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Neural Prediction of Multidimensional Decisions in Monkey Superior Colliculus

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SUMMARY To examine the function of the superior colliculus (SC) in decision-making processes and the application of its single trial activity for "neural mind reading," we recorded from SC deep layers while two monkeys performed oculomotor go/no-go tasks. We have recently focused on monitoring single trial activities in single SC neurons, and designed a virtual decision function (*VDF*) to provide a good estimation of single-dimensional decisions (go/no-go decisions for a cue presented at a specific visual field, a response field of each neuron). In this study, we used two *VDFs* for multidimensional decisions (go/no-go decisions at two cue locations) with the ensemble activity which was simultaneously recorded from a small group (4 to 6) of neurons at both sides of the SC. *VDFs* predicted cue locations as well as go/no-go decisions. These results suggest that monitoring of ensemble SC activity had sufficient capacity to predict multidimensional decisions on a trial-by-trial basis, which is an ideal candidate to serve for cognitive brain-machine interfaces (BMI) such as two-dimensional word spellers.

key words: *decision-making, prediction, brain-machine interface, go/no-go*

1. Introduction

Neurophysiological studies in behaving animals such as monkeys have disclosed neural substrates of highly cognitive functions. Those experiments often average single neuron activity over a number of trials intermixing difference experimental conditions. For these experiments, variability in a neuron's activity between trials with identical conditions is dismissed as "noise." It is, however, possible that the variability represent some unknown cognitive factors beyond our hypotheses [1]. Moreover, we have recently focused on monitoring single trial activities of neurons in the superior colliculus (SC) for "neural mind reading," one of the techniques in neurotechnologies [2].

The SC is located on the dorsal surface of the midbrain, and considered to be an important component of the oculomotor system [3]. Several studies have shown that neurons in the SC not only represent motor commands to execute saccadic eye movements but also the decision-making process for upcoming saccades [4]–[6].

An important component of movement control is the ability to withhold movements when appropriate. Recent experiments have looked at neural activity in the frontal eye field [7] and SC [2] in decision-making tasks that require the active suppression of saccades. These experiments suggest that many neurons in the oculomotor system exhibit selectivity for "go/no-go" decisions, that is, plans to make a saccade or to maintain fixation. The decision-making process is entirely internal and does not necessarily produce motor behavior. Studies on techniques to read out such an internal signal are closely related to brain-machine interface (BMI), especially cognitive BMI that might provide useful communication tools for patients with difficulty in expressing their intentions.

We recently addressed the issue of how well the activity of single SC neurons can predict, for individual trials, a monkey's decision to make a saccade or to maintain fixation in response to a peripheral cue [2]. We found that our methods correctly predicted the monkey's decision on about 83% of the trials. The prediction became more accurate when we recorded from multiple neurons ($N = 2$ to 5) at a single SC site [8]. For these studies, our single trial prediction was limited to the go/no-go cue in the specific visual field, which was covered by the response field of the recorded neuron(s).

In this study we attempted to record from the neurons in the both sides of the SC in order to increase the number of categories of decisions by presenting the cue at two locations. Here we report that simultaneous recording from both colliculi enables us to predict 4 categories (2×2; go/no-go at right/left position). Preliminary reports of these findings have appeared in abstract form [9].

2. Methods

2.1 Animal and Surgery

Two adult female Rhesus monkeys (*Macaca mulatta*) were used for this study. Each monkey received preoperative training followed by an aseptic surgery to implant a subconjunctival wire search coil, a plastic cilux recording cylinder aimed at the superior colliculus, and a titanium receptacle to allow the head to be held stationary during behavioral and neuronal recordings. All of these methods have been described in detail elsewhere [10]. Surgical anesthesia was induced with the short-acting barbiturate thiopental (5–7 mg/kg, *i.v.*), and maintained using isoflurane (1.0–2.5%) inhaled through an endotracheal tube. Northwestern University's Animal Care and Use Committee approved all animal protocols, which were in compliance with the NIH Guide for the Care and Use of Laboratory Animals.

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2.2 Behavioral Task

We used the REX system [11] running on a Dell Pentium II computer for behavioral control and eye position monitoring. Visual stimuli were generated by a second PC, which was controlled by the REX machine and rear-projected onto a tangent screen in front of the monkey by a CRT video projector (Sony VPH-D50, 75Hz non-interlaced vertical scan rate, 1024×768 resolution). We trained each monkey on an oculomotor go/no-go task (Fig. 1).

A trial was initiated by fixation of a central fixation spot (white spot; 0.5° diam.). Next, the fixation spot disappeared and simultaneously a peripheral stimulus ("cue"; 1° by 1° square) appeared. The monkey was trained to respond differently to the stimulus depending upon the color of the cue, that is, either make a saccade toward the stimulus within 800 ms (green cue; go trial) or maintain fixation for longer than 800 ms (red cue; no-go trial). A correct response was rewarded with a drop of water. During training, we presented the green or red cue at one of 24 locations that were in 8 directions (45° spacing) at 3 eccentricities (5, 10 and 15° away from the fixation point). All conditions were run in a pseudorandom fashion. During the recording sessions, we first presented all of these possible conditions to define the response fields of isolated neurons. Then, we presented the green/red cue only at the preferred location (near the center of the neuron's response field) and at the opposite location (rotated 180° with the same amplitude). This reduction of the number of conditions allowed us to record more trials with the responses of interest (usually more than 20 trials for each condition). In this study we focused on the response to the go/no-go cue at these two positions to allow us to predict multidimensional decisions.

2.3 Electrophysiological Recording

When the monkey's performance reached the criteria (> 85% over 3 successive days) in overall training history, we started recording from the SC. The location of the SC was confirmed by stereotaxic coordinates as well as by the response properties of isolated neurons. In this study, we focused on recording from two types of neurons, one with a response field that covered the right-side stimulus/rightward saccade, and the other with a response field that covered the left-side stimulus/leftward saccade. The SC has a topographically organized visual/motor map, making it possible to record simultaneous from these two neuron types (Fig. 2). Insulated tungsten microelectrodes (A-M Systems, Inc) were inserted into the SCs, through a hole drilled of the skull. The dura was pierced by stainless steel tubes, each of which guided one or two tungsten microelectrodes. To record simultaneously from both colliculi, right and left side electrodes were introduced through separate guide tubes, and manipulated by two separate Narishige microdrives. A 16-channel Plexon System was dedicated to accepting the electrode input, and could isolate 2 neuron waveforms from each of the electrodes. For these experiments, we obtained data from 7 sessions, in which multiple neurons were recorded in both left and right colliculi.

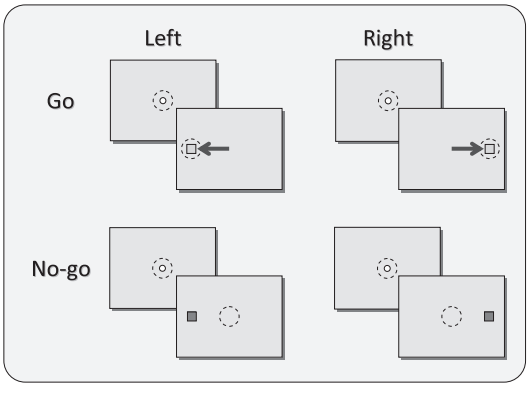

Fig. 1 Oculomotor go/no-go task. Go (saccade to a peripheral cue) or no-go (maintenance of fixation) response is required immediately following the appearance of the cue. The color of the cue indicates the type of the response (green for go; red for no-go).

2.4 Data Analysis

We analyzed data offline using programs written in Matlab. The original prediction method was developed with the single neuron's single trial activity to predict a binary (go/no-go) decision [2]. The method was then modified to handle multiple neurons' single trial activities [8]. The innovative aspect in this method was the introduction of the virtual decision function (*VDF*), which reflected the progress of decision making processes on individual trials (Fig. 3). Although it is very difficult to estimate when and how the internal decision was done with the raw activity, we can predict hem from the change of each *VDF*.

The major change in this study was the introduction of two *VDFs* for multi-dimensional decisions, one for the prediction of type of the cue (go/no-go), the other for the prediction of position of the cue (right and left).

As in the original method, we first calculated a spike density function of each of the recorded neurons by convolving single trial activity with a Gaussian kernel [12] with a sigma of 10 ms (36 ms spread of the spike density function). We measured the activity over a 500 ms interval, starting 100 ms before the cue onset and ending 400 ms after it. We used a linear model for each millisecond (t) of ensemble activities to produce two *VDFs* which was mostly common as follows:

$$y(t) = \frac{2}{1 + \exp\left(c(t) - \sum_{i}^{n} w_i(t) x_i(t)\right)} - 1 \qquad (1)$$

where independent variables, $x_i(t)$ were discharge rates of simultaneously recorded neurons (i, neuron ID; n, total number of neurons), $w_i(t)$ were unstandardized partial regression coefficients (weights), and $c(t)$ was a constant term

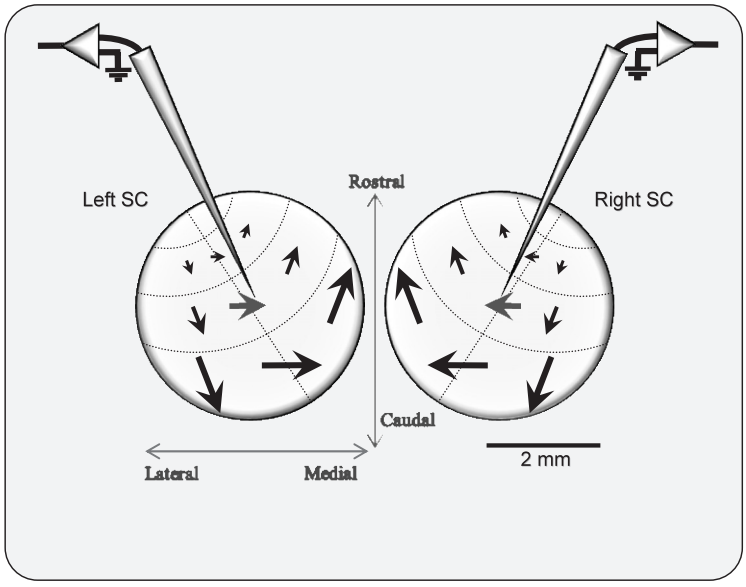

Fig. 2 Schematic drawing of simultaneous recording from neurons in both left and right superior colliculus (SC). Arrow vectors represent the approximate saccade vector map in each colliculus. Arrows adjacent to electrode tips provide examples of saccades that would be represented at two separate recording sites.

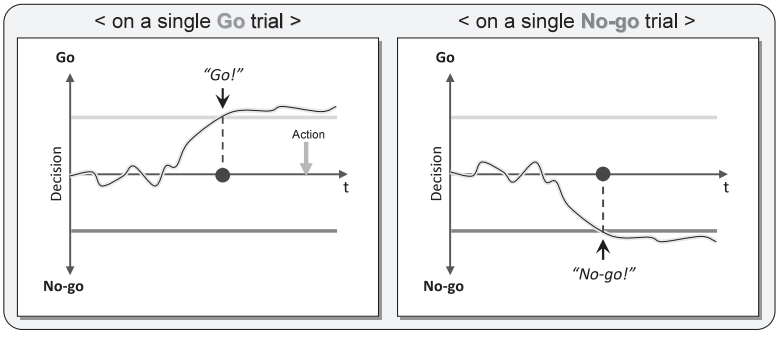

Fig. 3 Hypothetical virtual decision function (VDF) designed to estimate the progress of the decision making for "go" (left panel) or "no-go" (right panel) on single trial basis. Upper and lower horizontal lines mark the thresholds for go and no-go decisions respectively.

at the moment of t. In this study dependent/predicted variable, $y(t)$ was not only a desired go/no-go score but also a position score. While for go/no-go prediction its actual data (type of trial), z was set to either 1 on go trials or to -1 on no-go trials, for right/left prediction z was set to either 1 on right trials or to -1 on left trials. The z value was held constant throughout a given trial.

$$z = \begin{cases} 1: & \text{go or right trial} \\ -1: & \text{no-go or left trial} \end{cases} \tag{2}$$

A set of appropriate weights of the model were determined by the least square method which minimized the sum of the squared regression errors.

$$S_E(t) = \sum_{j=1}^{m} \left(z_j - y_j(t)\right)^2 \tag{3}$$

where z_j and $y_j(t)$ were respectively z (actual data) and $y(t)$ (fitted data) on each trial (j, trial ID; m, total number of trials). $S_E(t)$ represents the variation which is unexplained by the regression equation. On the other hand, the sum of squared errors from the mean represents the total variation.

$$S_T(t) = \sum_{j=1}^{m} \left(z_j(t) - \overline{y}(t)\right)^2 \tag{4}$$

The fitness of the model was evaluated by the coefficient of determination (R^2)

$$R^2(t) = 1 - \frac{S_E(t)}{S_T(t)} \tag{5}$$

which represents the proportion of variation that is explained by the model. R^2 may vary from 0 (no predictive power) to 1 (perfect prediction).

In this study, we repeated this analysis over the 500 ms interval beginning 100 ms before cue onset to determine

weights x_i, constant c and R^2 at a time t (sampled at 1 kHz). We used $R^2(t)$ as well as $y(t)$ to produce a $VDF(t)$ that was designed to reflect a single trial-based prediction.

$$VDF(t) = y(t)\, R^2(t) \tag{6}$$

R^2 represents how well the expected data fit the real data. It can be a good index for the confidence level of prediction but R^2 itself does not indicate the content of the prediction. Instead, $y(t)$ is the actual predictor although it lacks the information about "how well." Therefore, $y(t)$ and R^2 complement each other when those functions are multiplied.

To evaluate the success or failure of the predictions, we referred to a pair of criteria for cue location (e.g., +0.6 for "right" judgment vs. −0.6 for "left" judgment) as well as a pair of criteria for motor choice (e.g., +0.3 for "go" choice vs. −0.3 for "no-go" choice). Those two pairs of criteria were independently prepared. If the *VDF* reached either criterion, it was considered that the neurons had made a prediction. If the neuronal prediction matched the actual trial type (right/left for cue position and go/no-go for motor choice), the trial was considered to be one with a good prediction.

For each recording session, we set the criteria by simulations; out of 19 candidates of a pair of criteria (i.e., ±0.1, ±0.15, ±0.2 . . . ±1.0), we chose the "optimal" pair so that the number of good predictions was maximized. The pair of criteria for right and left decisions and those for go and no-go decisions were independently selected by the simulations.

We defined *decision time* as the first moment when the function reached either the upper (go or right) or the lower (no-go or left) criterion. A mismatch of neuronal prediction to stimulus location as well as actual behavior or (rarely) a trial where no neural prediction was made was considered to be a trial with a bad prediction. It was also incorrect if the *VDF* became 1 or −1 before the cue was presented, since it was unlikely that the monkey formed a decision before the instruction was presented. Therefore, we counted those trials (including the trials with the neural prediction made within 25 ms after the cue onset) as bad ones. We also set a time limitation of up to 400 ms after the cue presentation for inclusion of neuronal data in the analysis.

For the prediction above, we used the leave-one-out method, in which we removed single trials from the dataset $(n - 1)$, used the remaining trials to construct the model and then tested the model against the trial that had been removed. This procedure was repeated n times.

3. Results

3.1 General Property of SC Neurons

In total, 30 neurons were recorded during 7 recording sessions in 2 monkeys. For most of the sessions (6/7) we simultaneously recorded from 4 neurons (2 from right, and 2 from left SC). In the remaining session, we recorded simultaneously from 3 neurons in each colliculus. As described in previous studies [2], [8], [9], most SC neurons exhibited higher activity on go versus no-go trials when the cue was presented within the response field. Figure 4 shows examples of responses of two neurons with response fields in the left visual field (top panel) and right visual field (bottom panel), both of which were simultaneously recorded in the right and left SC respectively. Since SC neurons generally have response fields in the visual hemifield contralateral to the recording site, the combination of the responses of right and left SC neurons supplied enough information to predict the trial type in terms of position as well as the type of cue.

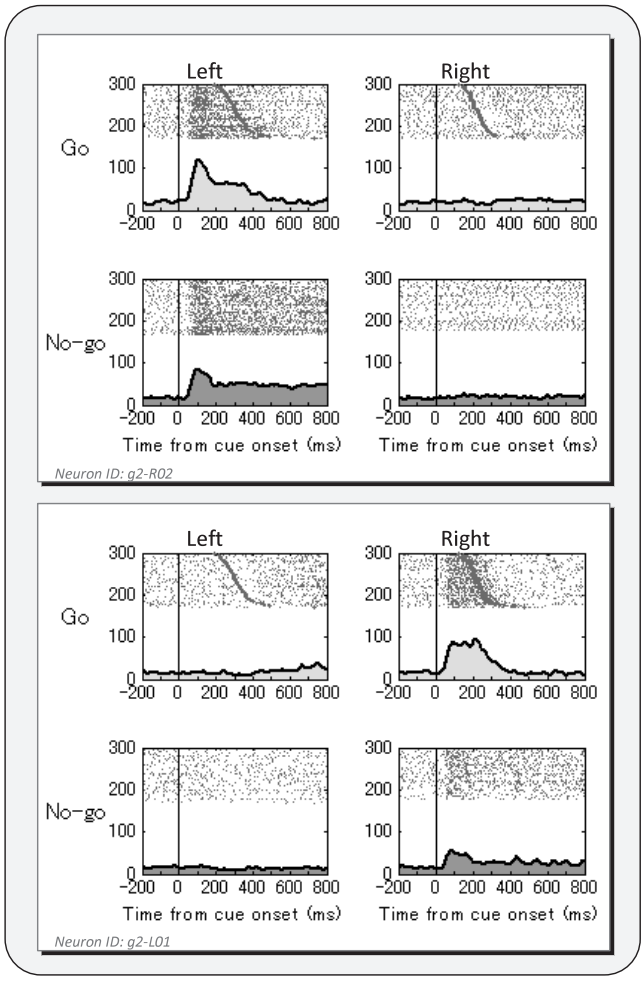

Fig. 4 Examples of the activity of neurons recorded from the right SC (top) and left SC (bottom). Each panel includes a raster and spike density histogram. For the raster, each horizontal line includes the activity for a single trial and each dot represents the time of occurrence of an action potential. All rows are aligned on the time of cue onset marked by the vertical line at time = 0. The larger dots positioned ~200–500 msec after cue onset mark the time for the beginning of the saccade in each trial. Spike density profiles represent an average of activity across all trials obtained by assigning a Gaussian distribution to the time of occurrence of each action potential with Sigma = 10 msec and averaging across trials. For each neuron, top panels plot activity for go trials, and bottom panels for no-go trials. Left column of panels for targets presented in the left hemifield, right column for right hemifield targets.

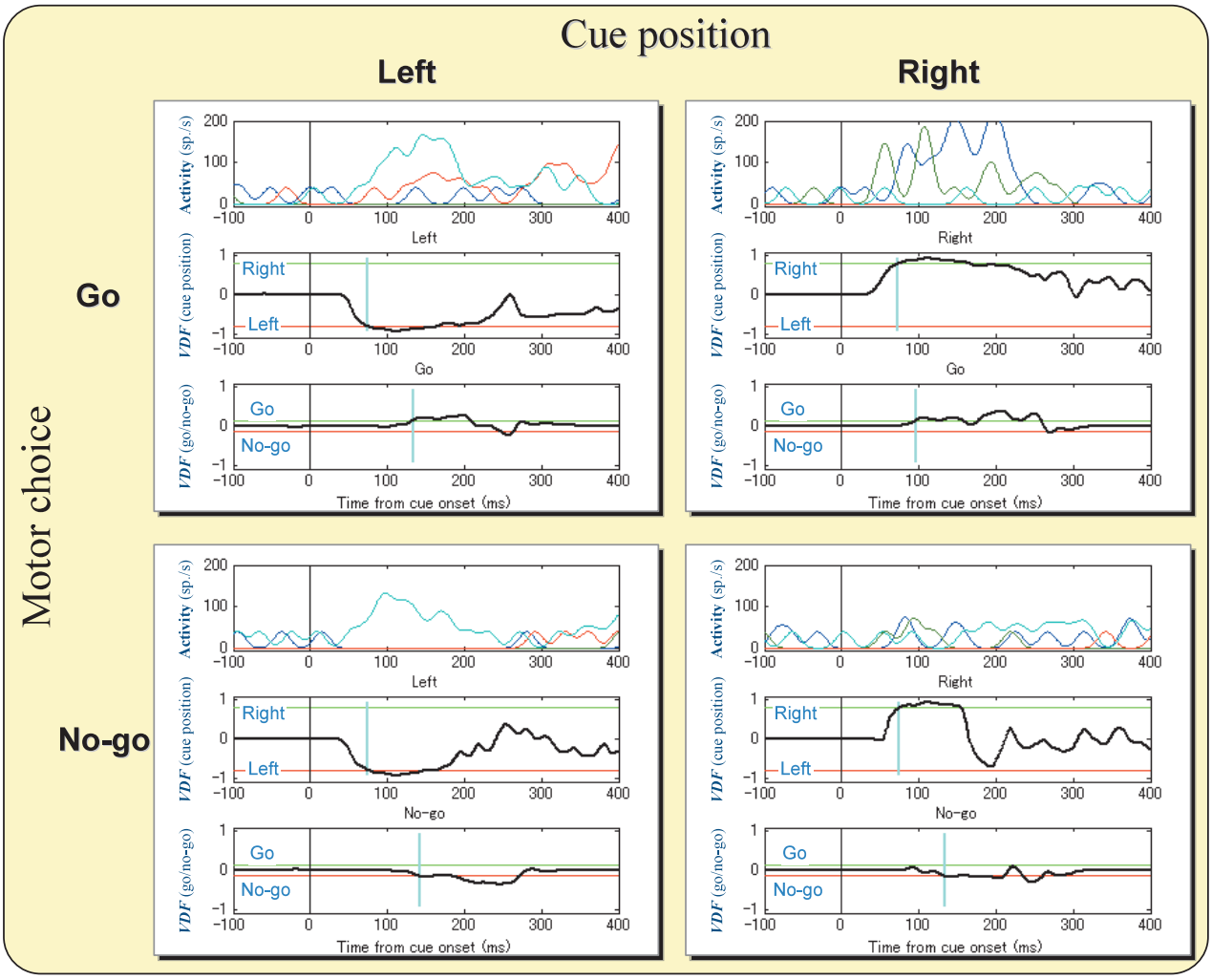

Fig. 5 Examples of successful predictions of multidimensional decisions. Four representative trials for 'go' and 'no-go' decisions (top and bottom rows) for the left and right cues (left and right columns) were used. On each panel single trial activities of four neurons are shown by spike density histograms aligned to cue onset (top), which produced the virtual decision function (*VDFs*) for predictions of the cue position (middle) and motor choice (bottom). A vertical line (cyan color) indicates the decision time which the *VDF* reached either the upper criteria (a green horizontal line for right or go decision) or the lower criteria (a red horizontal line for left or no-go decision).

3.2 Example of Predictions of Multidimensional Decisions

We used two *VDFs* (see Methods) to predict right/left cue position and go/no-go motor choice. Figure 5 shows representative successful predictions in the recording sessions, in which 4 neurons, including the 2 neurons shown in Fig. 4, were recorded. On each trial, in agreement with the actual trial type, the *VDF* reached either upper or lower criteria meaning "right" or "left" for prediction of cue position and "go" or "no-go" for that of motor choice. The model correctly predicted the cue position on 96% of trials (164/170), and the motor choice on 78% of trials (133/170). The percentage of trials, in which both cue position and motor choice were correctly predicted, was 75% (127/170). The median of the "decision time" (the time when the *VDF* reached the criteria) was 74 ms for the cue position and 139 ms for the motor choice, both of which were much faster than the median saccade latency on go trials (268 ms).

3.3 Summary of Predictions

Figure 6 summarizes the average accuracy and speed of the predictions for the total of 7 recording sessions. Although the number of simultaneously recorded neurons was a small group (4 to 6), the *VDFs* were proficient in predicting cue positions (93% on average) and motor choices (86% on average). Accuracy of the prediction of both cue positions and motor choices was 79% on average. A paired t test revealed that there was no significant ($P > 0.05$) difference between accuracies of cue positions and motor choices. The speed of

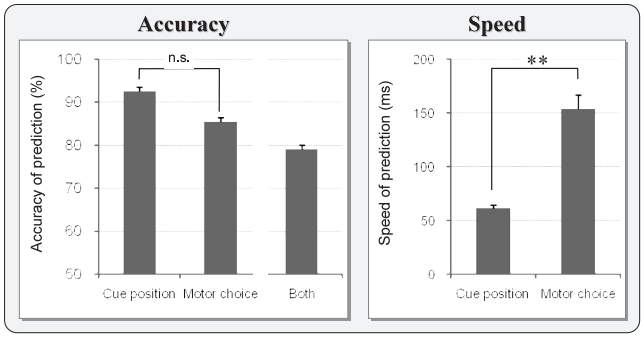

Fig. 6 Average accuracy (left panel) and speed (right panel) of the predictions for right/left and go/no-go decisions for the total of 7 recording sessions. Error bar indicates standard error of mean.

the prediction (decision time) of cue positions (62 ms on average) was, however, significantly ($P < 0.01$) faster than that of motor choices (154 ms on average). Those times were also significantly ($P < 0.01$) faster than the average of median saccade latencies (231 ms).

4. Discussion

4.1 History of the Development of the *VDF*

We used the *VDFs* to predict multidimensional decisions. The *VDF* was calculated using the regression analysis, which frequently has been used in neurophysiological studies to explain the variation of single trial neuronal activity as a dependent/predictor variable in relationship to cognitive, motivational or motor parameters as independent/explanatory variables [7], [13], [14]. The *VDF* was developed as a new decoding method based upon the single regressions with the activity of the single neuron (average spike density) as independent variables and a binary decision outcome (go/no-go score, 1 for go and −1 for no-go) as a dependent variable [2]. Then the *VDF* was modified to use the multiple neurons that were simultaneously recorded in the same side of the SC (2 to 5 neurons), simply expanding the model to perform the multiple regressions [8]. This expansion made the prediction accuracy 6% better on average (from 83% to 89% for the same population of neurons).

In these experiments with 7 recording sessions, the number of neuron recorded in the same side of the SC was smaller than it was for the earlier report (2 for 6 sessions and 3 for 1 session) and the prediction accuracy for the go/no-go decision was 86%. Nonetheless, we had an advantage in these sessions because the multiple neurons were recorded simultaneously from both colliculi, instead of from just one. As described in the Methods, neurons in the SC have response fields in the contralateral visual field, and simultaneous recording from both colliculi can monitor the responses for both left and right visual fields. We took advantage of this organization to develop the methods for prediction of the cue position as well as the behavioral meaning of the cue (motor choice). To our knowledge, this method for the prediction of multidimensional decisions using 2 *VDFs* is the first to demonstrate an estimation of the progress of internal decision-making processes for both sensory input and motor output on a millisecond timescale.

4.2 The SC's Signal for Cognitive BMI

Previous studies of BMI demonstrated that neural signals from motor-related areas could serve to control robot arms or computer cursors [15]–[18]. In addition to the control of output devices, it has been shown that muscle activities of subjects were reliably reconstructed by a small number of neurons recorded from the primary motor cortex [19], [20]. These "motor BMI" studies focused on the prediction of either kinematic parameters of movements (such as hand position and joint angle) or the muscle activities related to them. In contrast, our main goal has been to develop algorithms to predict, at neuronal level, cognitive decision signals which often result in the categorical selection of not only overt but also covert behaviors [21]–[23]. Such a high-order signal is compatible with the existing human-interface devices. Studies on non-invasive EEG-based brain computer interface (BCI) for human subjects have been developing spelling devices as a communication tool for patients [24]. Those BCI studies have focused on a late positive component of evoked potentials with the peak latency of about 300 msec (P300) which is affected by cognition. Direct access to neuronal signals by electrophysiological recording allowed us to obtain this information very quickly at roughly 150 ms after cue onset. For the sensory signals the timing was much faster −60 ms after cue onset. The risks inherent to invasive recording may present challenges to clinical application that must be overcome. Nevertheless, invasive BMI techniques continue to hold great promise for the development of high-speed communication tools, and warrant further study.

Acknowledgments

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