Rapid Communication

Conditional Oculomotor Learning: Population Vectors in the Supplementary Eye Field

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Chen, Longtang L., and Steven P. Wise. Conditional oculomotor learning: population vectors in the supplementary eye field. J. Neurophysiol. 78: 1160–1163, 1997. We have shown previously that the activity levels and preferred directions of supplementary eye field neurons change as monkeys learn to associate nonspatial visual information with a saccade (or the spatial target of that saccade). The present report describes changes in neuronal population vectors (PV) during such learning. PVs based on neuronal activity shortly before and after saccades predicted movement direction poorly in the earliest stage of learning, but as monkeys mastered novel stimulus-response mappings, PV accuracy and magnitude increased significantly.

Introduction

Conditional motor learning depends on the arbitrary mapping of a set of stimuli onto a set of actions. Such learning epitomizes the behavioral flexibility that advanced mammals bring to a rapidly changing environment: any stimulus or context that can be detected and discriminated can come to elicit any response within a behavioral repertoire. We have studied the activity of neurons in the supplementary eye field (SEF) during conditional motor learning (Chen and Wise 1995a, 1996). As monkeys learn novel stimulus-saccade mappings, the activity of one population of SEF neurons evolves in close correlation with the animals’ learning curve. In this report, we analyze population vectors (PVs) for this SEF population.

Methods

The behavioral, anatomic, and physiological methods have been described previously (Chen and Wise 1995a,b, 1996). Briefly, two rhesus monkeys (Macaca mulatta) learned to associate a visual stimulus with an eye movement or its target, having only reward or nonreward to guide learning. In each trial, the monkeys fixated a spot, after which four potential eye-movement targets simultaneously appeared: 7° from center (Fig. 1A). As the monkeys maintained fixation, a visual instruction stimulus (IS), which was a composite of several shapes, sizes, orientations, and colors, appeared foveally for 0.5 s. After 1.5–3.0 s, the disappearance of the fixation point served as the trigger (or ‘‘go’’) signal (Fig. 1A). The monkeys then had to make a saccade to the correct target and fixate it for 0.6 s to receive reinforcement. Retrivals were run after incorrect responses. There were four familiar ISs, one for each target. Novel ISs were added to that group, and the IS on each trial was selected randomly from a set containing three to four familiar ISs and one to three novel ISs.

Neuronal discharge during each trial was measured in two pairs of task periods (Fig. 1A): an instruction period, 80–320 ms after IS onset plus an instructed delay period from 400 to 1,200 ms before target acquisition (together termed the instruction + delay period) and a perisaccadic period, consisting of 20–200 ms before target acquisition (presaccadic activity) plus 200–600 ms after target acquisition (postsaccadic activity). Task-periods were paired because of the small number of neurons that could be studied adequately during learning for all four saccade directions. We measured activity in each task period separately (see Chen and Wise 1995a, 1996), and the present analysis is limited to cells with directionality as a main effect and a significant difference from background activity [two-factor analysis of variance (ANOVA), P < 0.05].

Four phases of learning were defined on the basis of the monkey’s performance. Neuronal and behavioral data were aligned on the first instance of three consecutive correct responses to each novel IS. The middle of those three trials was designated trial 0 (Fig. 1B). This procedure allowed averaging according to the stage of learning regardless of learning rate, which varied among the novel IS-saccade mappings. The first correctly executed trial was termed the early phase of learning, which always occurred more than two trials before trial 0. Correct trials −2 to +2 constituted the middle phase, trials 3–7, the late phase, and the last two trials the established phase of learning. We emphasize that this analysis included only correctly executed trials and that incorrectly performed trials were, especially in the early learning phases, interspersed with correctly performed ones.

PVs for each task period pair and learning phase were calculated, after Georgopoulos et al. (1983, 1989), as the weighted vector sum

$$\hat{\beta} = \sum w_i \cdot \hat{c}_i$$

where $\hat{c}_i$ is each cell’s preferred direction (PD), estimated as the circular mean resultant of the normalized vectors for each saccade direction (Batschelet 1981) and $w_i$ is the normalized activity modulation ($d_i - \bar{d}_i$). For each saccade direction for a given cell (i) $d_i$ is the square root transform of cell activity and $\bar{d}_i$ is the square root-transformed mean modulation. The square root transformation was applied, as in Georgopoulos et al. (1989), to stabilize variance. (We also computed PVs using alternative normalization methods, including some without square-root transformation, and the results were similar to those reported here.) In the computation of a PV, some assumption must be made about the PD to be used as a referent, $\hat{c}_i$, when that PD changes over task periods, learning phases or other experimental conditions (see Chen and Wise 1996; Wise et al. 1996b). For novel-IS trials, cross-referenced PVs were calculated with PDs from familiar-IS trials in a given task period and learning phase; self-referenced PVs were calculated with PDs calculated from novel-IS trials. PVs for familiar-IS trials were always calculated with PDs from familiar-IS trials.

Results

As reported elsewhere (Chen and Wise 1995a, 1996), the monkeys, on average, mastered each conditional motor
mapping problem in about a dozen trials, approximately half of which were executed correctly. Therefore, as shown in Fig. 1B, the monkeys reached a level of 95–100% correct performance in about six correct trials, with considerable variation among novel IS-saccade mappings. By the end of the middle phase of learning, the monkey’s performance had stabilized at a very high level, usually >90% correct (where chance performance is 25%).

The activity of 10 cells contributed to the instruction + delay period PVs; 12 to the perisaccadic period. The criterion for inclusion, distribution of PDs, and relative magnitudes can be found in Chen and Wise (1996). For the latter population, there was no significant directional bias in PDs in any phase of learning ($P > 0.05$, Rayleigh test) (Batschelet, 1981). For the former, there was no significant bias in the early, middle, or late phases of learning, but a significant directional bias did exist for the established phase ($P = 0.03$). In the description of results, below, we refer to the cross-referenced PVs based on novel-IS trials, unless otherwise noted.

Figure 2 shows the angular difference (i.e., error) between the PV and the direction of the saccade target. For perisaccadic activity, PV angle was highly inaccurate in the early learning phase but improved dramatically as learning progressed (Figs. 2A and 3A). As that angular error decreased, its relative amplitude increased (Figs. 2B and 3A) and came to resemble that for familiar-IS trials (ellipse in Fig. 2B). For the instruction and instructed delay periods, there was no improvement in the predictive accuracy of PVs (Fig. 2A) nor was such improvement seen for self-referenced PVs (not shown) or for PVs based on familiar-IS trials (Figs. 2A and 3B).

The circular correlation (Batschelet 1981) between the angle of each PV and the correct response direction is given in Table 1. Note especially the data for cross-referenced PVs and perisaccadic activity (PR + PO). In the early and middle phases of learning, taken together, the correlation of PV angle and saccadic direction was very low and not statistically significant. In later phases of learning, the correlation improved markedly and became highly significant.

Perisaccadic PVs usually predicted saccade direction better than those for the instruction + delay periods. The largest such difference was seen for cross-referenced PVs during the late and established learning phases (Fig. 2A, Table 1). In the early learning phase, however, perisaccadic PVs were substantially worse than those for the instruction + delay periods. This pattern of results explains why a previous PV analysis of these data, which averaged all task periods together, showed no significant learning-related trends (Wise et al. 1996a). The superiority of the perisaccadic period was also found for self-referenced PVs (ANOVA, $F(1,24) = 12.5, P < 0.002$; Fig. 2A, right), although a similar trend for PVs based on familiar-IS trials was not statistically significant ($F(1,24) = 3.0, P > 0.09$; Fig. 2A).

\[ A \]

\[ B \]

\[ C \]
TABLE 1. Circular correlation coefficients and average PV angular difference between the correct saccade direction and PVs

<table>
<thead>
<tr>
<th>PV Type</th>
<th>Task Period</th>
<th>Learning Phase</th>
<th>Correlation Coefficient (r)</th>
<th>Significance of Correlation (ρ)</th>
<th>PV Error (deg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Novel-ISs</td>
<td>IN + ID</td>
<td>E + M</td>
<td>0.65</td>
<td>0.02</td>
<td>34.4 ± 12.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>L + Es</td>
<td>0.66</td>
<td>0.02</td>
<td>33.7 ± 11.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PR + PO</td>
<td>0.32</td>
<td>0.65, NS</td>
<td>52.5 ± 18.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>L + Es</td>
<td>0.95</td>
<td>0.002</td>
<td>11.3 ± 4.0</td>
</tr>
<tr>
<td>Self-Referenced</td>
<td>IN + ID</td>
<td>E + M</td>
<td>0.82</td>
<td>0.01</td>
<td>28.8 ± 10.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>L + Es</td>
<td>0.76</td>
<td>0.002</td>
<td>9.2 ± 3.3</td>
</tr>
<tr>
<td></td>
<td>PR + PO</td>
<td>E + M</td>
<td>0.95</td>
<td>0.002</td>
<td>11.6 ± 4.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>L + Es</td>
<td>0.94</td>
<td>0.002</td>
<td>19.2 ± 6.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PR + PO</td>
<td>0.85</td>
<td>0.004</td>
<td>19.8 ± 7.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>L + Es</td>
<td>0.85</td>
<td>0.004</td>
<td>12.8 ± 4.5</td>
</tr>
<tr>
<td>Familiar-ISs</td>
<td>IN + ID</td>
<td>E + M</td>
<td>0.93</td>
<td>0.002</td>
<td>11.3 ± 4.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>L + Es</td>
<td>0.94</td>
<td>0.002</td>
<td>13.0 ± 4.0</td>
</tr>
</tbody>
</table>

Values are means ± SE. Learning phases: E, early; M, middle; L, late; Es, established. Task periods: IN, instruction; ID, instructed delay; PR, presaccadic; PO, postsaccadic. Other abbreviations: NS, not significant; PV, population vectors; IS, instruction stimulus.

DISCUSSION

The PV method developed by Georgopoulos and his colleagues is based on the assumptions that each member of a population contributes an activity-scaled “vote” in its PD and that serially recorded activity corresponds to simultaneous network activity. Recently developed models of conditional motor learning also assume, as does the PV method used here, that neurons “vote” for a movement in their PD, as defined during the performance of stable, well-learned mappings (Dominey et al. 1995; Wise et al. 1996a). Despite some controversy, the PV method has proven to be a useful measure of spatial information distributed across a neuronal population; one that can be used for testing specific hypotheses. Here, we have tested and confirmed the hypothesis that PVs based on a subpopulation of SEF neurons should predict eye-movement direction accurately. For familiar-IS trials, confirmation of this prediction was unsurprising given that no learning was taking place. However, for novel-ISs trials, the prediction was less straightforward given the lability in neuronal PDs and discharge rates during conditional motor learning (Chen and Wise 1995a, 1996). Despite that lability, we found that PVs for novel-IS trials were reliable predictors of saccade direction. Interestingly, PVs based on the perisaccadic task periods came to predict movement direction only after some conditional motor learning had occurred. We can only speculate about what neuronal populations might reflect saccade direction during the earliest phase of learning, when this SEF subpopulation does not. Other activity in the SEF, which appears exclusively the early phases of learning (see Chen and Wise 1995a) or perisaccadic activity in other cortical fields, such as the frontal eye field or prefrontal cortex, are among the possibilities.

We make no claim here about either a causal relationship between SEF PVs and saccades or the relative merit of various algorithms for estimating information distributed across a neuronal population (Salinas and Abbott 1994; Sanger 1996). Self-referenced PVs were generally more predictive of saccade direction than were cross-referenced PVs (Fig. 2A, right), as was to be expected (see E. E. Fetz, discussion, p. 133 in Georgopoulos 1987; Georgopoulos et al. 1988). However, we emphasize cross-referenced PVs here because they most resemble PVs that have been studied in the past (e.g., Schwartz 1993, 1994; Wise et al. 1996b). In most previous studies, PDs from a “standard” condition have been applied to another, experimental condition. Here we applied the PDs from familiar-IS trials to those on which novel ISs were presented.

The PVs for familiar-IS trials provided a guard against bias or artifact: no learning was taking place on those trials, but they were interleaved with trials in which novel ISs were presented. Those PVs were computed from the same task periods, thus the definition of those periods did not cause the observed properties of novel-IS PVs. For example, the fact that the early learning phase consisted of only one trial did not cause the inaccuracy of perisaccadic PVs: PVs for familiar-IS trials were computed identically and were highly predictive of saccade direction (Fig. 2A, Table 1), comparable in accuracy to those reported for primary motor cortex (Georgopoulos et al. 1983, 1989). Because of the difficulty in recording single-cell activity as monkeys learn conditional motor mappings for all four saccade directions, the number of neurons contributing to each of the PVs reported here was small (n = 10 and 12). However, the cells tested for all four directions resembled those tested for fewer directions in all relevant respects, and it has been shown in computational modeling studies that small numbers of hidden units (often as few as 8) are sufficient to encode spatial information accurately in distributed networks (Moody and Zipser 1997).

In the instruction + delay periods, i.e., substantially before the saccade is to be executed, PV accuracy appears to be relatively unaffected by learning (Fig. 2A). One interpretation of this finding is that, during those periods, the response is being selected and prepared, and it may be less important to achieve high spatial accuracy at those times. Later, near the time of movement, the accuracy of the PV improves dramatically as learning progresses. Thus the predictive capacity of the network appears to improve over two distinct time dimensions: within a trial, as monkeys near movement execution, and across trials, as monkeys accentuate reliance on nonspatial visual stimuli in their choice of response. This view accords with other physiological evidence that SEF activity is important when nonspatial visual information guides spatially directed action (Olson and Gettner 1996).
and supports the hypothesis that SEF neurons participate in a network subserving the long-term storage of arbitrary mappings that guide the selection, preparation and execution of flexible action.

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