by a neuron from the experimenter's point of view. The neuronal response is treated as the dependent variable, and the experimenter's goal is to determine the neuronal response for each feature within a set.

An alternative perspective is to attempt to determine the stimulus that caused each neuronal response, using the stimulus reconstruction or "decoding" approach (Bialek & Rieke 1992, Bialek et al 1991, Rieke et al 1997). In this paradigm, rather than analyzing what response each stimulus leads to, the experimenter decodes the neuronal response to provide a reconstruction of what feature of the stimulus was present preceding that response. This is not always merely the converse of constructing a tuning curve, as stimulus-response relationships need not be simple or one-to-one. This decoding is analogous to the task a neuron downstream might perform when "reading out" the spike trains that are its inputs. This approach reflects the organism's point of view, because it requires the experimenter to interpret the neuronal activity in the way that the organism itself is posited to interpret it.

One method of reconstructing the stimulus from neuronal signals uses a linear estimate provided by the reverse-correlation method (see below). In this method, the experimenter presents a rich variety of stimuli, typically many thousands of random combinations of different features, and determines the average stimulus configuration that drove spikes from a neuron. These methods allow the neuron, rather than the experimenter, to select the most relevant stimulus features from within a very broad ensemble. Better reconstructions can sometimes be obtained using nonlinear estimators, but the linear estimate provided by reverse correlation is often surprisingly good given the nonlinearities of neuronal processing. Both the tuning-curve and stimulus-reconstruction are methods of defining the content of neuronal signals, the information that the signals provide about some class of features.

## Function of Representations

As the initial examples illustrated, in order for a neuronal signal to have meaning for an organism, the signal must have projections that allow it to have a function in the organism's activities. The function of neurons or neural representations is not just to provide a highly correlated and information-rich mirror of the environment (Churchland et al 1994), except perhaps at the earliest stages of sensory processing, but to lead to adaptive behavioral results. The most faithful copy of sensory stimuli is on the sensory surface—from here on, information is only transformed or lost, it can never reflect external stimuli more accurately (Shannon 1949). Successive representations therefore serve not to add to the available information within a signal but to transform it, and to extract particular features from it that ultimately lead to relevant decisions, cognitive processes, or behavior.

Once the content of a neuronal signal has been measured, a second line of investigation must establish its function because to be a neuronal representation a signal must be able to lead to some behavioral or cognitive result. There are two main approaches to establishing the functional role of a signal: correlation and perturbation. First, in a behavioral task, the neuronal signal must be shown to be well correlated with a behavioral consequence, for example a particular perceptual choice. Second, perturbations of the signal must lead to different cognitive or behavioral consequences. For example, if a signal is blocked by tissue ablation, the resultant behavior or cognitive process may be impaired (Colombo et al 1990). If a signal is inserted into the system, perhaps by electrical stimulation, the resultant consequence may be mimicked (Penfield 1958; Penfield & Rasmussen 1950; Romo et al 1998; Salzman et al 1990, 1992). Additionally, studies of plasticity can be used as an indication of functional relevance, because the behavioral performance and the relevant neurophysiological signals can be observed to change in parallel (Buonomano & Merzenich 1998, Recanzone et al 1992a).

## Representation and Computation

***Representation*** To assess content and function, a representation can be understood as a signal that is used in a transformation of information. In the case of a simple stimulus-response behavior, this transformation may be from the input stimulus to the resultant action. The representational signal must carry information content about the input to the transformation, and it must have a function in determining the result or output of the transformation. Therefore, the signal must have a statistical relation to both the input and the output. One would ideally like to use a single statistical measure for representation that relates the signal to both the input and the output—to the transformation between the two. Several three-way statistical measures of this type have been considered for this process, but there is currently no widely accepted method (RC deCharms, M deWeese & P Latham, personal communication).

This statistical structure allows the distinction to be made between neuronal signals that have a functional role in representation and those that do not, even in some cases where perturbations of the system are not feasible. In the example presented in Figure 1, the signals of neurons B1 and B2 are highly similar. But assume that because of independent noise in each signal, they are not identical. The signal at B1, including all of its noise, is directly transformed into the behavior, so there is a tight correlation between the full signal and the behavioral output. In contrast, the signal at B2 and its noise are not driving behavior, so they will be less well correlated with behavioral output. Of course, if the two neurons have truly identical signals (identical noise in this case), then they will be statistically indistinguishable and can be functionally differentiated only through perturbation experiments. There have now been a number of experimental situations where the function of neuronal signals has been assessed using this statistical relation between individual cortical neuronal spike trains and resultant behaviors (see below).

The nervous system carries out many different transformations of information, so the concept of representation can be used in many very different contexts. The examples chosen thus far have illustrated the simple context of an organism perceiving a stimulus as input and producing a response as output (a stimulus-response task), but the concept of representation can be applied more generally. Neuronal representation can be defined and measured in any situation in which information is coded by neurons whose activity can be analyzed, and where a defined information transformation takes place. For additional examples, in the case of the intention or plan to make a movement, if motor cortical neurons are involved in the transformation of this plan into an actual movement, then motor representation can be measured. The motor cortical cells carry measurable information content about the intention or motor plan, and they have a measurable function because their signals affect the production of actual resultant movements. In different behavior, if a signal carries information content about a sensory object and is transformed into a subjectively experienced percept, then the signal's representational role can be measured because the neuronal signal has definable content with respect to the sensory input object, and it has a functional effect on the resultant experienced percept (see below).

A distinction is often made between explicit and implicit neuronal representation. Explicit representation is measured when a neuronal signal is analyzed using a defined decoding method and when the resultant decoded signal has measurable representational content and function, as described above. An implicit representation in a structure is a signal that is presumed by indirect evidence to carry representational information (e.g. because ablation disrupts function), but a signal that is not measured by a particular decoding strategy that retrieves appropriate content and function to meet the criteria for explicit representation. For example, if one brain area conveys a particular type of information to another downstream target area, then it is implicitly assumed that the information of the second area is represented in some fashion in the first area as well. However, the representation in the first area may be complex and indirect; there may be no explicit definition of how this information is decoded. Examples concerning implicit and explicit representation in retinal and cortical neurons are presented below.

***Computation*** Computation is the complement to representation, the process by which representations are transformed. The transformations of information that representations serve within would be impossible without computational processes. For example, neuronal representations are often transformed as they are projected from one cortical area to the next. Neural circuits represent information through their activity, and they transform these representations through computational processes.

A simple example illustrates the distinction between representation and computation. Consider a hypothetical neuron that generates a constant 10-Hz pacemaker signal necessary to synchronize activity in a neural circuit, thereby allowing the activity to propagate to a target neural structure. Without this pacemaker neuron, the circuit does not generate the appropriate input-output function—the circuit does not compute correctly. However, the activity in this pacemaker neuron is uncorrelated with both sensory input and motor output, and so it does not carry information about either. The spikes generated by this neuron, then, are a necessary part of the computational process, but not part of the representation of the input or output.

In practice, particular characteristics of neuronal spike trains could play either a computational or a representational role. For example, cortical neurons are capable of generating spikes with precise timing, which has led to the suggestion that this timing plays an important role in representation. Alternatively, this precise timing could serve a computational role. Indeed, the precise relative timing of spikes exerts powerful effects on synaptic plasticity (Hebb 1949, Levy & Steward 1983, Markram et al 1997, Markram & Tsodyks 1996, Merzenich & deCharms 1996, Recanzone et al 1992b, Singer 1995, Zhang et al 1998). This raises the possibility that relative spike timing may be essential to the operation and plasticity of the circuit—to computation—rather than containing information about the input or the output.

## THE CORTICAL CODE

Having considered how neuronal signals can serve as representations in transformations of information, we turn to particular coding strategies used in the cerebral cortex. This section explores coding mechanisms by which cortical neurons represent information, comparing firing rate and temporal coding in single neurons, and comparing independent and coordinated coding in cortical populations. We also consider whether there are significant similarities in physiological signaling mechanisms across different cortical areas (Creutzfeldt 1977, Roe et al 1990, Sur et al 1990), and we consider data bearing on the relevant timescales of coding in different cortical areas. Related issues have been previously briefly reviewed by deCharms (1998) and Merzenich & deCharms (1996), from which some of the following discussion is adapted.

## Single Neuron Coding

There is spirited debate over which characteristics of individual neuronal spike trains serve as the coding signals that carry information (Golomb et al 1994, McClurkin et al 1991, Rieke et al 1997, Shadlen & Newsome 1995, Shadlen & Newsome 1998, Softky 1995, Theunissen & Miller 1995, Tovee et al 1993). In this debate, two different views can be distinguished. The rate-coding hypothesis holds that it is the mean firing rate—the average number of spikes in some time bin—that carries the information, whereas the temporal-coding hypothesis holds that the precise placement of the spikes in time is also significant. On close inspection, this apparent distinction is just one of timescale rather than of category. Mean firing rate is defined as the average number of spikes over some time interval (Britten et al 1992, Tovee et al 1993). When the time bin is long compared with the length of time between spikes, the mean rate can be estimated reliably from a single spike train because many spikes occur in each bin. However, when the firing rate changes faster than a typical interspike interval, then the time bins required to capture these changes must be very small, so a typical bin will contain only one spike or no spikes. When using very small bins, one is effectively measuring the position of individual spikes in the bins rather than measuring large numbers of spikes in each bin, making it more a measure of spike timing than spike rate (Rieke et al 1997). The difference between rate coding and temporal coding for an individual spike train is a principled but arbitrary distinction that is based upon the interval chosen for counting the spikes. The choice of interval is often based upon timescales believed to be relevant to a particular circumstance, such as how quickly the stimulus changes, the integration time of a neural element, the mechanism of decoding, or the relevant behavioral timescale.

***The Rate-Coding Hypothesis*** The rate-coding hypothesis in its simplest form (Adrian 1928) posits that the only important characteristic of a spike train is its mean rate. This offers a dramatic simplification because it implies that an entire spike train—a complex time-varying signal comprising a long list of times at which a neuron fired—can be replaced by a single number, the mean rate. According to this view, both encoding and decoding are straightforward. The stimulus is encoded by setting the firing rate proportional to the value of some stimulus parameter, and the neuronal response is decoded by counting the spikes. The rate-coding hypothesis has provided the foundation for our current understanding of the cortical code, but this does not mean that its assumption of simplicity is fully justified.

***The Temporal-Coding Hypothesis*** The temporal-coding hypothesis posits that the temporal structure of a spike train carries additional information beyond that signaled by the mean firing rate. There is little debate that the temporal structure of spike trains can carry information about the temporal structure in stimuli, such as modulations in stimulus intensity (Bair & Koch 1996, Buracas et al 1998, Mechler et al 1998). For example, Figure 2 compares the temporal profile of the average firing rate for a neuron in cortical area MT (an extrastriate area sensitive to visual movement) for two different stimuli. In Figure 2*a*, the stimulus velocity is constant, and the neuronal response shows little temporal modulation. In Figure 2*b*, the stimulus velocity is rapidly modulated. Under these conditions, the temporal precision of the spike train is as high as 2–3 ms (measured as the standard deviation of individual spike times across trials). As this example shows, the MT neuron transmits information at rates approximately 20 times higher about the fine temporal structure of motion, as measured using spike timing, than about the constant direction of motion, as measured using the overall mean rate (Buracas et al 1998). When the stimulus varies on the same timescale as a typical interspike

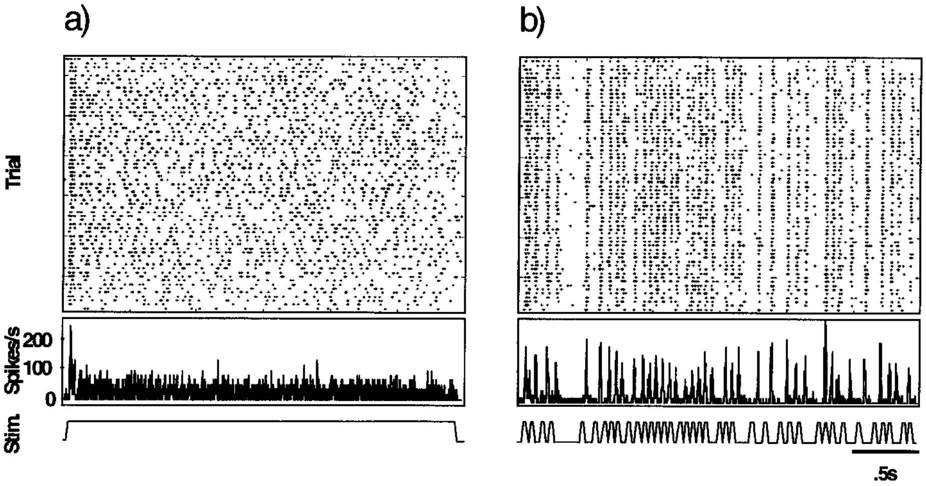

**Figure 2** The temporal structure of a cortical spike train can carry information about the temporal structure of the stimulus. (*a*) Response of a neuron in the middle temporal (MT) cortex of an awake macaque to a constant-velocity stimulus (*bottom*) in the preferred direction. (*Top*) The spike trains on 63 trials. There is no temporal structure apparent. (*Middle*) Average spike rate. (*b*) Response to a stimulus with temporal structure (*bottom*). The same MT neuron responds with fine temporal structure. [Adapted from Buracas et al (1998).]

interval, spike timing can carry significant information beyond the overall rate about the temporal structure of a time-varying stimulus.

A more controversial suggestion is that the temporal structure of spike trains can carry information about stimulus characteristics other than stimulus temporal structure, such as spatial form. It has been suggested that a significant fraction—approximately half—of the information about stimulus spatial pattern is carried by temporal components other than the mean rate in several visual cortical areas from the primary visual cortex to the inferotemporal cortex (McClurkin et al 1991; Optican & Richmond 1987; Richmond & Optican 1990, 1987; Richmond et al 1987, 1990). Experimenters presented monkeys with a set of static visual forms during visual fixation and measured the average time course of single-neuron firing rate for multiple presentations of each stimulus. Their proposal suggested that the temporal profile of firing rate carries information about the spatial stimulus presented. However, later data suggest that most of this "extra" information reflects the onset transient (the increase in the spike rate following the onset of the stimulus) (Tovee et al 1993). The question of whether the time course of cortical firing rate is used to reflect static stimulus features remains unresolved.

***Temporal and Spatial Scales for Sensory Cortical Areas*** As the preceding discussions suggest, it is important to define the timescales on which cortical representations are created and change, and to determine whether these timescales are similar or widely different in separate cortical areas. A behavioral neurophysiological experiment that has been conducted by Thorpe and colleagues (1996) suggests a time limit for how long cortical processing can take to make a sensory distinction. These authors demonstrated that when human subjects are presented with novel images of animals or nonanimals and asked to distinguish between the two, within 150 ms after the onset of the stimulus there are robust differences in neuronal signals corresponding to the perceptual judgment, (Hillyard et al 1998, Thorpe et al 1996) with behavior coming several hundred milliseconds later. This is only slightly longer than the first spike latencies, in monkeys, of the slower neurons in higher visual cortical areas such as the inferior temporal cortex (IT) (Rolls & Tovee 1994), which suggests a severe cortical processing time limit. The process of making complex perceptual distinctions can apparently be achieved through neuronal computational processes occurring just after the first burst of full activation reaches higher cortical areas, before extensive subsequent processing has begun.

The size of sensory stimulus features extracted by neurons in different cortical areas can be directly compared in their temporal and spatial extents. The spatiotemporal pattern of feature selectivity of early sensory cortical neurons can be linearly estimated using reverse correlation methods (DeAngelis et al 1995, Jones & Palmer 1987, Reid & Alonso 1995, Reid et al 1991, Ringach et al 1997). This approach was first used in the auditory periphery (DeBoer & Kuyper 1968) and early central stations (Eggermont et al 1983, Hermes et al 1981) and was later adapted for use in the primary visual (DeAngelis et al 1995, Jones & Palmer

1987, Reid & Alonso 1995, Reid et al 1991, Ringach et al 1997), auditory (deCharms et al 1998), and somatosensory (DiCarlo & Johnson 1999, DiCarlo et al 1998) cortex. In V1, reverse-correlation–based measures have confirmed and extended many previous findings regarding response selectivity, such as orientation and direction tuning. More recent experiments have probed the less-well-understood feature selectivity patterns of auditory and somatosensory cortical neurons. Examples of selectivity from each of these three modalities are shown in Figure 3 (see color insert).

Figure 3 shows the estimated preferred spatial stimulus for neurons in each primary cortical area (auditory neurons have no two-dimensional spatial pattern), and the preferred progression of the stimulus through time. There are significant similarities between the ways that cortical neurons decompose stimuli into component features across these three different cortical areas. Neurons from each area have spatially and temporally restricted response areas and can show complex feature selective structure. Neurons in each of these areas often show excitation driven by a stimulus in a central region that is flanked spatially by inhibition on one or both sides, or that is flanked in time by inhibition, which can create selectivity for temporal changes in stimulus intensity. Neurons can have multiple excitatory or inhibitory response zones that can be aligned in space and time so as to allow the detection of stimulus movement, as seen in the visual and auditory examples shown (DeAngelis et al 1993, deCharms et al 1998, McLean & Palmer 1989).

These plots are approximately evenly scaled by the perceptual discrimination capacity in each sensory continuum (Pasternak & Horn 1991, Recanzone et al 1993, Van Boven & Johnson 1994). This allows the plots to be compared against a common functional metric. In each of the cortical zones, the width of spatial tuning of individual cortical neurons is similar in magnitude to the discriminative capacity of the organism.

The timescale of stimulus decomposition is not identical across these areas (feature durations differ), but it is largely overlapping (DeAngelis et al 1993, deCharms et al 1998, DiCarlo & Johnson 1999, DiCarlo et al 1998, McLean & Palmer 1989). The neurons illustrated show differences in response patterns, particularly differences in duration, but this is partly an effect of the particular neurons shown, as similar magnitude differences in feature durations are observed for different neurons within a single cortical area (DeAngelis et al 1993, deCharms et al 1998, DiCarlo & Johnson 1999, DiCarlo et al 1998, McLean & Palmer 1989). In each area, the duration of cortical processing is on the order of 25–150 ms. The quantitative extent of similarity or differences of physiological response properties across multiple cortical areas remains to be fully quantified (Phillips et al 1983).

## Population Coding

It is now well appreciated that cortical representations involve the activities of large numbers of neurons (Deadwyler & Hampson 1997, deCharms 1998, Georgopoulos et al 1986, Hebb 1949, Knudsen et al 1987, Nicolelis et al 1995, Schwartz 1994b, Zohary et al 1994). Does the cortex function by pooling together large numbers of essentially independent neuronal signals, as in an election, or does the signal come about through the coordination of its elements, as in a symphony (Abeles 1991, Arieli et al 1996, deCharms 1998, Perkel et al 1967, Riehle et al 1997)?

***The Independent-Coding Hypothesis*** Independent coding suggests that each cortical neuron represents a separate signal. Cortical neurons are broadly tuned for features of the world, and a given sensory stimulus or motor act engages very large numbers of cortical cells (Arieli et al 1996, Deadwyler & Hampson 1997, deCharms 1998, Georgopoulos 1990). Although many neurons may be involved in coding a particular object, just as an election involves many voters, the essential characteristic of the independent-coding hypothesis is that all of the information that can be obtained from one neuron can be obtained from that one neuron alone, without reference to the activities of others. Independent signals may be overlapping, noisy, or redundant and may need to be pooled or averaged over large populations to become clear, but the signal carried by each neuron is carried independently.

The population vector method for computing predicted movement direction in the primary motor cortex from the activities of a large number of independently recorded neurons is a well-studied example of independent population coding (Georgopoulos 1990, Schwartz 1994a,b). Each neuron is presumed to "vote" independently for its own preferred direction of movement (deCharms 1998). The population vector method is an independent population code, not a coordinated code. There is sufficient information available in the independent signals of a population of neurons to determine a motor task (Georgopoulos 1990, Schwartz 1994a,b). There have also been additional attempts to define efficient means of extracting information from population signals (Abbott & Dayan 1998; Brunel & Nadal 1998; Pouget et al 1998, 1999; Sanger 1994; Zemel et al 1997, 1998). However, it is not yet clear whether information is primarily present in the pooled independent signals of individual neurons, or whether substantial or even greater information is available in the coordination of populations of neurons.

***Population Maps*** Representations in cortical populations are often arranged to form highly organized spatial maps (Buonomano & Merzenich 1998, Felleman & Van Essen 1991, Knudsen & Brainard 1995). It need not have been the case that the brain would be arranged into discrete processing areas that are similar in each individual of a species, or that neurons in these areas would be arranged topographically with adjacent cells representing similar features, but this has almost universally been found to be true. For example, the tactile sense of the body is mapped onto the primary somatosensory cortex (area 3b) just like geographic features are mapped onto a navigational chart, although the map is distorted to emphasize the most behaviorally important skin regions. This means that adjacent cortical neurons will respond to stimulation of nearly adjacent skin locations (Kaas et al 1979, Mountcastle 1957). Topographic spatial mapping has been found to be the rule for all of the primary sensory areas (Hubel & Wiesel 1962, Kaas et al 1979, Merzenich et al 1973) and for a number of secondary or tertiary sensory processing regions (Goldman-Rakic 1988), and it has been suggested to be true for later sensory processing (Fujita et al 1992) and association areas as well (Funahashi et al 1990). In each of these cortical zones, an environmental stimulus or movement is represented by an isomorphic spatial pattern in the cortex, and in a number of cases the spatial form of this mapping has been demonstrated to adaptively change to reflect changing levels of use or input from the relevant receptor surface (Buonomano & Merzenich 1998, Kaas 1991, Merzenich & deCharms 1996).

***Population Firing Rates*** The distribution of firing rates of neurons in different cortical areas gives an indication of the number of cells activated by stimuli (an indication of population size), as well as of the firing rate levels involved in signal coding. Figure 4 presents new analysis of data from previous studies on the distribution of firing rates in several different cortical areas during sensory stimulation. Individual cortical neurons have traditionally been studied in contexts designed specifically to drive maximal firing rate responses, which may lead to a significant bias in our view of typical cortical firing rates. The distributions shown necessarily depend on the stimuli and conditions chosen for each area, so differences observed may partially reflect differences in conditions. In this case, (*a*) V1 and IT neurons were stimulated during brief trials with an optimally oriented bar or spatial pattern in the receptive field, (*b*) AI neurons were stimulated continuously with a rapid tone stream including the preferred frequency of the neuron, and (*c*) SI cells were stimulated with embossed spatial patterns scanned continuously over the digits. These representative neurons were chosen to have near the median average firing rate of all neurons in a large sample collected from each area.

In each cortical area, cells spend the majority of time, and emit the majority of spikes, operating at rates in the range of tens of spikes/second or below. Data of this type cannot address the question of whether the smaller number of high rate spikes are most relevant for representation (Shadlen & Newsome 1994, 1998), or whether cortical signals are dominated by the preponderance of spikes emitted by the larger numbers of cells firing at low rates.

The data previously shown in Figure 3 bear on the issue of cortical population size as well by indicating the number of neurons in each cortical area that are engaged by a particular stimulus component. The number of primary cortical neurons with spatial response centers within the calibration bar shown (Gabbott & Stewart 1987, Merzenich et al 1984, Peters & Payne 1993, Recanzone et al 1993, Tusa et al 1978) provides an estimate, necessarily approximate, of the number of cortical neurons that will be activated by any individual spatial stimulus component, analogous to "point-spread" (Rolls & Cowey 1970, Wassle et al 1989). In each cortical area, populations on the order of $>$100,000 neurons are

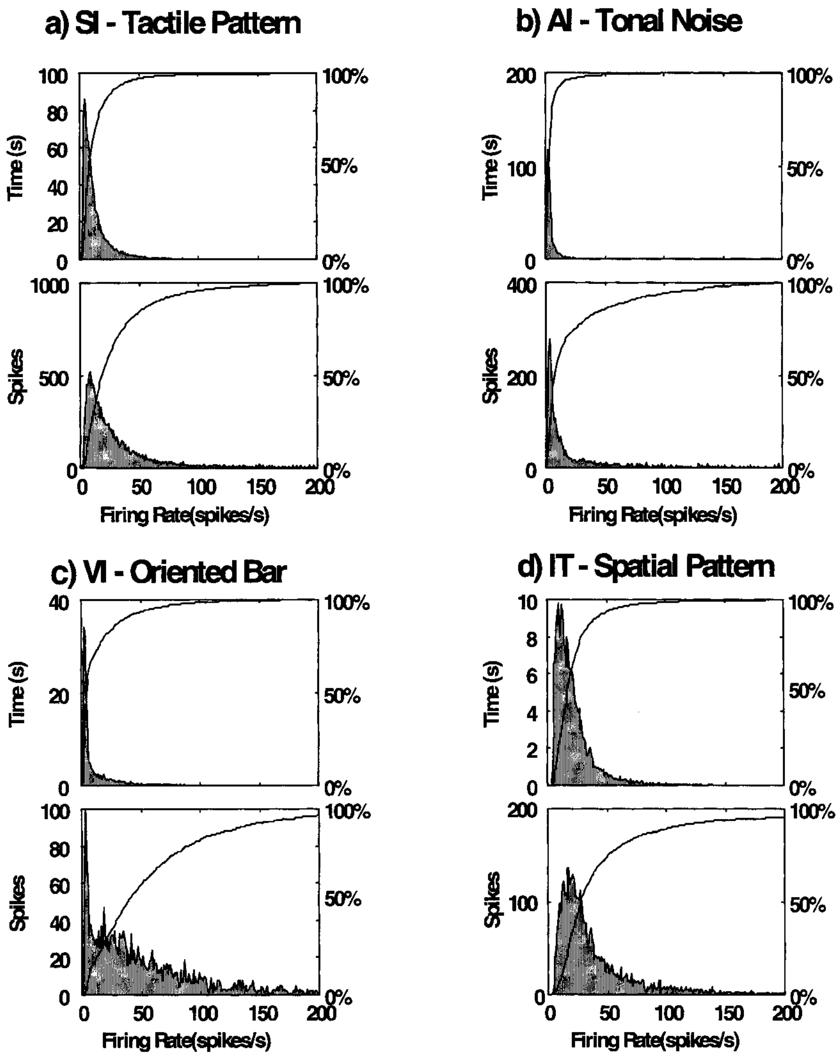

**Figure 4** Firing rate distributions for neurons from different cortical areas—reciprocal interval histograms in units of time and number of spikes versus firing rate. These plots are constructed from the interspike intervals (one per instantaneous firing rate) of action potentials of representative neurons in awake monkeys, taken from the cortical areas specified. (*a–d, upper plots*) The total amount of time accounted for by the sum of interspike intervals corresponding to the rate shown on the abscissa. (Thin upper line) Integral of shaded area normalized to the percentages (*right*), which corresponds to the percentage of time that the neuron spent below the corresponding firing rate. (*a–d, lower plots*) The number of spikes accounted for by each corresponding firing rate and (thin

(*continued*)

← **Figure 4** *continued.* upper line) the percentage of spikes occurring below each rate. In each case, the neuron presented had an overall mean firing rate near the median of the entire population recorded from the cortical area. SI data are taken from 121 neurons in cortical area 3b of an awake rhesus macaque while the corresponding digit was placed against a rapidly rotating drum containing embossed patterns (DT Blake & KO Johnson, personal communication). AI data were collected from 250 neurons in the primary auditory cortex of awake owl monkeys during the passive presentation of a broadband reverse-correlation stimulus (deCharms et al 1998). VI data were collected from 246 neurons in the primary visual cortex of awake macaques during ~2-s fixation periods with an optimally oriented bar present in the receptive field (S Martinez-Conde, SL Macknik, & DH Hubel, personal communication). Inferotemporal cortex (IT) data were collected from 19 neurons in awake macaques during the initial 300 ms of the presentation of one of a number of complex spatial patterns over the receptive field of the neuron during visual fixation (Eskandar et al 1992). In each case, data have been newly analyzed for the purpose of this figure.

active during the representation of any individual suprathreshold stimulus component on the epithelial surface (Das & Gilbert 1995, Grinvald et al 1994).

***The Coordinated-Coding Hypothesis*** The coordinated-coding hypothesis suggests that messages are conveyed at least in part by the many relationships among signals from multiple neurons within these large populations. The defining characteristic of coordinated coding is that the signal must be derived from the relations between multiple neurons in a population, whether this relation is spike synchrony or any other pattern (Carr 1993; deCharms 1998; Hopfield 1995, 1996). In order to decode the signal from one neuron, it must be compared with signals from other neurons. Coordinated information cannot be derived by tallying the independent votes of separate individuals.

One suggestion is that visual cortical neurons code the presence of visual features through their firing rates, but that they code the relationships among multiple features of the same object through their synchrony or oscillations (Gray et al 1989, Gray & McCormick 1996, Gray & Singer 1989, Singer & Gray 1995, von der Malsburg 1981). However, there has been a failure thus far of the research community to come together as a whole in either accepting (Singer 1995, Singer & Gray 1995) or rejecting (Horikawa et al 1994, Kiper et al 1996, Tovee & Rolls 1992a,b) this still-controversial view. Data from the visual cortex have been reviewed extensively elsewhere (Singer & Gray 1995, Usrey & Reid 1999) and are not considered in detail here.

Measures of neural synchrony have typically been made in the presence of changes in firing rate, leading to the question of whether changes in synchrony are important for coding in their own right. Figure 5 illustrates that many primary auditory cortical neurons in anesthetized animals do not change their overall mean firing rates during the ongoing phase of continuous stimuli, largely excluding independent-firing-rate coding for these neurons in this special circumstance. However, auditory cortical neurons can change their rate of temporally coordi-

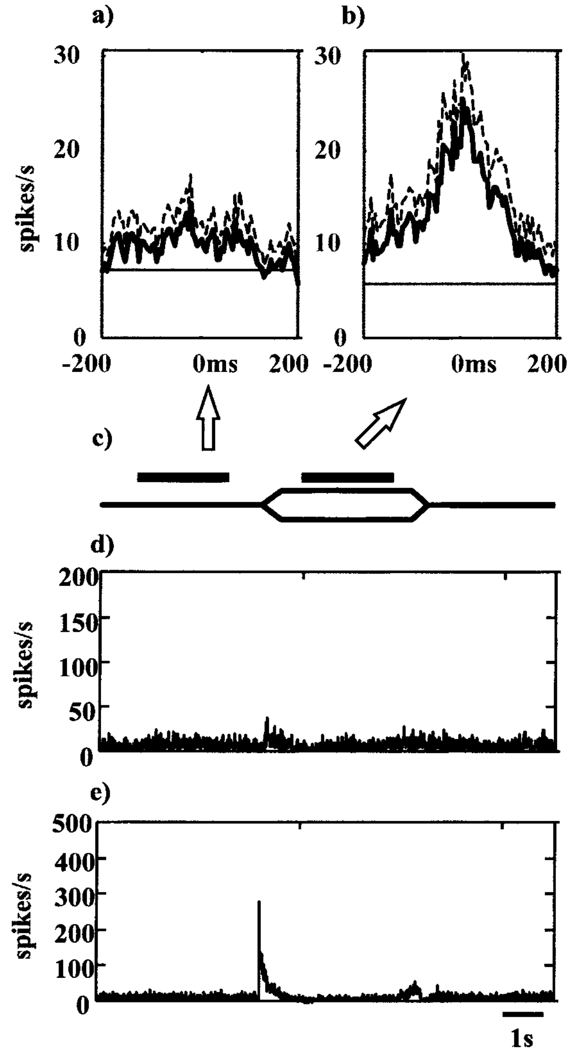

**Figure 5** Changes in mean firing rate and neuronal correlation in the primary auditory cortex of anesthetized primates during continuous pure-tone stimuli. A 4-kHz, 70-dB pure-tone stimulus with the amplitude envelope (*c*) was presented binaurally during multisite neuronal recording. Histograms of ongoing mean neuronal firing rates (in spikes/second) for two cortical locations (*d, e*) and neuronal cross correlations between the two locations (*a, b*), all constructed from 100 repetitions of the stimulus sequence. (*a*) The rate of correlated discharge (in spikes/second) between the two locations during an initial silent period (with 95% confidence limits); (*b*) the 3-s constant phase of a ramped pure tone. (bars) The time windows for cross correlation. The cross correlogram calculations excluded a full second after stimulus onset to avoid transient components. A shift-predictor calculation showed no stimulus-locked component of the correlation peak (not shown). This example had a particularly broad correlation peak; the median half-width was 11.2 ms. [Adapted from deCharms & Merzenich (1996).]

nated spikes during these stimuli, and these changes in synchrony (*a*) are stimulus-frequency specific, (*b*) follow the time course of ongoing stimuli, and (*c*) are systematically mapped across the cortical surface (deCharms & Merzenich 1996). This suggests the possibility of the systematic representation of features by the comodulation of cortical neuronal firing rates on a timescale of 5–15 ms in the absence of overall increases in firing rate. Presumably, temporal coordination could also be called into play during more natural stimuli that also cause changes in mean overall rate. As with the synchrony data described above, these data are limited by their lack of direct connection to a function in behavioral performance.

Attempts to duplicate these experimental methods in behaving animals have thus far not yielded clear results because, in awake animals, many neurons show changes in both firing-rate and spike-time coordination, removing the critical firing rate control from the anesthetized experiments (RC deCharms, unpublished observation).

Related examples of changes in coordination in the absence of changes in rate have also been found in the frontal and motor cortex (Abeles et al 1993, 1995; Hatsopoulos et al 1998; Murthy & Fetz 1992; Prut et al 1998). For example, Vaadia et al (1995) found that neurons in the frontal cortex of monkeys performing a motor task could show changes in their number of synchronous spikes that related to behavior, and Riehle et al (1997) have observed synchronous patterns across multiple frontal cortical neurons. An early hypothesis as to the function of cortical synchrony was that the propagation of neural activity in precisely timed bursts through successive populations of neurons, dubbed synfire chains, was a stable means of signal propagation and an important feature of cortical coding (Abeles 1991, Abeles et al 1993, Prut et al 1998, Seidemann et al 1996). Given the tremendous noise in cortical signals, it is straightforward to imagine that synchronous discharge of a population of neurons enhances signal saliency (Abeles 1991, Merzenich & deCharms 1996, Singer 1995, von der Malsburg 1981). This would likely increase the fidelity of transmission of signals through a noisy cortical system using a mechanism similar to the synchronous burst of activity that propagates through sensory cortex following a stimulus transient.

Independent and coordinated signaling are typically found intermixed, they are overlapping in properties, and it is often not clear how to separate the two. For example, at stimulus or movement onsets, many neurons fire action potentials and, thereby, may signal these events using independent coding. However, because these spikes are nearly coincident, the relevant signal could also be the synchronous burst across the population. Some investigators prefer to call bursts from multiple neurons in a population temporal coordination (deCharms & Merzenich 1996, Senn et al 1998), whereas others prefer to describe it as the rate modulation of multiple inhomogeneous poisson-like processes (Shadlen & Newsome 1994, 1998). This semantic distinction between coordinated coding and rate coding may be more of an obstacle than an aid to understanding. Neurons integrate their inputs temporally as well as spatially, so it is clear that at the level of synapses, both the number and the timing of input spikes determine postsynaptic response.

***Coordinated Noise in Cortical Populations*** Investigations of the noise in cortical signals can give insight into the sources of temporal coordination of cortical populations. Neurons in all cortical areas fire very irregular spike trains, i.e. spike trains that are observed to contain a mixture of interspike intervals of different lengths. The source of this noise has posed a puzzle because irregular firing is incompatible with the simplest view of cortical processing (Softky & Koch 1993, Softky 1995). Softky & Koch (1993) studied the outputs of an "integrate-and-fire" model cortical neuron (a simple model that sums inputs until it reaches a threshold and then fires a spike) while it received independent irregular inputs. As shown in Figure 6*a*, the output predicted by this model is much more regular than the input because the time taken by the neuron to count up a large number of spikes is roughly constant, even when the individual spikes arrive at irregular intervals. However, cortical neurons at all processing levels fire outputs with high irregularity, rather than becoming more regular at each successive stage.

There have been several resolutions proposed for this conundrum. Softky & Koch (1993) proposed that the spike-generating mechanism of cortical neurons

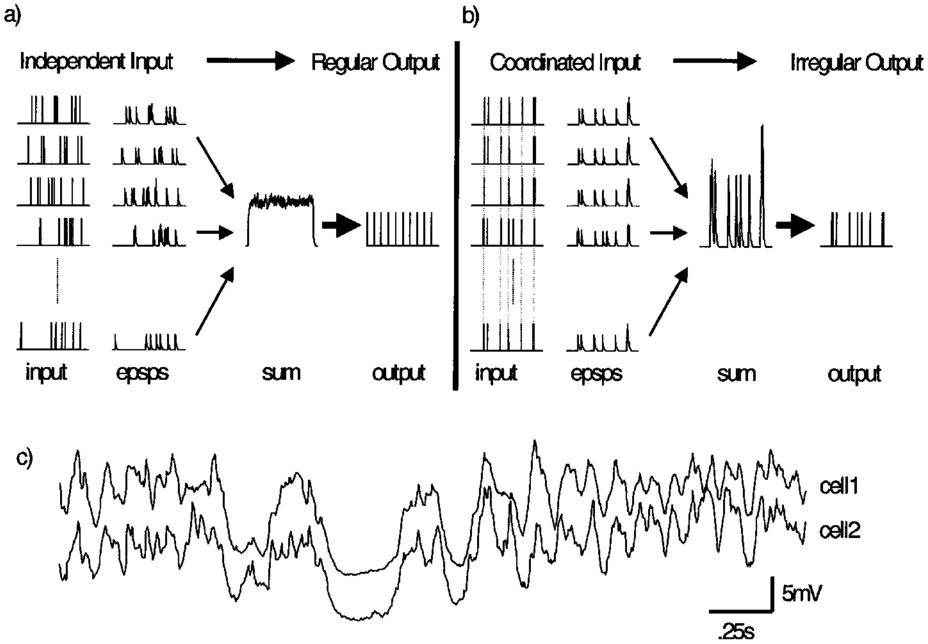

**Figure 6** Cartoon of mechanisms of irregular firing in cortical neurons. (*a*) A simple model of cortical circuitry incorrectly predicts that neurons should fire regularly. The input to a cortical neuron consists of spike trains from approximately 10000 other cortical neurons firing independently and irregularly. Each action potential causes a postsynaptic current. These are summed at the soma and passed through a spike-generating mechanism to produce an output spike train. This model predicts regular spike trains because it assumes that the output spike generator acts as an integrator and therefore averages away the input variability (presumably increasingly as signals pass through successive cortical processing areas). (*b*) If the inputs are assumed to arrive in an irregular but coordinated fashion, the output is similarly irregular. (*c*) The model proposed in *b* predicts that fluctuations in membrane potential are large and that input to nearby neurons is correlated because they receive input from coordinated populations. Simultaneous patch-clamp recordings of membrane potentials from nearby neurons in the visual cortex of anesthetized cats support this prediction. [Modified from Lampl et al (1999).]

might be more complex than a simple integrator, and that cortical neurons might decode the temporal structure of their inputs. Another set of resolutions emphasized the importance of inhibitory inputs (Shadlen & Newsome 1994, Tsodyks et al 1994), while suggesting that temporal coordination was not an important determinant in cortical signals. In this second generation of models, inputs increase the rate of both excitatory and inhibitory drive, leading to more action potentials through a "random walk," but also maintaining irregularity in spike timing. Another resolution focuses on the spike-generating mechanism (Troyer & Miller 1997), with a particular emphasis on the effect of the refractory period. These attempted resolutions were, like the original Softky-Koch (1993) study, based on theoretical models of neuronal firing.

Recent experimental data now suggest that the irregularity in cortical spike times may not be due primarily to the spike-generating mechanism, as proposed in these models (Nowak et al 1997, Stevens & Zador 1998) but may instead arise because of temporally coordinated inputs to cortical cells arriving at irregular intervals (Figure 6*b*) (Shadlen & Newsome 1998, Stevens & Zador 1998). If cortical neurons receive large coordinated bursts of action potentials from many input neurons at once, then they will spike at times that match the coordinated input times, which can be irregular. This irregularity will be propagated through successive cortical processing stages. Injecting synthetic synaptic current designed to mimic this situation in cortical neurons in slices, Stevens & Zador (1998) showed that only large inputs, indicative of coordinated bursts from many input cells, can generate the large current fluctuations requisite for experimentally observed spike output irregularity. Direct measurement of membrane potentials in vivo further supports the notion that ongoing input fluctuations are large (Azouz & Gray 1999) and, thereby, likely arrive simultaneously from many sources. Single-trial optical imaging experiments have suggested that the inputs to cortical neurons over significant areas are comodulated and that this may explain much of the variability in single-neuron cortical signals (Arieli et al 1996). Finally, simultaneous dual in vivo whole cell recordings support the view that the synaptic inputs that drive cortical neurons consist of large, synchronous barrages that are similar for nearby cortical neurons (Figure 6*c*) (Lampl et al 1999). These data suggest that the temporal coordination of inputs may be an important determinant in cortical signaling mechanisms.

## LINKING MENTAL AND NEURAL REPRESENTATIONS

Because neural representations exist to perform functions, our understanding of representation and coding cannot end with the exploration of neural signals themselves but must explain how signaling mechanisms underlie cognitive and behavioral processes. Attempting to understand neuronal representation in the absence of cognition and behavior is akin to analyzing the mathematical patterns in a musical score without ever listening to the music—it misses entirely the reasons that particular patterns exist. This section introduces selected examples illustrating the link between neuronal representations and the cognitive/behavioral processes that they mediate. Neuronal representations and internal mental representations, whether subjective experiences such as sensory percepts or behavioral templates such as motor plans, can both be measured in terms of the same two representational characteristics: content and function. Because both neuronal representations and internal mental representations can be measured using directly parallel terms, it is possible to draw explicit links between these two areas, between cognition and neurophysiology.

## Linking the Contents of Mental and Neural Representations

Internal mental representations have content, whether of sensory percepts (Green & Swets 1966, Parker & Newsome 1998), memories (Goldman-Rakic et al 1990, Brewer et al 1998, Schacter 1996, Schacter et al 1993), or plans (Andersen et al 1997, Georgopoulos 1991, Georgopoulos et al 1989). Within philosophy and psychology, this property of having content is called intentionality, and it is broadly considered the principle hallmark of all subjective mental processes (see Dennett 1987). We have noted that content is also a principle hallmark of neuronal representations, so this central, measurable feature of both can serve as the link that allows the two to be directly aligned and compared.

The content of internal representations can be empirically measured during perception using standard psychophysical experiments somewhat analogous to the construction of a neuronal tuning curve (Cutting 1987, deBoer & Dreschler 1987, Fechner et al 1966, Gescheider 1976, Stebbins 1970). More complex aspects of the content of subjective mental representations can also be measured and thereby compared with neuronal signals. For example, a large body of psychophysical literature now supports the finding that subjects can directly and accurately estimate the magnitude of their own subjective experiences in some detail (Stevens & Atkinson 1988), such as directly estimating the magnitude of how hot something feels to them, or how intense a purely subjective ringing in their ears might seem (Bolanowski et al 1991). Many other details of internal mental representation have also been measured empirically, such the velocities of rotation of spatial mental images (Shepard & Metzler 1971), their spatial form (Farah 1989a,b; Farah et al 1988; Kosslyn 1988), and their spatial interactions (Farah 1989a, Hebb 1968) or the affects of spatial attention (Colby 1991, Desimone & Duncan 1995, Kastner et al 1998, Moran & Desimone 1985, Posner & Petersen 1990). More recent experiments have begun to answer the long-controversial question of where the internal representations of our subjective experiences reside (Posner & Raichle 1998, Raichle 1994), leading the way toward measurement of their corresponding mechanisms. For example, Kosslyn and colleagues (1995) have discovered that visual areas, including the primary visual cortex, are selectively and topographically activated in subjects undergoing mental imagery tasks, as shown in Figure 7*a.* This list of examples was selected to illustrate the measurement of the content of cognitive and behavioral representations, which neuronal representations mediate, and with which the content of neuronal signals must be compared in order to be understood.

In early experiments explicitly showing the link between the content of individual cortical signals and a sensory percept, Mountcastle et al (1967, 1969, 1990a,b) discovered that the perceptual performance of rhesus monkeys on a tactile discrimination task was closely related to the performance of individual cortical neurons in somatosensory area 3b. Further experiments linking the content of neuronal and perceptual representations in a selection of structures in the peripheral and central nervous system have been reviewed extensively elsewhere (Parker & Newsome 1998). Here, we present a single recent example illustrating this link.

To make the link between the contents of neural signals and the contents of perception clear, it has been especially useful to consider cases where the contents of perception differ from external stimuli, such as in optical illusions. In these circumstances, it is possible to ask whether neural activity matches the stimuli or whether it matches what is perceived (for experiments on cortical responses to illusory contours, see Peterhans & von der Heydt 1991, von der Heydt et al 1984). During the condition of binocular rivalry, separate images are presented simultaneously to the two eyes, and human subjects experience an alternating percept, first perceiving one image and then the other, rather than a fusion of the two. Data strongly support that monkeys experience a similar alternating subjective percept (Leopold & Logothetis 1996, Logothetis 1998, Logothetis et al 1996, Logothetis & Sheinberg 1996). These experiments explored a situation in which the measured contents of a binocular rivalry subjective percept alternates between two states while the sensory stimulus is constant and found that some cortical neuronal signals alternated with the alternating percept, whereas others were static, like the static stimulus (Leopold & Logothetis 1996, Logothetis 1998, Logothetis et al 1996, Logothetis & Sheinberg 1996). As shown in Figure 7, the firing rates of some neurons in the visual cortex are directly matched to the alternating perceptual representation (particularly neurons in IT cortex). These neurons fire in response to the particular stimulus that the monkey indicates it perceives, rather than the unchanging stimulus that is presented. These authors were able to predict a novel perceptual phenomenon from their neuronal data, suggesting that binocular rivalry is not a perceptual rivalry between the two eyes, as had long been believed (Blake 1989), but a rivalry between simultaneously present neuronal representations. They demonstrated that a rivalrous percept could be achieved even when the two images were not statically segregated between the two eyes (Logothetis et al 1996), and thereby they created a new class of bistable percept. This example illustrates a direct linking of the content of neuronal signals with the content of subjective experiences, as well as the possibility of even predicting the content of novel subjective experiences based upon an understanding of neuronal representation.

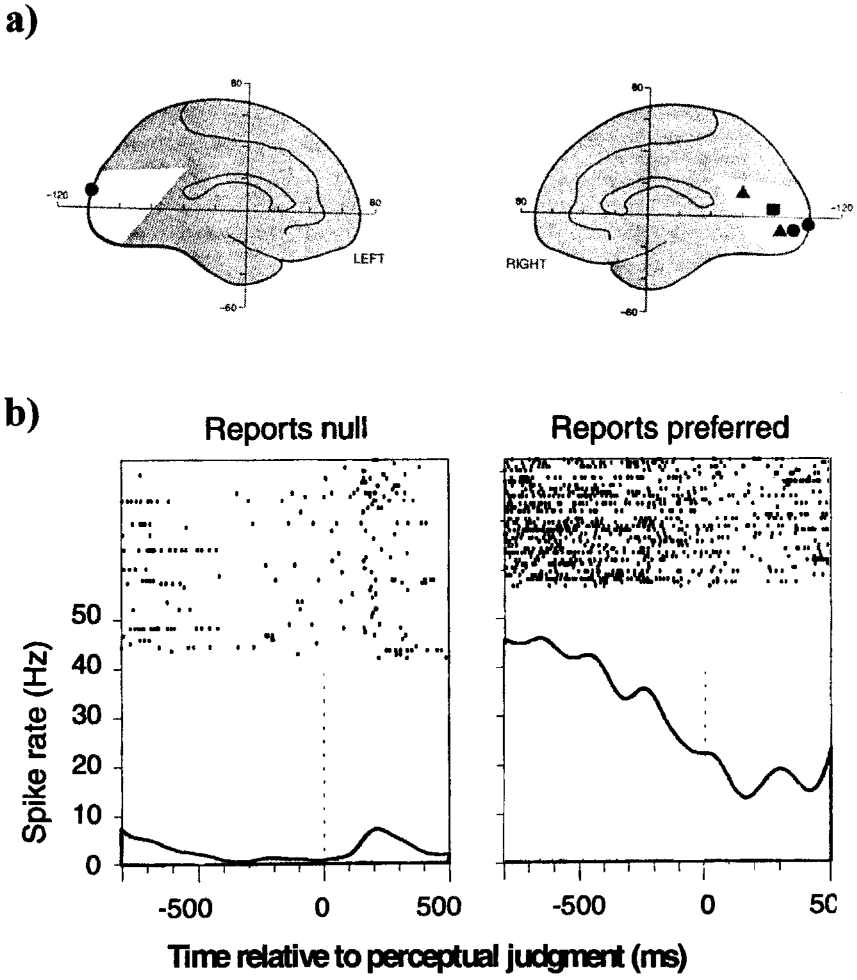

**Figure 7** Neural activation of representations of subjective percepts. (*a*) Activation of the left and right medial occipital cortex measured by positron emission tomographic imaging. (Points) The most activated pixel with a Z-score >3.0(Kosslyn et al 1995). Imagery of a small object (circle), imagery of a medium object (square), imagery of a large object (triangle). This spatial activation pattern is consistent with the larger images activating a larger region of the primary visual cortex, with a correspondingly more anterior center (toward center of figure in both plots). (*b*) Activation of a visual cortical neuron (from area V1 or V2) during the subjective percept of a grating stimulus of orientation matched to the cell's response selectivity (Logothetis 1998). This cell was selective for gratings oriented at 45° and unresponsive for –45° gratings (data not shown). Data were collected while a monkey was presented with both of these gratings simultaneously, one

(*continued*)

← **Figure 7** *continued.* to each eye, and the animal indicated which grating it perceived by pressing a corresponding lever. When the animal indicated perceiving a grating with orientation that matched the cell's response selectivity (*right*), the cell responded more vigorously than when the animal indicated perceiving an orthogonal grating (*left*). (Dashed line) Time the animal indicated its perception. (Tic marks) The individual records of action-potential trains, aligned to the time of behavioral response. (Smooth line) Average firing rate from all of the trains.

## Linking the Functions of Mental and Neural Representations

The second principle link between mental representations and neural representations is their function—how they are used and thereby affect behavior. The suggestion has been made that because subjective experience is not completely understood by biology, perhaps it has no function at all (Block 1995, Block et al 1997), is impossible to comprehend (Chalmers 1977, Shear 1997), or is principally a mystical or religious matter (Tart 1992). Internal subjective mental representations are natural processes of living organisms, this much is clear. Our belief is that until demonstrated otherwise, they are to be presumed to have evolved to serve an adaptive function like any other biological mechanism.

Many examples throughout this review have made the point that neuronal representations serve cognitive and behavioral functions. Therefore, the internal mental representations that neuronal signals mediate necessarily share these same functional properties. Neurophysiological research has the power to demonstrate that internal representations are not just paintings on our internal walls that mirror the outside world for our distraction or illumination—they are part and parcel of neural signaling mechanisms that have functional roles in adaptive behavior (Crick 1994). There are several critical questions to ask of mental representations. What is the purpose of a particular mental phenomenon, experience, or representation? What exactly is awareness *for*? What behavioral abilities does subjective experience confer that are impossible without it? What is its adaptive function, and how can it be linked with its underlying neuronal signals?

Recent experiments in both animals and humans have explored the link between perceptual representations and neural representations at the very detailed level of the correspondence of the activity of individual neurons or populations with their adaptive behavioral outcomes, individual perceptual decisions. For example, a series of experiments have shown that the activity of neurons in the primate cortical area MT correlates with the individual perceptual decisions made by monkeys during a visual motion discrimination task. In these experiments, animals were required to indicate the direction of motion of moving random-dot visual stimuli near the threshold of perceptual motion detection, and the signals of single neurons in area MT were recorded. The responses of single neurons were strongly correlated with the perceptual judgments made by the animals. In fact, the responses of single neurons could be used to predict individual perceptual decisions with modest reliability (Britten et al 1992, 1996; Shadlen et al 1996). This is an example of the use of the statistical relation of a neuronal signal with a behavioral outcome to assess representational function. Experiments exploring the link between single-neuron coding and perceptual decisions are reviewed elsewhere (Barlow 1972, 1990; Parker & Newsome 1998). A recent class of experiments performed using imaging methods has also demonstrated trial-by-trial covariation of cortical activity with learning on single trials in humans (Brewer et al 1998, Wagner et al 1998). These experiments provide examples of the correlational link that can be made between (*a*) cognitive phenomena, including subjective experiences such as measured percepts; (*b*) the neuronal processes that mediate these phenomena; and (*c*) the behavioral functions that result, such as perceptual judgments or learning.

The strongest link to be drawn between the function of neural representations and mental representations is a causal link. Early experiments demonstrated that stimulation of cortical structures was able to directly and reproducibly induce internal mental representations analogous to recollections (Penfield 1958, Penfield & Rasmussen 1950) or sensory percepts (Dobelle et al 1979, Libet 1982). This issue has recently been explored in much greater detail using stimulation experiments that intend to create highly specific perceptual consequences by activating neuronal representations (Salzman et al 1990, 1992; Salzman & Newsome 1994). For example, Romo and colleagues (1998) asked monkeys to compare percepts of tactile stimuli with percepts induced through cortical microstimulation. These authors found that monkeys performing a tactile frequency discrimination task are able to make discriminations equally well either between pairs of real tactile stimuli or between a tactile stimulus and a pattern of cortical microstimulation intended to mimic a tactile stimulus. The direct creation or altering of mental representations by selectively activating neural representations is an indication of the progress made in linking these two once disparate areas.

## SUMMARY AND EXAMPLES—NEURAL REPRESENTATION

We end this article with an answer to the question that began it: What does it mean to say that a neural signal is a representation? We also return to our initial example, determining whether activity in a particular neural area is involved in the perceptual representation of visual experience. In order to ask this question, one must define a perceptual task involving transformation of information. If we are interested in measuring elements of subjective experience that may not otherwise have a clear behavioral outcome, such as a mental image or illusory percept, we operationally construct a task to make as direct a measurement of this subjective experience as possible, through either verbal report or some other overt behavior. We then define a measure of neuronal activity that we hypothesize to be involved in representation. We analyze the statistical relationship between the input to the representation (such as a stimulus), the neuronal signal, and the resultant output (behavior or subjective report). We determine whether the signal carries content related to the input, and whether its function affects the behavioral output, and we attempt perturbation experiments such as mimicry, disruption, or ablation.

Returning to concrete neuronal examples, we ask the question: Is a retinal cone cell involved in the neural representation of visual experience? To answer this, the particular form of representation and circumstance being considered must be defined. If the question is whether the neuron is involved in the representation of an individual point of luminance on the retina and its transformation into a corresponding contrast signal in its target structure, then the retinal cell may well be involved in neural representation for this particular transformation. The activity of the neuron will be highly correlated with the point of luminance (thus carrying content about this input) and will be highly correlated with the resultant output of this transformation into a contrast signal (thus having a function).

For a more complex case, such as the representation of upward movement direction in the transformation of visual stimuli into an experienced motion percept, the retinal cone cell is not explicitly involved in representation. Although the cell may fire to moving stimuli, the activity of the neuron will be poorly correlated with the direction of movement. Furthermore, the activity of the neuron will not be a good indicator of the resulting percept, because many stimuli will activate the neuron that do not lead to a percept of upward movement.[1] However, a neuron in cortical area MT, believed to be involved explicitly in the representation of movement, would likely meet these criteria. For a broad range of different stimuli, the MT neuron's response will be well correlated with movement direction (high content). Furthermore, the activity of the neuron will be well correlated with the resultant experienced percept of motion (functional relevance).

Representational signals can be carried by cortical neurons using a number of potential codes. For single neurons, these codes include the firing rate of the cell and the temporal structure of neuronal spike trains. For larger populations of neurons, coordinated codes involve the relationships among the activities of individual neurons whereas independent codes involve the pooling of separate signals from separate cells. Through measurements of the contents and functions of neuronal signals, these signals can be directly linked to the behavioral and cognitive processes that they mediate.

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[1] However, one might rightly suggest that signals in the retinal cones as a whole carry an implicit representation of motion, i.e. that the information is there but a defined decoding algorithm is not specified that extracts a signal well correlated with movement direction and the resultant motion percept.

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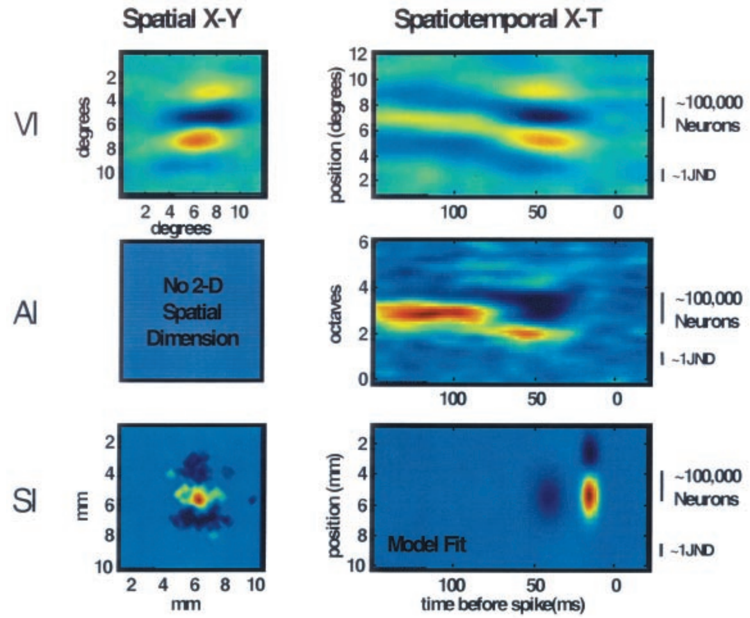

**Figure 3** Spatial and spatiotemporal receptive fields from neurons in the primary visual, auditory, and somatosensory cortex. (*Left*) The spatial pattern of increases in firing rate (*red, light colors*) and decreases in firing rate (*blue, dark colors*) caused by stimuli at different locations on the receptor surface. In the visual case, this corresponds to the spatial feature selectivity in degrees; in the auditory case, this plot is undefined because the receptor surface is essentially one dimensional; and in the somatosensory case, this corresponds to the spatial pattern of feature selectivity on the skin in millimeters (but see below). (*Right*) Spatiotemporal plots of the activity evolving over time. This gives an indication of the change in selectivity over time of the neuron along one spatial dimension (visual angle, distance along the skin, or difference in frequency measured in octaves, corresponding to a single *vertical line* through the plot at *left*). (*Right*) The psychophysically measured just noticeable differences between similar stimuli in each sensory modality (the achievable behavioral output) (Pasternak & Horn 1991, Recanzone et al 1993, Van Boven & Johnson 1994). Also, a calibration is presented (*right*) of the approximate number of primary cortical neurons with response centers within the calibration bar shown. For details of data collection and stimulus presentation methods, the reader is referred to the original papers, from which these are adapted. The VI neuron was an anesthetized cat simple cell with motion selectivity (Reid et al 1997), the Al neuron was an awake owl monkey frequency-sweep selective cell (deCharms et al 1998), and the SI neuron was an awake macaque area 3b cell (DiCarlo & Johnson 1999, DiCarlo et al 1998). The spatial and spatiotemporal data presented for the SI neuron were not obtained directly for technical reasons (the experimental method scanned stimuli along the receptor surface, so space and time are not independent variables) but was computed by a model designed to fit data from several scanning velocities and directions (J DiCarlo, personal communication).

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