

Analyzing Neuronal Processing Locus in Stimulus–Response Association Tasks

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If a neuron is being recorded while a trained animal performs a 2×2 stimulus–response association task, how can we decide whether it is related more to the encoding and analysis of the sensory stimulus, to the preparation and execution of the motor response, or to the animal's decision that associates the two? The difficulty arises because, within a single task, stimulus and response are intrinsically confounded per task instruction; it is only through proper analysis of errors in performance (behavioral noise) and variance in recorded neural activity (neuronal noise) that one can identify the sensorimotor significance of such activity. A quantitative technique is proposed here, based on the framework of signal detection theory, to determine the sensorimotor "locus" of a neural process when recorded simultaneously with the animal's performance on a trial-by-trial basis. The premise is that a pure sensory process should be influenced only by the nature of the sensory stimulus regardless of the nature of the behavioral response, and vice versa for a pure motor process. From the recorded neural activity, we calculate the prediction or discriminability (by an ideal operator) for the stimulus categories and for the response categories. These discriminability values are then compared with each other to infer whether the neural process is more related to stimulus or to response. An index is derived that quantitatively specifies the processing locus of a given neural process along the sensorimotor continuum, with pure sensory and pure motor processes at the two extremes. In between lies the locus of decision-related processes whose activities allow equal (but not chance) prediction for stimulus and response categories. The technique is applied to single-unit activities recorded in monkey primary motor cortex (MI) while the monkey performed a simple go/nogo task involving visual stimulus and hand/wrist movement. We find that sensorimotor

indices of MI neurons are widely distributed, with a preponderance of motor-related units (that better predict go/nogo response than go/nogo stimulus) but also sensory-related ones (with predictabilities reversed). © 1997 Academic Press

1. INTRODUCTION

Understanding neuronal processes that mediate an animal's perception and action has long been of interest. Although numerous single-unit recording studies have compared the selectivity and sensitivity of individual neuron response to the animal's (or human's) perceptual judgments under comparable stimulus conditions (e.g., Tolhurst, Movshon, & Dean, 1983; Parker & Hawken, 1985; Barlow, Kaushal, Hawken, & Parker, 1987, Bradley, Skottun, Ohzawa, Sclar, & Freeman, 1987; Vogels & Orban, 1990), not until recently was this comparison performed directly on a trial-by-trial basis in awake, trained animals performing simple stimulus-response association tasks. For example, in the visual discrimination paradigm of Newsome and his colleagues (Newsome, Britten, Movshon, & Shadlen, 1989a; Newsome, Britten, & Movshon, 1989b; Britten, Shadlen, Newsome, & Movshon, 1992), a monkey was rewarded for making a correct eye movement to one of two locations in response to random-dot stimuli moving toward the corresponding direction. Single-neuron activity in area MT, a region of extrastriate visual cortex known to be involved in extracting global motion signals, was recorded concomitantly with the monkey's behavioral performance as stimulus strength was systematically manipulated. In the go/nogo choice reaction-time (RT) task, Miller, Riehle, & Requin (1992) trained a monkey to perform a rapid wrist

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flexion/extension rotation whenever there was a color light illuminated at one spatial location or to maintain the arm at its starting position whenever a light was illuminated at a different location. Single-unit activity in primary motor cortex (MI) was recorded along with the behavioral context on every trial. Both examples have the following common characteristics: (a) Neuronal activity was recorded in an awake monkey during the performance of a simple 2×2 stimulus-response association task. (b) Neuronal activity, which may mediate perception, action, and/or their connection within a task, was recorded for each trial along with the knowledge of exact sensory stimulus and motor response. This trial-by-trial comparison of neurophysiological measurement with its behavioral context provides both an opportunity and a challenge in understanding the nature of information processing in the nervous system. The opportunity is that the neuronal activity so recorded can now be scrutinized with respect to the trial-specific behavioral context, i.e., the nature of the stimulus and the response, and whether or not stimulus-response association has been successfully made. The challenge is how we then infer the role of these recorded neurons in mediating the stimulus or the response aspect of the task—whether an individual neuron serves to encode and analyze sensory stimuli, to prepare and execute motor responses, or to interface and translate between the two.

Newsome *et al.* (1989a,b) attempted to quantitatively relate the firing rate of visual sensory neurons (in area MT) to the behavioral performance of the monkey using the above paradigm. Specifically, the *strength* of the motion signal was manipulated, and the resulting psychophysical performance of the animal (measured by the threshold for discriminating opposite motion directions) and the activity of single neurons (measured by spike-rate distributions over the two directions of the motion stimulus) were compared. By applying computational techniques from signal detection theory (Peterson, Birdsall, & Fox, 1954; Tanner & Swets, 1954; Swets, Tanner, & Birdsall, 1964; see also Green & Swets, 1966), it was shown (Newsome *et al.*, 1989a,b; Britten *et al.*, 1992) that the changes in the differential firing activity of most MT neurons parallel the changes in the monkey's perceptual judgment of motion signals, indicating that indeed those MT neurons may mediate the monkey's psychophysical performance during each trial of the task (even during those incorrect trials when the stimuli had been misjudged). This parallelism between an animal's performance and activity of its neurons was also observed during task reacquaintance, where short-term improvement in perceptual sensitivity mirrored the improvement of neuronal sensitivity (Zohary, Celebrini, Britten, & Newsome, 1994). Furthermore, microstimulation of sites in area MT (by passing electric current into restricted cortical tissues, thereby enhancing the firing rate of selected groups of neurons) biased the animal's judgments of motion direction

in favor of the direction being encoded by neurons at the stimulation site (Salzman, Britten, & Newsome; 1990; Salzman, Murasugi, Britten, & Newsome, 1992; Salzman & Newsome, 1994). This analysis, based on a well-established signal detection framework, shed important light on how the role of an individual neuron in a sensorimotor task can be evaluated from a trial-by-trial examination of its firing activities in the context of the animal's performance.

However, the application of signal detection analysis in its current form to neuronal data (as performed by Newsome and his colleagues) suffers from a conceptual deficiency: it is often difficult to conclude from this analysis *per se* whether the neuronal activity is more related to the encoding and analysis of sensory stimulus, to the preparation and execution of the motor response, or to the animal's decision translating a specific stimulus to a specific response. This is due to the existence of an intrinsic correlation, on a trial-by-trial basis, between sensory stimuli and motor responses, after the animal has been successfully trained. The firing of a neuron is no more attributable to the nature of the stimulus than to the nature of the animal's response, whenever the stimulus-response association is correctly made. It is only through analyzing the neuronal activity on error trials that the sensorimotor characteristics of such activity can be determined.

Here, the signal detection approach will be extended to address this issue. We have developed a method for systematically identifying the role of a single neuron in stimulus-response association tasks when both neuronal and behavioral data are available for single trials. Specifically, neuronal activity (e.g., mean or peak spike rate) in each trial of the experiment has been sorted in *two* different ways: first, according to the stimulus and, second, according to the behavioral response on a trial. For each neuron, a stimulus-related and a response-related operational curve can be generated. The stimulus-related operational curve is just the standard receiver-operating characteristic curve (or ROC curve) in signal detection theory; the response-related operational curve is calculated similarly, but using the behavioral/motor category rather than the stimulus category. These curves describe the accuracy of single-trial predictions from spike rate to stimulus or response category. The curves can be compared to determine with which category the neuronal activity is better correlated. An index can be derived to characterize the processing "locus" of an individual neuron along a sensorimotor processing continuum for that particular task, from pure sensory neurons at one end to pure motor neurons at the other, with those related to sensorimotor "decisions" (i.e., processes that translate the animal's perception to its action) lying in between. The primary concern of this paper is how to interpret properly neurophysiological data obtained when the animal is performing a simple 2×2 stimulus-response association task, i.e., a task where an animal is rewarded for

generating a particular motor response as a reaction to the presentation of one of the possible stimuli, and where the only behavioral “tags” or context on an individual trial associated with the recorded activity are stimulus and response categories.

2. MATHEMATICAL FORMULATION

2.1. Background

We first briefly review the basic concepts and mathematical techniques of signal detection theory (see Green & Swets, 1966). The basic assumption is that the activation of a sensor by sensory stimuli is a stochastic process associated with intrinsic noise. Therefore, with respect to two different stimulus conditions S_1 and S_0 (here stimulus condition could refer either to one of the two preselected, equally probable stimuli, or to the presence/absence, with equal probability, of a single stimulus), the sensor’s activation (e.g., mean or peak spike rate), can be described by two probability density functions, $p(\tau)$ for stimulus S_1 and $q(\tau)$ for stimulus S_0 , over all possible activation levels or values τ (Fig. 1). Denote the decumulative probability distributions $Y(\tau_0)$ and $X(\tau_0)$ as the probabilities of the sensor’s activation value greater than a certain level τ_0 upon the presentation of stimulus S_1 (e.g., the signal-plus-noise stimulus condition) and S_0 (e.g., the noise-alone stimulus condition), respectively:

$$Y(\tau_0) = \int_{\tau_0}^{\infty} p(\tau) d\tau, \quad X(\tau_0) = \int_{\tau_0}^{\infty} q(\tau) d\tau. \quad (1)$$

The “separation” of the two distributions is determined by the extent to which the two stimulus conditions differ, as well as by the intrinsic sensitivity of the sensor in question; it reflects how reliable the sensor is in discriminating S_1 from S_0 . When plotted against each other, the curve $(X(\tau), Y(\tau))$, with running parameter τ , is called the receiver-operating characteristic (ROC) curve. When the parameter τ is interpreted as a preselected cutoff criterion an ideal observer would use in performing a stimulus discrimination judgment, $Y(\tau)$ and $X(\tau)$ represent, respectively, the probability of a “hit” and the probability of a “false alarm”; this assumes that the ideal operator makes a judgment about the stimulus category by comparing the sensor’s activation level on a given trial with the cutoff criterion he has selected. The area under the receiver-operation characteristic curve

$$A = \int_{\tau=\infty}^{\tau=-\infty} Y(\tau) dX(\tau) = \int_{X=0}^{X=1} Y dX \quad (2)$$

is a value ranging from 0 to 1.0 (with 0.5 representing chance) and can be shown to equal the probability of

correct judgment by the ideal observer in a two-alternative forced-choice situation where the same sensor’s measurements on *two* stimulus presentations (signal-plus-noise and noise) are available and made to compare against each other instead of based on the sensor’s single measurement (Green & Swets, 1966). This area A is also a quantitative characterization of “separation” between the two probability distributions $Y(\tau)$ and $X(\tau)$ and therefore is said to be related to the discriminability (from the stimulus perspective) or predictability (from the observer’s perspective) of the two stimulus categories. Sophisticated statistical tests on the variance of this area estimator are available (Bamber, 1975).

Though the framework of signal detection theory primarily deals with the capacities of sensors and the performance of an ideal observer based on these sensors, the mathematical analysis behind it, namely, (a) the notion of categorical discriminability and predictability associated with the two probability distributions of activation value, and (b) the areal measure that quantitatively specifies the separation between these two probability distributions, can be conveniently borrowed to address broader issues in a stimulus–response association task. In general, each trial of an experiment may be “tagged,” for the purposes of data analysis, by the nature (or category) of the sensory stimulus the experimenter delivers and the nature (or category) of the animal’s motor response. Suppose the animal is trained on a go/nogo task (see Section 3 for a detailed description of the experimental paradigm):

The animal is rewarded for performing a go-response (e.g., moving its hand/wrist) whenever there is a go-stimulus (e.g., a light at one location) and for performing a nogo-response (e.g., doing nothing) whenever there is a nogo-stimulus (e.g., a light at another location).

For each trial, the category of the stimulus (go-stimulus or nogo-stimulus) and the category of the response (go-response or nogo-response) are known and recorded, along with the activity of a single neuron. Of course, in some trials the animal makes a correct stimulus–response association; on others the animal’s association is incorrect. It is conceivable that neuronal activity under these four behavioral conditions (go/nogo-stimulus \times go/nogo-response) will be different. The goal is to analyze and interpret these differences of neural activity in the context of information processing of the stimulus–response association task itself.

2.2. Stimulus-Related and Response-Related Operational Curves

Let $\mathcal{D}_\sigma(\tau)$ denote the decumulative probability distribution function (also called the survivor function) of spike-rate

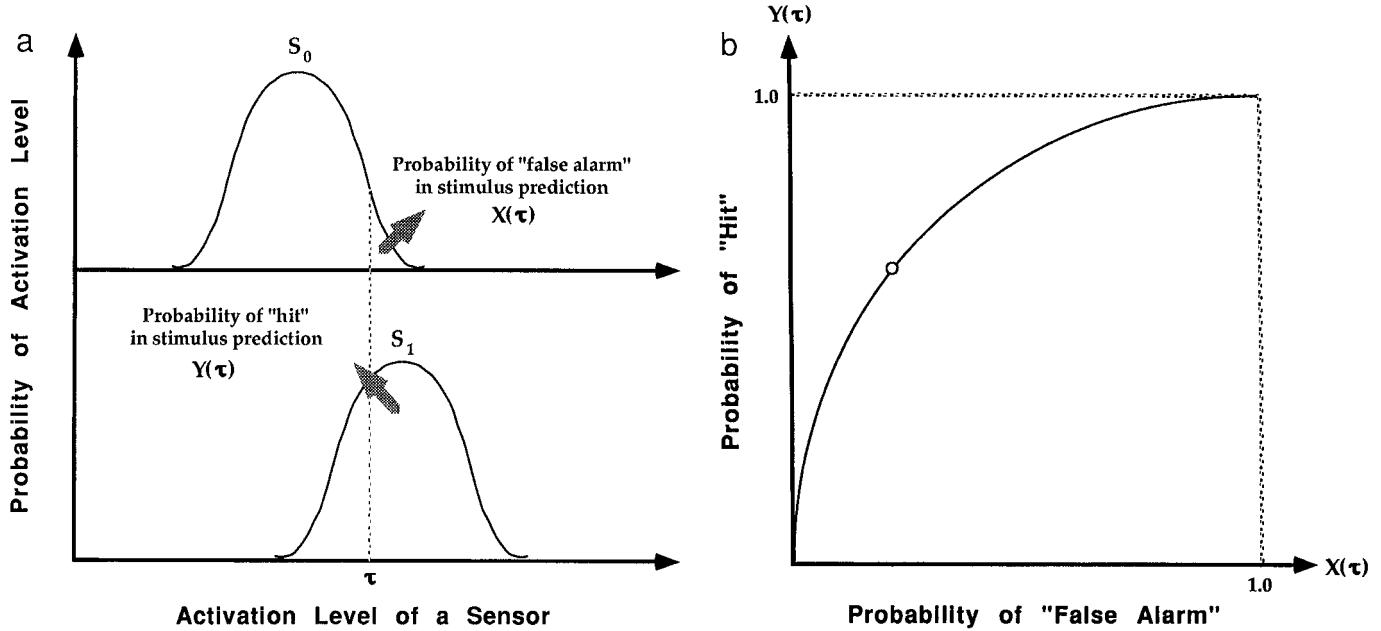


FIG. 1. (a) Probabilistic activation of a sensor by stimulus S_1 (e.g., “signal-plus-noise”) or by S_0 (e.g., “noise”). The knowledge of these probability distributions allows an ideal observer to predict, with a chosen criterion τ , the two stimulus categories based on the sensor’s activation level on a given trial. (b) The “hit” and “false alarm” probability of such prediction can be plotted against each other, resulting in an operational curve of the ideal observer when the pre-selected criterion is varied. The empty circle on this ROC curve corresponds to the chosen criterion in (a).

value above a certain cutoff value τ , with $\sigma = 1, 2, 3, 4$ representing the following four distinct stimulus-response contexts (“tags”):

- $\sigma = 1$: go-stimulus and go-response, called “hit”;
- $\sigma = 2$: go-stimulus and nogo-response, called “miss”;
- $\sigma = 3$: nogo-stimulus and go-response, called “false-alarm”;
- $\sigma = 4$: nogo-stimulus and nogo-response, called “correct-rejection.”

“Hit” ($\sigma = 1$) and “correct-rejection” ($\sigma = 4$) trials are rewarded, “miss” ($\sigma = 2$) and “false-alarm” ($\sigma = 3$) ones are not. “Miss” trials and “hit” trials share the same kind of stimulus; “miss” trials and “correct-rejection” trials share the same kind of response. Analogously, “false-alarm” trials and “hit” trials share the same kind of response; “false-alarm” trials and “correct-rejection” trials share the same kind of stimulus. The total count of each tag σ over many repeated trials of an experiment is denoted N_σ . Note that “hit,” “false-alarm,” etc., are tags (labels) of individual trials. They should not be confused with $Y(\tau)$ and $X(\tau)$, the probability of “hit” and probability of “false-alarm” that concern the response prediction that an ideal operator makes based on certain preselected criterion (see last subsection).

First, we sort the ensemble of trial-by-trial neuronal activities (operationalized as spike rate) into two distributions based on the category of the stimulus, that is, whether

a given trial contains a go-stimulus or a nogo-stimulus, *regardless* of the response category for that trial. The two spike-rate histograms (i.e., number of trials having a particular spike rate versus the spike rate) compiled in this way are called *stimulus-sorted* spike-rate histograms. Each may be properly normalized, with respect to the total number of go-stimulus trials or nogo-stimulus trials, to become frequency histograms and reflect the percentage of trials having such a spike rate. These stimulus-related histograms represent estimates of the probability density function of particular spike rates given (i.e., conditioned on) the go-stimulus or the nogo-stimulus, regardless of the animal’s behavioral response. The associated decumulative probability distributions, denoted as $Y_s(\tau)$ and $X_s(\tau)$, thus represent the probability of neuronal spike-rate values exceeding τ during go-stimulus or nogo-stimulus trials. Formally written,

$$\begin{aligned} Y_s(\tau) &= (1 - \alpha_s) D_1(\tau) + \alpha_s D_2(\tau), \\ X_s(\tau) &= \beta_s D_3(\tau) + (1 - \beta_s) D_4(\tau), \end{aligned} \quad (3)$$

where

$$\alpha_s = \frac{N_2}{N_1 + N_2}, \quad \beta_s = \frac{N_3}{N_3 + N_4}. \quad (4)$$

The two constants α_s , β_s are, respectively, the stimulus-referenced “miss” rate (proportion of trials, among all go-stimulus trials, in which the animal fails to act when

the response should be go) and the stimulus-referenced “false-alarm” rate (proportion of trials, among all nogo-stimulus trials, in which, the animal acts when the response should be nogo). Both are behavioral variables that assume a value between 0 (no failure) and 1.0 (always failure) (with 0.5 representing chance performance.) A value of 1.0 could occur, for instance, if the animal reversed the stimulus-response mapping instruction by generating a nogo-response to the go-stimulus and vice versa.

Next, we sort the same ensemble of trial-by-trial spike-rate measurements into two distributions based on the category of the response, that is, whether a given trial involves a go-response or a nogo-response. The two histograms thus obtained are called *response-sorted* histograms. After normalization with respect to the total number of go-response trials or nogo-response trials, the histograms become estimates of probability density functions for response categories, indicating the probability of a certain spike-rate value given (i.e., conditioned upon) the animal’s go-response or nogo-response, regardless of what the stimulus is for each trial. The decumulative probability distribution (i.e., the probability that the spike rate exceeds τ) is denoted $Y_r(\tau)$ for go-response trials or $X_r(\tau)$ for nogo-response trials. Then,

$$\begin{aligned} Y_r(\tau) &= (1 - \alpha_r) \mathcal{D}_1(\tau) + \alpha_r \mathcal{D}_3(\tau), \\ X_r(\tau) &= \beta_r \mathcal{D}_2(\tau) + (1 - \beta_r) \mathcal{D}_4(\tau), \end{aligned} \quad (5)$$

where

$$\alpha_r = \frac{N_3}{N_1 + N_3}, \quad \beta_r = \frac{N_2}{N_2 + N_4}. \quad (6)$$

The two constants α_r , β_r are, respectively, the response-referenced “false-alarm” rate (proportion of trials, among all go-response trials, in which the animal acts when the stimulus is actually nogo) and the response-referenced “miss” rate (proportion of trials, among all nogo-response trials, in which the animal fails to act when the stimulus is actually go). Both are behavioral variables, ranging from 0 to 1.

When plotted against each other, the curve $(X_s(\tau), Y_s(\tau))$ with floating parameter τ is called the *stimulus-related operational curve*, and the curve $(X_r(\tau), Y_r(\tau))$ is called the *response-related operational curve*.¹ The former indicates

¹ There is a subtle yet crucial difference between the response-related operational curve constructed here and the sender-operation-characteristic (SOC) curve constructed in Newsome *et al.* (1989a). The response-related operational curve is constructed from the two probability distributions $X_r(\tau)$ and $Y_r(\tau)$ of spike rate conditioned on the response categories and therefore is based on all trials involving both stimulus categories, whereas the SOC curve is from the two probability distributions $\mathcal{D}_1(\tau)$ and $\mathcal{D}_3(\tau)$, or from $\mathcal{D}_2(\tau)$ and $\mathcal{D}_4(\tau)$, which are based on only those trials involving one stimulus category.

how the neuronal firing on a trial is related to the nature of the stimulus and how it predicts the go/nogo stimulus category of that trial, whereas the latter indicates how it predicts the response category. The area under the stimulus-related operation curve (denoted A_s) and the area under the response-related operation curve (denoted A_r) can be calculated from (2). They are quantitative measures of stimulus/response predictability or discriminability from the knowledge of a neuron’s firing rates. Intuitively, for a sensory neuron or sensory process, $A_s > A_r$, whereas for a motor neuron or motor process, $A_s < A_r$. Yet the response predictability/stimulus predictability will *not* be zero even for a pure sensory/pure motor neuron, because there is an intrinsic behavioral correlation between sensory stimulus and motor response performed by a trained animal.

2.3. Pure Sensory and Pure Motor Processes

A pure sensory process or sensor will react to (or be activated by) the nature of the stimulus only, regardless of the behavior of the animal. Whether the behavior is go-response or nogo-response, the sensor gives the same activation (e.g., spike rate). This definition implies $\mathcal{D}_2(\tau) = \mathcal{D}_1(\tau)$, $\mathcal{D}_3(\tau) = \mathcal{D}_4(\tau)$, see Fig. 2(a). Thus (3) becomes

$$\begin{aligned} Y_s(\tau) &= \mathcal{D}_1(\tau), \\ X_s(\tau) &= \mathcal{D}_4(\tau), \end{aligned}$$

and (5) becomes

$$\begin{aligned} Y_r(\tau) &= (1 - \alpha_r) \mathcal{D}_1(\tau) + \alpha_r \mathcal{D}_4(\tau), \\ X_r(\tau) &= \beta_r \mathcal{D}_1(\tau) + (1 - \beta_r) \mathcal{D}_4(\tau). \end{aligned}$$

The (Y_r, X_r) -pair is related to the (Y_s, X_s) -pair through

$$\begin{aligned} Y_r(\tau) &= (1 - \alpha_r) Y_s(\tau) + \alpha_r X_s(\tau), \\ X_r(\tau) &= \beta_r Y_s(\tau) + (1 - \beta_r) X_s(\tau). \end{aligned}$$

We now compute the area A_r under the response-related operation curve:

$$\begin{aligned} A_r &= \int_0^1 Y_r \, dX_r \\ &= \int_0^1 ((1 - \alpha_r) Y_s + \alpha_r X_s) \, d(\beta_r Y_s(s) + (1 - \beta_r) X_s). \end{aligned} \quad (7)$$

Making use of the identities

$$\begin{aligned}\int_0^1 Y_s \, dY_s &= \frac{1}{2} \int_0^1 d(Y_s)^2 = \frac{1}{2}; \\ \int_0^1 X_s \, dX_s &= \frac{1}{2} \int_0^1 d(X_s)^2 = \frac{1}{2}; \\ \int_0^1 Y_s \, dX_s + X_s \, dY_s &= \int_0^1 d(Y_s X_s) = 1\end{aligned}$$

as well as the area A_s under stimulus-related operational curve

$$A_s = \int_0^1 Y_s \, dX_s, \quad (8)$$

Eq. (7) can be simplified as

$$A_r = \frac{\alpha_r + \beta_r}{2} + (1 - \alpha_r - \beta_r) A_s. \quad (9)$$

We introduce the *response-referenced error-rate*

$$\varepsilon_r = \alpha_r + \beta_r. \quad (10)$$

This is a behavioral variable that describes all incidents of performance failure from the perspective of response generation—proportion of “false-alarm” among all go-responses plus proportion of “miss” among all nogo-responses; therefore it ranges from 0 (no failure) to 1.0 (chance performance) to 2.0 (always failure). For convenience, we also define *stimulus-related discriminant* Σ_s and *response-related discriminant* Σ_r :

$$\Sigma_s = 2(A_s - 0.5), \quad \Sigma_r = 2(A_r - 0.5). \quad (11)$$

The relative magnitudes of Σ_s and Σ_r reflect the reliability in predicting stimulus or response categories from the knowledge of the neuron’s spike rate of a given trial. As such, these quantities can be regarded as the correlation between neuronal activity and stimulus (for Σ_s) or between neuronal activity and behavioral response (for Σ_r). They range from 1.0 (perfect correlation) to 0 (no correlation) to -1.0 (perfect anti-correlation). From (10) and (11), Eq. (9) becomes

$$\Sigma_r = (1 - \varepsilon_r) \Sigma_s \quad \text{for a pure sensory process.} \quad (12)$$

This quantitative relationship between neural variables Σ_s , Σ_r on the one hand, and behavioral variable ε_r on the other hand, characterizes a “pure” sensory process or sensor. In fact, Eq. (12) says that the correlation of a sensor’s activity with the response category, Σ_r , equals its correlation with the stimulus category, Σ_s , multiplied by the behavioral

correlation between the stimulus and the response, $1 - \varepsilon_r$. Since $|1 - \varepsilon_r| < 1.0$, the activity of a sensor is always less predictive of the response category than of the stimulus category. In fact, it will not be predictive of the response category at all ($\Sigma_r = 0$) before the animal has been trained on the task ($\varepsilon_r = 1$). These conclusions agree with the intuitive considerations of a sensor or pure sensory process.

The above derivation can be applied to the analysis of a pure motor process or effector whose activities, by definition, are related to the nature of the motor response of the animal but not the nature of the sensory stimuli that are delivered. In other words, $\mathcal{D}_3(\tau) = \mathcal{D}_1(\tau)$, $\mathcal{D}_2(\tau) = \mathcal{D}_4(\tau)$ for an effector or pure motor process (see Fig. 2b). Define *stimulus-referenced error rate* as

$$\varepsilon_s = \alpha_s + \beta_s. \quad (13)$$

As a counterpart of (10), it describes all incidents of performance failure from the perspective of stimulus reception—proportion of “miss” among all trials in which the go-stimulus is delivered, plus proportion of “false-alarm” among all trials in which the nogo-stimulus is presented. Similar calculation shows that a pure motor process or an effector can be characterized by

$$\Sigma_s = (1 - \varepsilon_s) \Sigma_r \quad \text{for a pure motor process.} \quad (14)$$

The activity of a pure motor process is always less predictive of the stimulus category than of the response category ($|\Sigma_s| < |\Sigma_r|$), so long as the behavioral correlation between the stimulus and the response is not perfect (i.e., the animal makes errors in its behavioral performance).

2.4. Sensorimotor Index of a Neural Process

Sensors and effectors lie at two ends of the sensorimotor processing continuum. In general, neurons involved in the information processing of a task are neither sensors (pure sensory processes) nor effectors (pure motor processes). Rather they are positioned somewhere between the two. We will here develop an index, based on the above analysis, that will “localize” an individual neuron along this sensorimotor continuum for any task when trial-by-trial comparison of neurophysiological data and behavioral data is possible (but unavoidably corrupted by noise).

We introduce a scalar λ and assume that for a sensorimotor neuron, in general, its activities on those error trials shared a mixed resemblance, in proportions of $1 - \lambda$ and λ in the case of miss trials, and λ and $1 - \lambda$ in the case of false-alarm trials, to its activities on a hit and on a correct-rejection trial:

$$\begin{aligned}\mathcal{D}_2(\tau) &= (1 - \lambda) \mathcal{D}_1(\tau) + \lambda \mathcal{D}_4(\tau), \\ \mathcal{D}_3(\tau) &= \lambda \mathcal{D}_1(\tau) + (1 - \lambda) \mathcal{D}_4(\tau).\end{aligned} \quad (15)$$

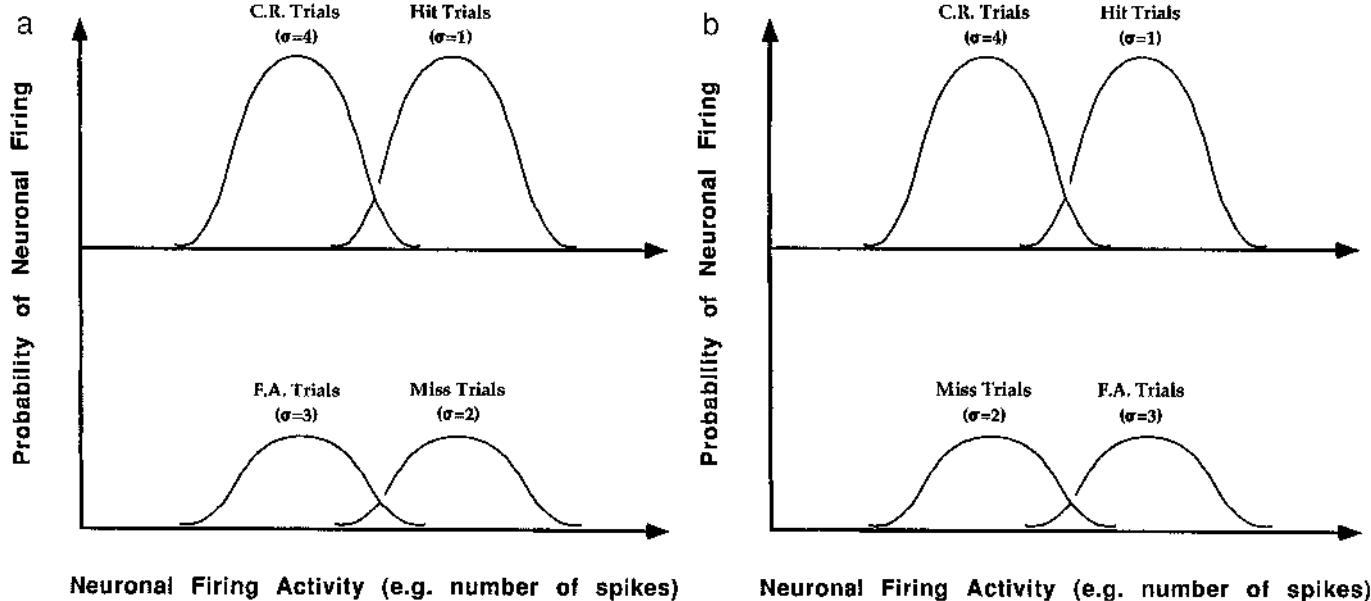


FIG. 2. Pattern of firing of a pure sensory neuron (a) and that of a pure motor neuron (b). Probability distribution of neuronal firing activity (e.g., number of spikes) for the hit, miss, false-alarm (f.a.) and correct rejection (c.r.) trials are depicted hypothetically. Note that the hit/miss trials, as well as the f.a./c.r. trials, share same stimulus category, whereas the hit/f.a. trials, as well as miss/c.r. trials, share same response category. The relative height for distributions associated with correct (hit and c.r.) and incorrect (miss and f.a.) trials are schematically drawn to reflect the different number of trials for these conditions (i.e., N_1 and N_4 are greater than N_2 and N_3 after task training).

For a pure sensory process, $\lambda = 0$; for a pure motor process $\lambda = 1$. For other neurons interfacing between sensors and effectors, we expect λ to be between 0 and 1: $0 < \lambda < 1$ (the meaning of $\lambda < 0$ and $\lambda > 1$ will be discussed shortly). Note that in (15), the two distributions over error trials ($\mathcal{D}_2(\tau)$ for miss trials, $\mathcal{D}_3(\tau)$ for false-alarm trials) are assumed to be symmetric in their mixing proportions of the two correct-trial distributions. We call this the *symmetric mixture hypothesis*. This hypothesis simply means that neuronal activity on the correct (hit and correct-rejection) trials and incorrect (miss and false-alarm) trials is somehow balanced. A neuron that encodes stimulus or response information, or specific stimulus-response mapping, will follow this hypothesis, whereas a neuron that monitors the reward aspect of the task (whose firing is different in correct and incorrect trials) will not satisfy this assumption. The meaning of this hypothesis is further elaborated in subsection 2.8. An empirical test for this hypothesis is conducted in subsection 3.3.

There can be another group of neurons that satisfy the symmetric mixture hypothesis but in a different form; that is, the distributions over the two correct trials $\mathcal{D}_1(\tau)$, $\mathcal{D}_4(\tau)$ are linear mixtures, in proportion of $1 - \lambda$ and λ , respectively, of the distributions over the two incorrect trials $\mathcal{D}_2(\tau)$, $\mathcal{D}_3(\tau)$ ($0 \leq \lambda \leq 1$):

$$\mathcal{D}_1(\tau) = (1 - \lambda) \mathcal{D}_2(\tau) + \lambda \mathcal{D}_3(\tau),$$

$$\mathcal{D}_4(\tau) = \lambda \mathcal{D}_2(\tau) + (1 - \lambda) \mathcal{D}_3(\tau).$$

The above equations may be recast in the form of (15)

$$\begin{aligned} \mathcal{D}_2(\tau) &= (1 - \tilde{\lambda}) \mathcal{D}_1(\tau) + \tilde{\lambda} \mathcal{D}_4(\tau), \\ \mathcal{D}_3(\tau) &= \tilde{\lambda} \mathcal{D}_1(\tau) + (1 - \tilde{\lambda}) \mathcal{D}_4(\tau), \end{aligned}$$

with an equivalent $\tilde{\lambda}$

$$\tilde{\lambda} = \lambda / (2\lambda - 1), \quad \lambda = \tilde{\lambda} / (2\tilde{\lambda} - 1).$$

Here, $\tilde{\lambda}$ lie outside the range of 0 and 1: $\tilde{\lambda} < 0$ or $\tilde{\lambda} > 1$. Furthermore, whenever λ is close to 1 (or 0), $\tilde{\lambda}$ is also close to 1 (or 0). In fact, the transformation

$$\mathcal{M}: \lambda \leftrightarrow \frac{\lambda}{2\lambda - 1} \quad (16)$$

maps $0 \leftrightarrow 0$, $1 \leftrightarrow 1$, and $\pm \infty \leftrightarrow 0.5$. This transformation allows us to identify a unique sensorimotor locus between 0 and 1 regardless of whether the neuron has a better predictability for the correct trials or for the incorrect trials. We now proceed to derive an expression for λ under (15).

In order to relate λ to neural variables (that is, Σ_s , Σ_r) and behavioral variables (that is, ε_s , ε_r), (15) may be conveniently written in vectorial notations:

$$\begin{bmatrix} \mathcal{D}_2 \\ \mathcal{D}_3 \end{bmatrix} = \begin{bmatrix} 1 - \lambda & \lambda \\ \lambda & 1 - \lambda \end{bmatrix} \begin{bmatrix} \mathcal{D}_1 \\ \mathcal{D}_4 \end{bmatrix}.$$

From (3),

$$\begin{aligned} \begin{bmatrix} Y_s \\ X_s \end{bmatrix} &= \begin{bmatrix} (1-\alpha_s) \mathcal{D}_1 \\ (1-\beta_s) \mathcal{D}_4 \end{bmatrix} + \begin{bmatrix} \alpha_s \mathcal{D}_2 \\ \beta_s \mathcal{D}_3 \end{bmatrix} \\ &= \left(\begin{bmatrix} (1-\alpha_s) & 0 \\ 0 & (1-\beta_s) \end{bmatrix} + \begin{bmatrix} \alpha_s & 0 \\ 0 & \beta_s \end{bmatrix} \begin{bmatrix} 1-\lambda & \lambda \\ \lambda & 1-\lambda \end{bmatrix} \right) \begin{bmatrix} \mathcal{D}_1 \\ \mathcal{D}_4 \end{bmatrix} \\ &= \begin{bmatrix} 1-\lambda\alpha_s & \lambda\alpha_s \\ \lambda\beta_s & 1-\lambda\beta_s \end{bmatrix} \begin{bmatrix} \mathcal{D}_1 \\ \mathcal{D}_4 \end{bmatrix} \end{aligned}$$

or

$$\begin{aligned} Y_s &= (1-\lambda\alpha_s) \mathcal{D}_1 + \lambda\alpha_s \mathcal{D}_4, \\ X_s &= \lambda\beta_s \mathcal{D}_1 + (1-\lambda\beta_s) \mathcal{D}_4. \end{aligned}$$

Following the derivation of (9), we have

$$A_s = \frac{\lambda\alpha_s + \lambda\beta_s}{2} + (1-\lambda\alpha_s - \lambda\beta_s) A_0,$$

where A_0 is defined as

$$A_0 = \int_0^1 \mathcal{D}_1 d\mathcal{D}_4.$$

Therefore, Σ_s may be expressed as

$$\Sigma_s = (1-\lambda\varepsilon_s) \Sigma_0$$

or

$$\lambda = \frac{\Sigma_0 - \Sigma_s}{\varepsilon_s \Sigma_0} \quad (17)$$

with

$$\Sigma_0 = 2(A_0 - 0.5).$$

An analogous derivation of Σ_r gives

$$\Sigma_r = (1 - (1-\lambda)\varepsilon_r) \Sigma_0$$

or

$$1 - \lambda = \frac{\Sigma_0 - \Sigma_r}{\varepsilon_r \Sigma_0} \quad (18)$$

Equation (17) or (18) is the formula for calculating λ based on Σ_0 , Σ_s , and ε_s (variables related or referenced to stimulus) or Σ_0 , Σ_r , and ε_r (variables related or referenced to response). In fact Σ_0 may be eliminated from these two equations to yield

$$\lambda = \frac{(\Sigma_r - \Sigma_s) + \varepsilon_r \Sigma_s}{\varepsilon_r \Sigma_s + \varepsilon_s \Sigma_r}. \quad (19)$$

The dimensionless scalar λ computed above (or through (17) or (18) if Σ_0 is also calculated) is called the *sensorimotor index* of a neuron. It depends on neurometric data Σ_s , Σ_r (which are themselves computed from the stimulus-sorted and response-sorted spike-rate histograms) along with the behavioral data ε_s , ε_r . The index can then be used to infer to what extent a particular neuron is classifiable as a sensory or a motor neuron. When $\lambda = 0$, (19) reduces to (12), the case for a pure sensory process; when $\lambda = 1$, (19) reduces to (14), the case for a pure motor process.

2.5. Task Relevance of a Neural Process

Obviously not all recorded neurons participate in a given sensorimotor association. It is important to define and evaluate the degree of relevance of a neural process to the particular stimulus-response task in question. To avoid confusion, we say a neural process is task relevant if and only if its activity is *differentially* related to a specific stimulus, a specific response, or a combination thereof. Since we are not dealing here with the time course of neural processes and only have one neural measure (one number) per trial, we require that this measure be nonuniform across the 2×2 stimulus-response combination to qualify for its task relevance. A uniform activity profile over the four distinct trial configurations will imply that any change in neural activity during a trial (as compared against spontaneous activity) merely reflects an overall modulation related to the general aspect of the task such as alertness rather than the processing of the specific stimulus and/or response in individual trials.

We adopt, for simplicity, the discriminant for the two kinds of correct trials (hit trials and correct-rejection trials), Σ_0 , to characterize the task relevance of neuronal activity (see subsection 2.4). Eliminating λ , and solving for Σ_0 in (17) and (18), we have

$$\Sigma_0 = \frac{\varepsilon_r \Sigma_s + \varepsilon_s \Sigma_r}{\varepsilon_s + \varepsilon_r - \varepsilon_s \varepsilon_r}. \quad (20)$$

We can see that Σ_0 would be small (close to 0) if and only if both Σ_s and Σ_r are small. This situation implies that the recorded neuronal process is task unrelated, since the prediction from its activity for either the stimulus category or the response category is at chance ($\Sigma_s \simeq \Sigma_r \simeq 0$).

Equation (20) may be recast into

$$\frac{\Sigma_0 - \Sigma_s}{\varepsilon_s \Sigma_0} + \frac{\Sigma_0 - \Sigma_r}{\varepsilon_r \Sigma_0} = 1, \quad (21)$$

a conserved quantity for arbitrary λ . This is a direct consequence of the symmetric mixture hypothesis of (15). Indeed, we may test the symmetric mixture hypothesis by performing correlations between $(\Sigma_0 - \Sigma_s)/(\varepsilon_s \Sigma_0)$ and $1 - (\Sigma_0 - \Sigma_r)/(\varepsilon_r \Sigma_0)$.

2.6. Effects of Performance Error

The behavioral error rates are related to, among other factors, the amount of behavioral training. Before being trained on a novel stimulus-response association task, an animal can only guess and thus makes incorrect associations about half the time in a two-stimulus, two-choice task (assuming there is no prior, automatic response tendency toward the two stimuli that could bias the animal's choice). Hence, before training, $\varepsilon_s = \varepsilon_r = 1$. During training, stimulus-referenced and response-referenced error rates decrease, reflecting an increasing mastery of correct stimulus-response associations. For individual neurons, the improvement in behavioral performance is reflected by the values of Σ_s and Σ_r approaching each other—this can be seen from the following identity, easily derived from (17) and (18):

$$\frac{\Sigma_r - \Sigma_s}{\Sigma_0} = \lambda \varepsilon_s - (1 - \lambda) \varepsilon_r.$$

The values Σ_s and Σ_r will be identical if the animal achieves perfect performance, i.e., when $\varepsilon_s = \varepsilon_r = 0$. In this case, there is no difference between sorting the trial-by-trial spike rates according to stimulus category and sorting them according to response category; there is perfect correlation between the two, resulting in identical spike-rate histograms. The proposed method then fails. To identify the sensorimotor locus λ , our method relies on the premise that animals (even when well trained) make errors in their behavioral performance. In fact, error trials are not only convenient but *necessary* for producing a difference in stimulus-based and response-based sorting and eventually for calculating the sensorimotor index. As such, our method is best applied to paradigms in which an animal's error rates are high instead of low (for example, during training).

The stimulus-referenced error rate ε_s and the response-referenced error rate ε_r are two different ways of characterizing the animal's performance, the former from the perspective of stimulus deliverance and the latter from that

of response generation. Their values need not be equal. From (4), (6), (10), and (13), we can derive

$$\varepsilon_s - \varepsilon_r = \frac{(N_1 - N_4)(N_2 - N_3) N_2 N_3}{(N_1 + N_2)(N_1 + N_3)(N_2 + N_4)(N_3 + N_4)}.$$

When the stimulus presentation (which is controlled by the experimenter) is balanced, $N_1 + N_2 = N_3 + N_4$ or $N_1 - N_4 = -(N_2 - N_3)$,

$$\varepsilon_s - \varepsilon_r \leq 0 \quad \text{for balanced stimulus.}$$

On the other hand, when the response generation (which is controlled by the animal) is unbiased, $N_1 + N_3 = N_2 + N_4$ or $N_1 - N_4 = N_2 - N_3$,

$$\varepsilon_s - \varepsilon_r \geq 0 \quad \text{for unbiased response.}$$

When both conditions are satisfied (i.e., balanced stimulus and unbiased response), then

$$\varepsilon_s = \varepsilon_r = \varepsilon.$$

Define in this case the sensorimotor discriminant of a neuron to be the ratio of its stimulus-related discriminant over its response-related discriminant

$$k_\lambda = \Sigma_r / \Sigma_s; \quad (22)$$

then

$$k_\lambda = \frac{1 - (1 - \lambda) \varepsilon}{1 - \lambda \varepsilon}.$$

Note that k_λ is a measure that takes into account the amount of behavioral training ε , and λ is an index intrinsic to the sensorimotor task:

$$\lambda = \frac{k_\lambda - 1 + \varepsilon}{\varepsilon(k_\lambda + 1)}.$$

Since (from (12) and (14), respectively)

$$k_0 = 1 - \varepsilon, \quad k_1 = (1 - \varepsilon)^{-1},$$

we have

$$k_\lambda = k_1 \frac{k_0 + \lambda(1 - k_0)}{k_1 + \lambda(1 - k_1)}.$$

For small error rates, k_λ is given by

$$k_\lambda \simeq 1 + \varepsilon(2\lambda - 1).$$

2.7. Identifying the “Decision” Process

Given the sensorimotor index, it is tempting to identify a certain intermediate value of λ as representing the locus for decision-related neurons, i.e., neurons through which the sensorimotor association or mapping is mediated. Intuitively, a decision process involves the activation and then application of an appropriate stimulus-response mapping rule of a task to generate a motor intent and select a motor program on a trial-by-trial basis. Operationally, a decision neuron can be defined as a cell whose neuronal activity allows neither better nor worse (but systematically better than chance) prediction of the nature of the stimulus than of the nature of the response. Assuming that the stimulus presentation is balanced and the response generation is unbiased, the above operational definition of a decision process amounts to requiring that its stimulus-related operational curve coincides with its response-related curve. For a less stringent requirement, we merely consider the areas associated with these operational curves. Setting $\Sigma_s = \Sigma_r$, along with the assumption of balanced stimulus and unbiased response ($\varepsilon_s = \varepsilon_r$), the sensorimotor index for decision-related neurons indeed turns out to be

$$\lambda_{\text{decision}} = 0.5. \quad (23)$$

When stimulus presentation is unbalanced and/or response generation is biased, the stimulus-referenced and response-referenced error rates are no longer equal $\varepsilon_s \neq \varepsilon_r$. For (23) to still hold (i.e., for decision locus to be at 0.5), we can derive from (19)

$$\Sigma_s \left(1 - \frac{\varepsilon_r}{2}\right) = \Sigma_r \left(1 - \frac{\varepsilon_s}{2}\right) \quad \text{for a decision-related process.} \quad (24)$$

This can be compared with (12) for a pure sensory process and (14) for a pure motor process.

Requiring $\lambda = 0.5$ for decision-related processes implies (as derived from (15))

$$\mathcal{D}_2(\tau) = \mathcal{D}_3(\tau) = \frac{\mathcal{D}_1(\tau) + \mathcal{D}_4(\tau)}{2}.$$

In general, whenever $\mathcal{D}_2(\tau) = \mathcal{D}_3(\tau)$, i.e., the neuron has identical spike-rate distributions for miss trials and for false-alarm trials, the stimulus-sorted and response-sorted histograms will be identical, and $\Sigma_s = \Sigma_r$. So, in effect,

decision-related neurons are those that have indistinguishable firing patterns on the two incorrect (miss and false-alarm) trials.

2.8. Symmetric Mixture Hypothesis and Reward-Related Process

The derivation of the sensorimotor index relies on an assumption about the underlying distribution of neuronal spike rates on error trials—the symmetric mixture hypothesis (15). Here we analyze the condition under which it holds, the implication for neuronal data, and possible relaxation of this hypothesis.

A direct consequence of (15) is

$$\mathcal{D}_2(\tau) + \mathcal{D}_3(\tau) = \mathcal{D}_1(\tau) + \mathcal{D}_4(\tau), \quad (25)$$

which implies that the neuronal spike-rate distribution is the same for correct trials ($\mathcal{D}_1(\tau) + \mathcal{D}_4(\tau)$) as for error trials ($\mathcal{D}_2(\tau) + \mathcal{D}_3(\tau)$). That is, the recorded neuron does not carry information related specifically to the correct/incorrect aspect of a trial. In previous subsections, we have analyzed the sensorimotor aspect of a simple stimulus-response association task. However, in addition to the representation of sensory stimuli and motor responses themselves, there is yet another aspect, namely the reward contingencies of the task that specify the rule of mapping a stimulus to a correct response. The sense of “correctness” in evaluating the performance (a particular stimulus-response association) derives from the reward aspect of the behavioral task. A neuron or neural process is a purely reward-related one, that is, it mediates and only mediates the reward aspect of the task, if its activities are the same for the two correct trials (“hit” and “correct rejection”), are the same for two incorrect trials (“miss” and “false alarm”), but differ for the two occasions. The symmetric mixture hypothesis precludes the analysis of reward-related neurons, in that (25) dictates that all neurons under analysis may not be reward sensitive. In the same spirit, the situation of $\Sigma_0 = 0$ has been interpreted as being task unrelated, rather than simply sensorimotor unrelated (and possibly reward related).

We now relax the symmetric mixture hypothesis and assume instead a *linear mixture hypothesis*: we assume that the neural activities $\mathcal{D}_\sigma(\tau)$ in the four (2 stimuli \times 2 responses) kinds of trials (tagged by σ) obey a binary mechanism so that the probability of spike-rate distribution of each trial type is a linear mixture of two underlying fundamental (basis) distributions. Let $P(\tau)$, $Q(\tau)$ denote the two basis functions of decumulative probability, and λ_σ the constant of mixture for trial type σ :

$$\mathcal{D}_\sigma(\tau) = (1 - \lambda_\sigma) P(\tau) + \lambda_\sigma Q(\tau), \quad \sigma = 1, 2, 3, 4. \quad (26)$$

Analogous to the derivation of (11), we may calculate the area under the operational curve related to the tags μ and ν ($\mu, \nu = 1, 2, 3, 4, \mu \neq \nu$):

$$\int \mathcal{D}_\nu d\mathcal{D}_\mu - 0.5 = (\lambda_\mu - \lambda_\nu) \left(\int P dQ - 0.5 \right).$$

Define the between-tag discriminability (μ against ν) for an ideal operator

$$\begin{aligned} \Sigma_{\mu\nu} &= 2 \left(\int \mathcal{D}_\nu d\mathcal{D}_\mu - 0.5 \right), \\ \Sigma_{00} &= 2 \left(\int P dQ - 0.5 \right); \end{aligned} \quad (27)$$

we have

$$\Sigma_{\mu\nu} = (\lambda_\mu - \lambda_\nu) \Sigma_{00}, \quad \mu, \nu = 1, 2, 3, 4, \quad \mu \neq \nu. \quad (28)$$

Under the linear mixture hypothesis (26), the values $\Sigma_{\mu\nu}$ obey anti-symmetry²

$$\Sigma_{\mu\nu} = -\Sigma_{\nu\mu},$$

and transitivity

$$\Sigma_{\mu\sigma} + \Sigma_{\sigma\nu} = \Sigma_{\mu\nu}.$$

Moreover, (28) implies the existence of an interval scale (Stevens, 1946) such that $\Sigma_{\mu\nu}$ represents the linear distance between the two loci λ_μ and λ_ν on that scale. A pure sensory, motor, or reward process, corresponds to

$$\begin{aligned} \lambda_1 &= \lambda_2, \lambda_3 = \lambda_4 \quad \text{for a pure sensory process,} \\ \lambda_1 &= \lambda_3, \lambda_2 = \lambda_4 \quad \text{for a pure motor process,} \\ \lambda_1 &= \lambda_4, \lambda_2 = \lambda_3 \quad \text{for a pure reward process.} \end{aligned} \quad (29)$$

Collectively, they are called *primary processes* for a stimulus-response task. In general, a neural process may be adequately characterized by the quadruplet $(\lambda_1, \lambda_2, \lambda_3, \lambda_4)$. The discriminability or predictability from the neural activity to behavioral context is determined by these four λ 's on an interval scale (i.e., subject to an arbitrary affine transform $\lambda'_\sigma = a\lambda_\sigma + b$ with constants a, b).

To describe the stimulus-related, response-related, and reward-related components of the neural activity, we

² The negative sign merely reflects that if the tags μ and ν are switched (or trials types are relabeled), then the quality of an operator's performance, i.e., predicting the tag on a particular trial based on the recorded neural activity, will be reversed—the predictability value of 1.0 (perfect correlation between the predicted and actual tag on individual trials) becomes a value of -1.0 (perfect anti-correlation).

introduce the three-dimensional vector space (Zhang, Riehle, Requin, and Kornblum, 1997) defined by

$$\begin{aligned} X &= (\lambda_1 + \lambda_2 - \lambda_3 - \lambda_4) \Sigma_{00}, \\ Y &= (\lambda_1 - \lambda_2 + \lambda_3 - \lambda_4) \Sigma_{00}, \\ Z &= (\lambda_1 - \lambda_2 - \lambda_3 + \lambda_4) \Sigma_{00}. \end{aligned} \quad (30)$$

Define the task-related activity measure

$$R^2 = X^2 + Y^2 + Z^2 = (\Sigma_{00})^2 \sum_{\mu \neq \nu} (\lambda_\mu - \lambda_\nu)^2;$$

the spherical coordinates $(X, Y, Z)/R$ can be used to characterize the functional locus of neural activity for a stimulus-response association task. For a pure sensory process, the spherical locus is $(1, 0, 0)$; for a pure motor process, it is $(0, 1, 0)$; and for a pure reward process, it is $(0, 0, 1)$. The general position on this sphere determines the functional relevance of a neural process subserving the stimulus-response association task, where R specifies the task relatedness of neuronal activity. It can be shown that, under (26), the symmetric mixture hypothesis is equivalent to

$$\begin{bmatrix} 1 - \lambda_2 & \lambda_2 \\ 1 - \lambda_3 & \lambda_3 \end{bmatrix} = \begin{bmatrix} 1 - \lambda & \lambda \\ \lambda & 1 - \lambda \end{bmatrix} \begin{bmatrix} 1 - \lambda_1 & \lambda_1 \\ 1 - \lambda_4 & \lambda_4 \end{bmatrix}$$

or

$$\begin{aligned} \lambda_2 &= (1 - \lambda) \lambda_1 + \lambda \lambda_4, \\ \lambda_3 &= \lambda \lambda_1 + (1 - \lambda) \lambda_4. \end{aligned}$$

Therefore

$$\lambda_1 + \lambda_4 = \lambda_2 + \lambda_3$$

under the symmetric mixture hypothesis; the Z -component (reward component) has been assumed to be zero.

One question remains: How would one derive the set of numbers λ_σ from the recorded neural activities $\mathcal{D}_\sigma(\tau)$? Without knowing $P(\tau)$, $Q(\tau)$, it is theoretically impossible to obtain the λ 's. To get around this problem, we may take an arbitrary linear *functional* of both sides of Eq. (26) (a functional \mathcal{F} maps a function to a number):

$$\mathcal{F}[\mathcal{D}_\sigma(\tau)] = \mathcal{F}[P(\tau)] + (\mathcal{F}[Q(\tau)]) - \mathcal{F}[P(\tau)] \lambda_\sigma.$$

In particular, we may take the mean activity (firing rate) averaged across trials (remember the probability density function, or spike-rate histograms, is obtained from

the decumulative distribution $\mathcal{D}_\sigma(\tau)$ via a differentiation $d\mathcal{D}_\sigma/(-d\tau)$)

$$\langle D_\sigma \rangle = \int_{\tau=-\infty}^{\tau=+\infty} \tau \left(-\frac{d\mathcal{D}_\sigma}{d\tau} \right) d\tau$$

and

$$\langle P \rangle = \int_{\tau=-\infty}^{\tau=+\infty} \tau \left(-\frac{dP}{d\tau} \right) d\tau, \quad \langle Q \rangle = \int_{\tau=-\infty}^{\tau=+\infty} \tau \left(-\frac{dQ}{d\tau} \right) d\tau$$

to obtain

$$\langle D_\sigma \rangle = \langle P \rangle + (\langle Q \rangle - \langle P \rangle) \lambda_\sigma. \quad (31)$$

Equation (31) indicates that λ_σ is linearly related to the mean activity (average spike rate) $\langle D_\sigma \rangle$ and may therefore be substituted, on the interval scale, by $\langle D_\sigma \rangle$, even though $\langle P \rangle$, $\langle Q \rangle$ remain unknown. As a result, the (X, Y, Z) -coordinates may be calculated by using the set of numbers $\langle D_1 \rangle, \langle D_2 \rangle, \langle D_3 \rangle, \langle D_4 \rangle$ in place of $\lambda_1, \lambda_2, \lambda_3, \lambda_4$.

The linear mixture hypothesis (26) assumes that the intrinsic, trial-by-trial variation (albeit the same tag σ) in neural activity, namely, neural noise, is caused by two underlying processes, perhaps related to the activated and the quiescent states characteristic of a binary code. When the linear mixture hypothesis is not valid, (26) no longer holds. We may use the following alternative formula for calculating the coordinates of neural activity vector:

$$\begin{aligned} X &= \Sigma_{13} + \Sigma_{24} + \Sigma_{14} + \Sigma_{23}, \\ Y &= \Sigma_{12} + \Sigma_{34} + \Sigma_{14} + \Sigma_{32}, \\ Z &= \Sigma_{12} + \Sigma_{43} + \Sigma_{13} + \Sigma_{42}; \end{aligned} \quad (32)$$

where $\Sigma_{\mu\nu}$ ($\mu, \nu = 1, 2, 3, 4$) are pairwise discriminant values related, through (27), to $\mathcal{D}_\sigma(\tau)$ over the four tags ($\sigma = 1, 2, 3, 4$). Of course, (32) and (30) are identical when (28) holds under linear mixture hypothesis.

2.9. Summary of the Mathematical Framework

The mathematical framework presented above is aimed at determining the sensorimotor processing locus of individual neurons whose firing activity (in terms of mean firing rate) on the 2×2 combinations of stimulus and response conditions is known. After a brief review of the signal detection theory (subsection 2.1), we proposed the construction of a stimulus-related operational curve (traditionally, the ROC curve) by sorting individual trials based on stimulus category and a response-related operational curve (the response analogue of the ROC curve) by sorting individual trials based on response category (subsection 2.2). The areas under these curves (and after a

linear transformation, the discriminant values Σ_s and Σ_r) are, respectively, measures of correlations of an individual neuron's firing rate to stimulus and to response. We then derived the theoretical relationships between these two measures for pure sensory neurons and pure motor neurons (subsection 2.3). For neurons between these two extremes, an index λ was derived to characterize their resemblance of their firing patterns to a pure sensory and to a pure motor neuron (subsection 2.4). This value was calculable from Σ_s and Σ_r as well as the behavioral error rates ε_s and ε_r , and could be normalized such that $0 \leq \lambda \leq 1.0$. Thus, along the sensorimotor continuum, the value λ determines the processing locus for this simple 2×2 task. A measure to characterize a given neuron's extent of participation in the stimulus and response aspects of the task (task-relevance measure Σ_0) was also derived (subsection 2.5). Also discussed in that subsection was a procedure to test the hypothesis underlying the definition and derivation of sensorimotor index—the symmetric mixture hypothesis. The effect of task training on the sensorimotor index, and a related measure, is discussed (subsection 2.6), and we attempted to derive operationally the locus for a decision-related (homuncular) processes (subsection 2.7). Finally, since the symmetric mixture hypothesis forms the heart of our analysis, the condition under which it holds, as well as a relaxation of it, is provided (subsection 2.8).

3. AN ILLUSTRATIVE APPLICATION

In this section, we have applied the framework developed above to analyze single-unit activity recorded from the motor cortex of a monkey during the performance of a go/nogo task. Since it is generally believed that the motor cortex is not directly involved with processing of reward aspect of a stimulus-response association task, the single neurons there are good candidates for the analysis of sensorimotor locus and for the test of the symmetric mixture hypothesis.

3.1. Experimental Paradigm

A monkey (*Macaca fascicularis*) performed a go/nogo task involving wrist rotation while single-unit activity in primary motor cortex (MI) was being simultaneously recorded (Fig. 3a). The monkey was trained to grasp and rotate a vertical handle by performing wrist flexion and extension movements in the horizontal plane in response to visual stimuli and was rewarded with a drop of fruit juice for performing a rapid (within 1s of stimulus onset) wrist flexion/extension rotation for about 40° (go-response) or maintaining the handle (within 3°) at the starting position for at least 1s (nogo-response) as a reaction to red LEDs (filled circles) illuminated at different spatial locations that

represent go-stimulus and nogo-stimulus, respectively. The stimulus (whether go or nogo) could be presented either as an extension movement signal or as a flexion movement signal. Each trial began with a warning signal (another set of green LEDs, open circles) given 1 s prior to go/nogo signal (stimulus, one of the four red LEDs). For details of procedures, see Miller *et al.* (1992). Simultaneously during this behavioral task, single-unit activity in the hand-wrist area of the left primary motor cortex (Fig. 3b, dashed area) of the monkey was recorded using glass-insulated tungsten microelectrodes that were transdurally inserted contralaterally to the performing (right) arm and controlled by a hydraulic micromanipulator. Recording sites were determined by means of intracortical microstimulation and reconstructed *post mortem* (Riehle & Requin, 1989).

3.2. Data Analysis

Neuronal spike trains on individual trials were recorded at a precision of 1 ms. The peak spike rate on a given trial is determined by applying a 150-ms window that is moved across the whole spike train in steps of 1 ms, counting the total number of action potentials within this (150-ms) scoring window, and finding an interval that contains maximal spike count. The total number of spikes thus obtained (peak spike count) is used as a scalar measure of "neuronal activity" or "spike rate" of a trial. Spike-rate histograms are constructed by counting the incidence of trials with peak spike counts falling within each prespecified bin, in increments of 1 spike per 150 ms for successive bins (corresponding to a bin width of 6.67 spikes/s).

A total of 118 units had a task-related modulation in firing activities (the flexion and extension movement of a single neuron have been treated as two separate "units"). From this pool, 75 units were selected based on the criterion that there should be only a single peak (as identified by the

moving window method) in the poststimulus time histogram (PSTH), which is better time locked (across the ensemble of trials) either to the onset of the stimulus or to the onset of behavioral response (Seal & Commenges, 1985). Two units were discarded because there were no behavioral errors, making them inappropriate for the current analysis. Thus, a total of 73 units were further analyzed for their sensorimotor loci in the processing of the go/nogo task, as described above.

3.3. Results

We first show examples of MI cells with their operational curves for this go/nogo task (Figs. 4 and 5). The stimulus-related operational curves are drawn as solid lines with empty circles, and the response-related operational curves are drawn as dotted lines with filled circles. For all units in Fig. 4, the response-related operational curves are above the stimulus-related ones, suggesting that an ideal operator (e.g., other neurons monitoring their outputs) could make a better prediction regarding go/nogo response rather than go/nogo stimulus for a given trial. Thus, each unit is possibly related more to preparing a motor response than to encoding sensory information. For the units in Fig. 5, the relationship between the two operational curves is reversed, suggesting that those units may be related more to stimulus encoding than to motor preparation.

Figure 6 shows an example of a unit whose stimulus-related and response-related operational curves coincide. The firing rate of this unit predicts the stimulus and the response categories equally well (both not at chance). This suggests that the unit lies somewhere in the middle of the information flow between a stimulus and a response and, thus, this unit can be thought of as connecting sensory stimulus to behavioral response, or effecting a "decision" for sensorimotor transformation (also see discussion in subsection 2.7).

To facilitate the analysis of sensorimotor properties of the entire population, we calculated the areas under the operational curves using a trapezoid approximation. For any given cell, a pair of areal measures were obtained, one from the stimulus-related operational curve and one from the response-related operational curve. These numbers were then converted into the stimulus and response discriminants (Σ_s , Σ_r) using Eq. (11). As discussed in subsection 2.3, these discriminants range from -1 to 1 and reflect the correlation of neuronal firing rate with the behavioral (stimulus or response) category. The scatter plot of (Σ_s , Σ_r) for the 73 units in MI is shown in Fig. 7. Linear regression analysis reveals that the two values are highly correlated (Pearson's $r = 0.861$), and that MI is inclined toward the motoric side on this go/nogo task (slope $k = 1.254 > 1$).

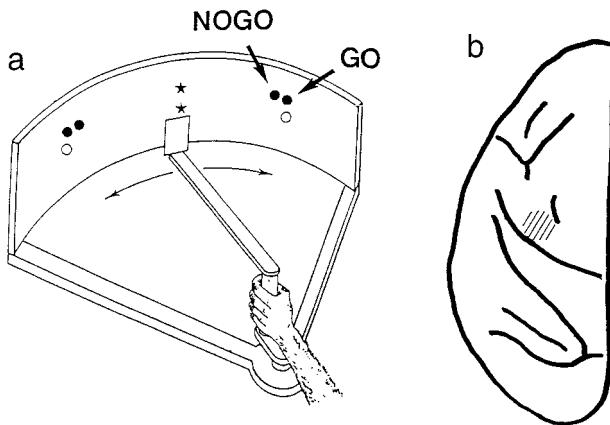


FIG. 3. (a) Experimental paradigm for the go/nogo task and (b) the site of microelectrode recording of an awake, trained monkey. Shaded area corresponds to the area in the left MI in which neurons are recorded.

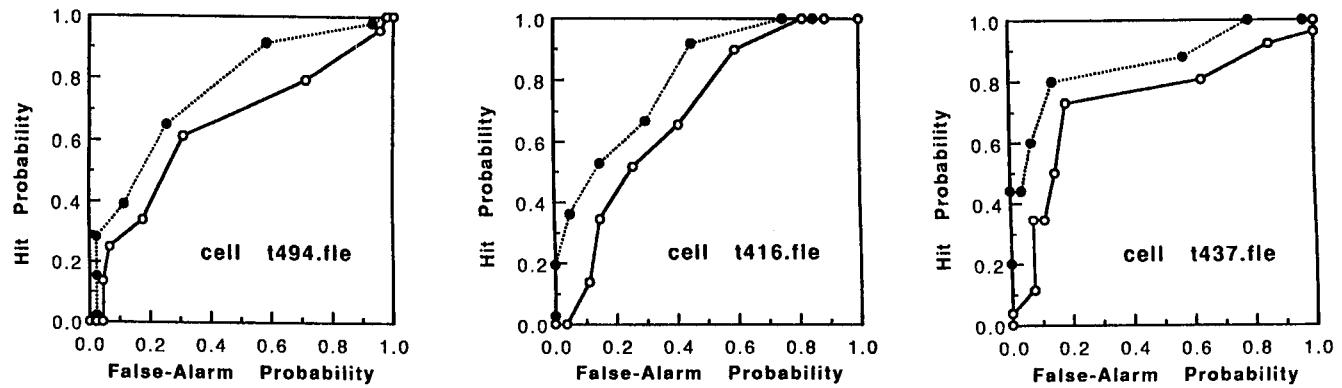


FIG. 4. Operational curves related to stimulus categories (solid lines with empty circles) and response categories (dotted lines with filled circles) of three units in primary motor cortex. Note that for these three units, the stimulus-related operational curves lie *below* the response-related operational curves.

The stimulus-related and response-related discriminants represent accuracy of behavioral predictions (i.e., prediction about stimulus or response category on each trial) based on the activity of a neuron. (A negative-valued discriminant, resulting from the area under an operational curve being less than 0.5, simply means that the neuron has a lower rather than a higher peak spike rate for go category trials compared with nogo category trials.) The high correlation between Σ_s and Σ_r is attributed in part to the relatively low behavioral error rates in our go/nogo paradigm. In other words, the covariance between the stimulus-related and response-related discriminability values results from the monkey's almost error-free performance in this relatively easy task. Were there no error trial at all, there would have been no difference between stimulus-based and response-based sorting: go-stimulus is accompanied by a go-response and nogo-stimulus by a nogo-response for each and every trial. Therefore the two discriminability values are always equal. With increasing error trials, they become unequal in quite different ways depending on the nature of the neuron. Therefore, it is necessary to specify the intrinsic processing locus of a neuron after factoring out the effects due to error rates.

Before deriving the sensorimotor index λ of a cell, we need to test the validity of symmetric mixture hypothesis (sub-sections 2.4 and 2.8). Figure 8 is a scatter plot of the two terms on the left-hand side of (21), $x = (\Sigma_0 - \Sigma_s)/(\varepsilon_s \Sigma_0)$ against $y = (\Sigma_0 - \Sigma_r)/(\varepsilon_r \Sigma_0)$. Theoretically, $x = 1 - y$ according to symmetric mixture hypothesis; see Eq. (21). Linear regression reveals that the two values indeed obey $x + y = 1$, with $r^2 = 0.953$. If the linear regression is restricted to one parameter only (i.e., of the form $y = k(1 - x)$), a value of $k = 1.037$ is found, which also conforms to the identity $x + y = 1$. This establishes the validity of the symmetric mixture hypothesis and reinforces the notion that MI activities are not solely discriminating the correct versus incorrect trials; they are not representing reward contingencies, but rather sensorimotor transformation of this 2×2 task.

The sensorimotor indices of the 73 units in MI are shown in Fig. 9. Here λ is the arithmetic average of the two estimates from Eqs. (17) and (18) which, taken together, are equivalent to (19) and which, if necessary, have been subject to transformation (16) in order to accommodate the two complementary expressions of symmetric mixture hypothesis. It can be seen that while there is a larger proportion of

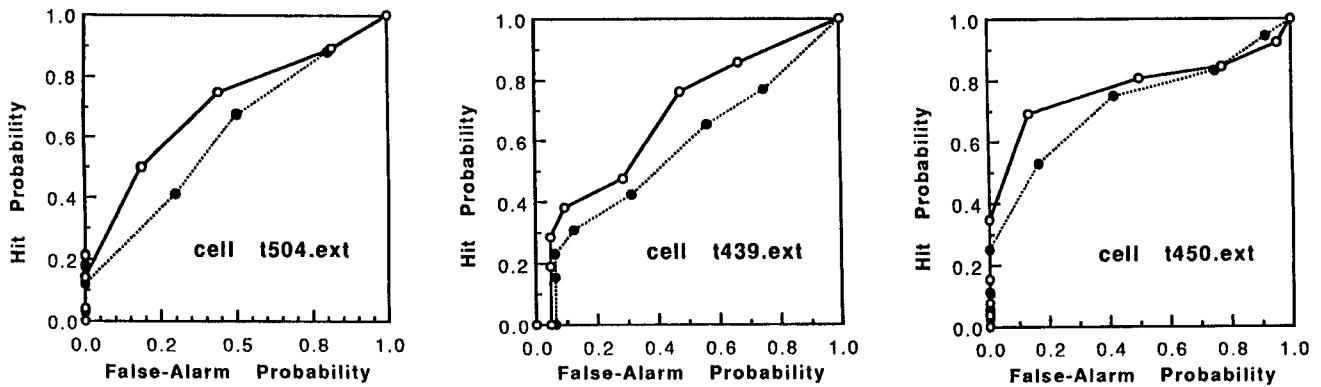


FIG. 5. Operational curves related to stimulus categories (solid lines with empty circles) and response categories (dotted lines with filled circles) of three different units in primary motor cortex. Note that for these three units, the stimulus-related operational curves lie *above* the response-related operational curves.

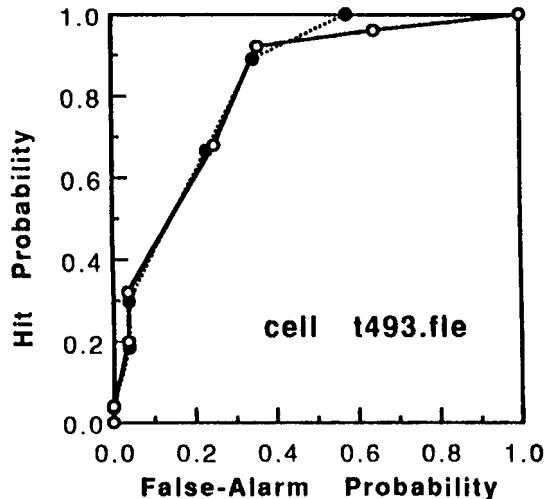


FIG. 6. Operational curves related to stimulus categories (solid lines with empty circles) and operational curves related to response categories (dotted lines with filled circles) of another unit in primary motor cortex. Note the stimulus-related operational curve almost coincides with its response-related operational curve.

response-related neurons than stimulus-related neurons, our sample contains a wide variety, from those that appear to purely mediate the behavioral meaning of a stimulus (in the context of this go/nogo task) to those that appear to purely mediate the behavioral reaction of the animal, as well as decision-like neurons that may mediate the transition between the two.

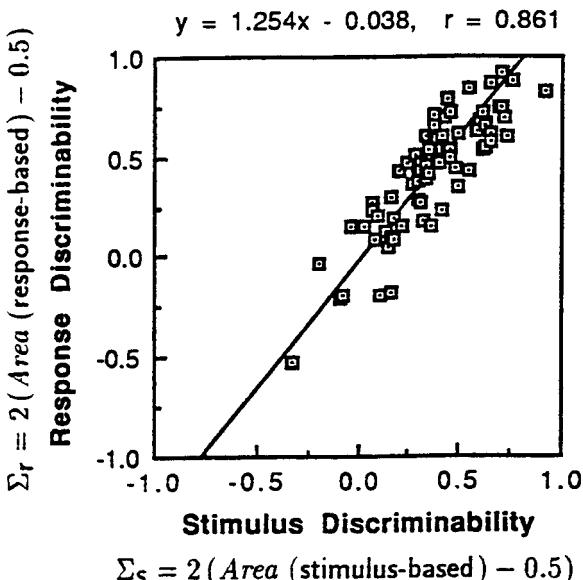


FIG. 7. Scatter diagram of the stimulus-related discriminant (Σ_s) and response-related discriminant (Σ_r) for the 73 units recorded from the monkey primary motor cortex. These discriminants reflect correlations of neuronal spike-rate with either stimulus or response categories. Each dot in the plot represents a single unit.

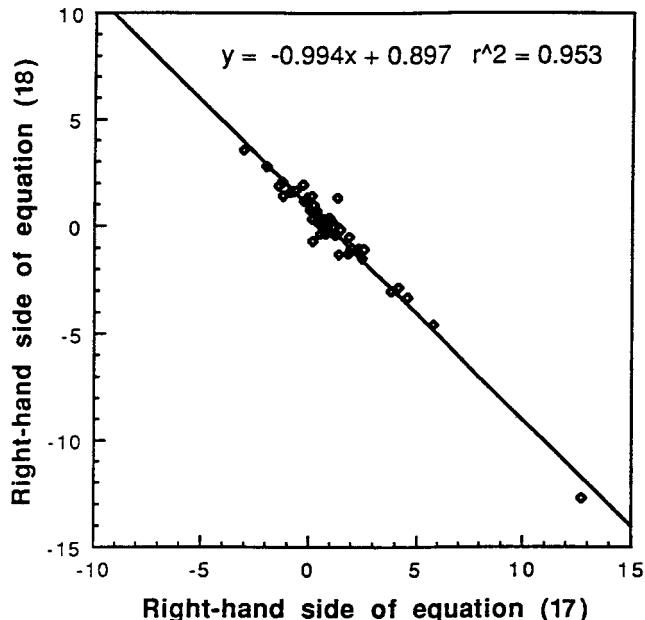


FIG. 8. Test of the symmetric mixture hypothesis. The two terms on the left-hand side of Eq. (21), $x = (\Sigma_0 - \Sigma_s)/(\epsilon_s \Sigma_0)$ and $y = (\Sigma_0 - \Sigma_r)/(\epsilon_r \Sigma_0)$, is plotted as a scatter diagram for the 73 units. Each symbol in the plot represents a single unit. The symmetric mixture hypothesis will predict that they sum to 1.0.

Note that the proper interpretation of the pure sensory locus ($\lambda = 0$) and the pure motor locus ($\lambda = 1$) should be constrained by the nature of contextual descriptions (i.e., behavioral tags) available for individual trials of an experiment. In our go/nogo paradigm, each trial is labeled by the visual stimulus (the location of a colored LED signal) and

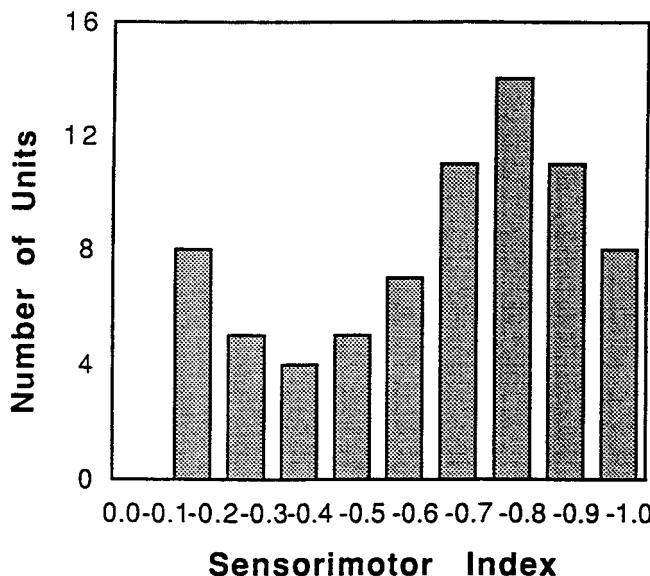


FIG. 9. Distribution of the sensorimotor indices for the 73 units recorded from monkey primary motor cortex. Each bin in the histogram represents an accumulation of index values within a 0.1 interval, starting from 0 (index for pure sensory neuron), to 1 (index for pure motor neuron).

the overt movement (the rotation of the wrist). The pure sensory locus ($\lambda = 0$) can therefore represent either a neuron that was selective to the physical attributes of such stimulus (i.e., the sidedness of the LED light) or a neuron whose activity differentially encoded the behavioral meaning transmitted by those LED signals (i.e., a stimulus calling for an appropriate go- or nogo-response). Additional experiments (e.g., using different stimulus attribute) are needed to distinguish a neuron's involvement in either of these perceptual stages. Similarly, the pure motor locus ($\lambda = 1$) can represent either a neuron whose activation indicated the animal's preparation of a selected motor act by programming its parameters or a neuron that was actually involved in the overt execution and expression of the movement.

3.4. Discussion

We have applied the mathematical framework of Section 2 to determine the sensorimotor processing locus of a population of neurons in MI recorded during a go/nogo task involving wrist movements to visual stimuli. The demonstration of a wide variation in the sensorimotor loci of MI neurons (though with a predominance of motor-related neurons) is in agreement with previous studies which also suggested the existence of three different types of units in the MI, namely, input or sensory neurons that process relevant stimulus information; output or motor neurons that execute overt (behavioral) response; and interfacing or sensorimotor neurons that supposedly connect the two (Lecas, Requin, Anger, & Vitton, 1986; Riehle & Requin, 1989; Miller *et al.*, 1992). These previous studies, however, relied on quantitative comparisons of temporal relationships between the time of peak neuronal response and the time of stimulus onset or movement initiation on go trials (Seal & Commenges, 1985; Requin, Riehle, & Seal, 1988), whereas our present analysis is based on trial-by-trial comparison of neuronal firing rates with the behavioral context of a trial.

In our analysis, we have chosen the "peak firing" as the measure of neuronal activity to carry out the proposed analysis of sensorimotor locus. The selection of such measure is motivated by earlier studies in which the variances of the stimulus-locked and the response-locked time-to-peak distributions were compared for determining sensory and motor neurons (Seal & Commenges, 1985; Miller *et al.*, 1992). However, one drawback is that it precludes the analysis of the time course of neuronal activity. It has been shown (Zhang *et al.*, 1997) that MI neurons change dynamically from sensory to "decisional" to motor loci during the evolution of a trial. The selection of the "peak firing" measure serves to demonstrate how our computational scheme might work; other trial-by-trial measure of neuronal firing activity can be used for application of the current technique.

4. GENERAL DISCUSSION

This paper addresses the following question (Section 1): If neural activity is being recorded while a trained animal performs a two-stimulus, two-choice task, how could the functional role of the neuron in the processing of the sensory, motor, or decision aspect of the behavioral task be inferred? An analysis has been proposed, based on the conceptual framework of signal detection theory, to localize the function of a neural process along the sensorimotor continuum (Section 2). Specifically based on how similar the recorded neural process is to a pure sensory process versus a pure motor process, an index can be calculated from the recorded neural activity to represent the processing stage along the directed information flow of the stimulus-response task (from sensor to effector). The method was then applied to single neuron activities recorded in MI of a monkey trained to perform a go/nogo task involving hand/wrist movements in response to visual signals (Section 3). Although there are a variety of units with widely distributed sensorimotor indices, a preponderance of them are movement-related ones. The working hypothesis (i.e., symmetric mixture hypothesis) that underlies the definition and derivation of the sensorimotor index was demonstrated to be valid within this recorded neuronal population. The method, therefore, provides a novel framework with which to characterize quantitatively the processing locus of a neuron (or neural process) in a 2×2 stimulus-response association task.

Previously, the basic difficulty for determining whether the neuronal response is primarily mediating stimulus or response processing has been due to the intimate association and intrinsic correlation between the stimulus and response categories themselves in a trained animal. From correlations of neuronal firing to the stimulus categories or to the response categories (the stimulus and response discriminant values or areas under respective operational curves in the text), one needs to "remove" the behavioral correlation between stimulus and response in order to ascertain and properly attribute the underlying causation of neuronal firing. This is the motivation behind the derivation of the sensorimotor index λ , which has theoretically "corrected" for the amount of behavioral correlation.

This method has certain limitations in its practical application. First, the method as it now stands applies only to the 2×2 stimulus-response mapping tasks. The neural measure to be analyzed is not restricted to the firing activities of single neurons, and other task-related neurophysiological measures (such as peak latency or peak amplitude in event-related brain waves, amount of metabolites taken up in brain imaging, etc.) can be dealt with in an analogous way to address whether such measures are more related to the stimulus aspect or to the response aspect of a task. However, the method is indeed highly

specific for the simple (and widely adopted) 2×2 experimental paradigm; extensions to more general situations remain to be worked out. Second, our proposed analysis relies on the premise that animals (even those well trained on a task) make errors in their behavioral performance, and those errors are not due to some inadvertent mistakes of the animal (e.g., eye-blink) where the stimulus is not even processed! The error trials that are prerequisites for calculating the sensorimotor index refer to the failure of correctly associating a certain response to a certain stimulus (whether due to failure in perception or failure in action selection). Therefore this analysis is best applied to neuronal recordings obtained during training sessions in connection with the acquisition of stimulus-response association.

Despite these drawbacks, the signal-detection-based technique has certain advantage over more traditional approaches, such as the two-way (stimulus category \times response category) analysis of variance (ANOVA) technique. Under ANOVA, neuronal activity could be found significantly different both for the stimulus factor and for

the response factor merely because of the fact that the stimulus and response categories are significantly correlated on the behavioral level! Therefore, it is impossible to infer from ANOVA per se whether the differential activity of the neuron is causally linked to the stimulus processing or the response processing. On the other hand, our signal-detection-based technique allows such attribution. The foundations of the signal detection theory is the Bayesian framework of statistical inference and decision making, which has been shown in a variety of applications to be advantageous (or at least complementary) to the classic statistical approach involving testing a null hypothesis (for a review, see Bernardo and Smith, 1995). Our adaptation of the signal detection theory to the analysis of neuronal activity not only allows the determination in some quantitative way of the sensorimotor locus of a neuron and neuronal population, but also motivates the operational definition for the class of decision-related neurons, which supposedly mediate an animal's sensorimotor transformation from its perception into action.

APPENDIX: LIST OF SYMBOLS AND NOTATIONS

Symbol	Definition	Equation
τ	A number representing neural activity (e.g. spike rate)	(1)
σ	Behavioral characterization ("tag") of a trial, in terms of "hit" ($\sigma = 1$), "miss" ($\sigma = 2$), "false-alarm" ($\sigma = 3$), and "correct-rejection" ($\sigma = 4$)	(3)–(6)
$D_\sigma(\tau)$	Decumulative probability distribution of τ for trials carrying tag σ	(3), (5)
N_σ	Total number of trials carrying tag σ	(4), (6)
$X_s(\tau)$	Probability of "false-alarm" in stimulus prediction at criterion τ	(3)
$Y_s(\tau)$	Probability of "hit" in stimulus prediction at criterion τ	(3)
$X_r(\tau)$	Probability of "false-alarm" in response prediction at criterion τ	(5)
$Y_r(\tau)$	Probability of "hit" in response prediction at criterion τ	(5)
α_s	Stimulus-referenced "miss" rate	(4)
β_s	Stimulus-referenced "false-alarm" rate	(4)
α_r	Response-referenced "false-alarm" rate	(6)
β_r	Response-referenced "miss" rate	(6)
ε_s	Stimulus-referenced error-rate	(13)
ε_r	Response-referenced error-state	(10)
A_s	Area under stimulus-related operational curve ($X_s(\tau), Y_s(\tau)$)	(8)
A_r	Area under response-related operational curve ($X_r(\tau), Y_r(\tau)$)	(7)
Σ_s	Stimulus-related discriminant (i.e. correlation with stimulus categories)	(11)
Σ_r	Response-related discriminant (i.e. correlation with response categories)	(11)
Σ_0	Discriminant for "hit" and "correct-rejection" trials only	(17), (18)
λ	Sensorimotor index (independent of performance error)	(15), (19)
k_λ	Sensorimotor discriminant (dependent on performance error)	(22)
$P(\tau)$	Basis function of decumulative probability under the linear mixture model	(26)
$Q(\tau)$	Basis function of decumulative probability under the linear mixture model	(26)
λ_σ	Proportional constant in the (P, Q) mixture for trials of tag σ	(26)
$\Sigma_{\mu\nu}$	Discriminant between tag μ and tag ν	(27)
Σ_{00}	Discriminant between P and Q	(27)

REFERENCES

- Bamber, D. (1975). The area above the ordinal dominance graph, the area below the receiver operating characteristic graph. *Journal of Mathematical Psychology*, **12**, 387–415.
- Barlow, H. B., Kaushal, T. P., Hawken, M., & Parker, A. J. (1987). Human contrast discrimination and the threshold of cortical neurons. *Journal of the Optical Society of America A*, **4**, 2366–2371.
- Bernardo, J. M., & Smith, A. F. M. (1995). *Bayesian theory*. New York, Wiley.
- Bradley, A., Skottun, B. C., Ohzawa I., Sclar, G., & Freeman, R. D. (1987). Visual orientation and spatial frequency discrimination: a comparison of single cells and behavior. *Journal of Neurophysiology*, **57**, 755–772.
- Britten, K. H., Shadlen, M. N., Newsome, W. T., & Movshon, J. A. (1992). The analysis of visual motion: A comparison of neuronal and psychophysical performance. *Journal of Neuroscience*, **12**, 4745–4765.
- Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York, Wiley.
- Lecas, J. C., Requin, J., Anger, C., & Vitton, N. (1986). Changes in neuronal activity of the monkey precentral cortex during preparation for movement. *Journal of Neurophysiology*, **56**, 1680–1702.
- Miller, J., Riehle, A., & Requin, J. (1992). Effects of preliminary perceptual output on neuronal activity of the primary motor cortex. *Journal of Experimental Psychology, Human Perception and Performance*, **18**, 1121–1138.
- Newsome, W. T., Britten, K. H., & Movshon, J. A. (1989a). Neuronal correlates of a perceptual decision. *Nature (London)*, **341**, 52–54.
- Newsome, W. T., Britten, K. H., Movshon, J. A., & Shadlen, M. (1989b). Single neurons and the perception of visual motion. In D. M-K. Lam and C. D. Gilbert (Eds.), *Proceedings of the Retina Research Foundation Symposia, Vol. 2, Neural Mechanisms of Visual Perception*, (pp. 171–198), Woodlands, TX: Portfolio Publishing.
- Parker, A., & Hawken, M. (1985). Capabilities of monkey cortical cells in spatial-resolution tasks. *Journal of the Optical Society of America A*, **2**, 1101–1114.
- Peterson, W. W., Birdsall, T. G., & Fox, W. C. (1954). The theory of signal detectability. *Transactions of the IRE Professional Group on Information Theory*, PGIT-4, 171–212.
- Requin, J., Riehle, A., & Seal, J. (1988). Neuronal activity and information processing in motor control: From stages to continuous flow. *Biological Psychology*, **26**, 179–198.
- Riehle, A., & Requin, J. (1989). Monkey primary motor and premotor cortex: Single-cell activity related to prior information about direction and extent of an intended movement. *Journal of Neurophysiology*, **61**, 534–549.
- Salzman, C. D., Britten, K. H., & Newsome, W. T. (1990). Cortical microstimulation influences perceptual judgements of motion direction. *Nature (London)*, **346**, 174–177.
- Salzman, C. D., Murasugi, C. M., Britten, K. H., & Newsome, W. T. (1992). Microstimulation in visual area MT: effects on direction discrimination performance. *Journal of Neuroscience*, **12**, 2331–2355.
- Salzman, C. D., & Newsome, W. T. (1994). Neural mechanism for forming a perceptual decision. *Science*, **264**, 231–237.
- Seal, J., & Commenges, D. (1985). A quantitative analysis of stimulus-and movement-related responses in the posterior parietal cortex of the monkey. *Experimental Brain Research*, **58**, 144–153.
- Swets, J. A., Tanner, W. P., & Birdsall, T. G. (1964). Decision process in perception. *Psychological Review*, **68**, 301–340.
- Tanner, W. P., Jr., & Swets, J. A. (1954). A decision-making theory of visual detection. *Psychological Review*, **61**, 401–409.
- Tolhurst, D. J., Movshon, J. A., & Dean, A. F. (1983). The statistical reliability of signals in single neurons in cat and monkey visual cortex. *Vision Research*, **23**, 775–785.
- Vogels, R., & Orban, G. A. (1990). How well do response changes of striate neurons signal differences in orientation: A study in the discriminating monkey. *Journal of Neuroscience*, **10**, 3543–3558.
- Zohary, E., Celebrini, S., Britten, K. H., & Newsome, W. T. (1994). Neuronal plasticity that underlies improvement in perceptual performance. *Science*, **263**, 1289–1292.
- Zhang, J., Riehle, A., Requin, J., & Kornblum, S. (1997). Dynamics of single neuron activity in monkey primary motor cortex to sensorimotor transformation. *Journal of Neuroscience*, **17**, 2227–2246.

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