

Direction-selective visual responses in macaque superior colliculus induced by behavioral training

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Received 16 March 2004; received in revised form 14 May 2004; accepted 22 May 2004

Abstract

In a previous report, we described a heretofore undetected population of neurons in the intermediate and deep layers of the monkey superior colliculus (SC) that yielded directionally selective visual responses to stimuli presented within the central 4° of the visual field. We observed these neurons in three monkeys that had been extensively trained to perform a visual direction discrimination task in this region of the visual field. The task required the monkeys to report the perceived direction of motion by making a saccadic eye movement to one of two targets aligned with the two possible directions of motion. We hypothesized that these neurons reflect a learned association between visual motion direction and saccade direction formed through extensive training on the direction discrimination task. We tested this hypothesis by searching for direction-selective visual responses in two monkeys that had been trained to perform a similar motion discrimination task in which the direction of stimulus motion was dissociated from the direction of the operant saccade. Strongly directional visual responses were absent in these monkeys, consistent with the notion that extensive training can induce highly specific visual responses in a subpopulation of SC neurons. © 2004 Elsevier Ireland Ltd. All rights reserved.

Keywords: Superior colliculus; Macaque; Learning; Plasticity; Vision; Direction selectivity

While studying the responses of intermediate and deep layer superior colliculus (SC) neurons during performance of a visual motion direction discrimination task, we observed a small population of neurons with novel visual response properties. These neurons exhibited standard movement fields that are typical of SC neurons, but they also yielded direction-selective visual responses to random dot motion stimuli presented in the central 4° of the visual field. Importantly, the visual direction selectivity was related systematically to the topographic location of the movement field: each neuron responded best to motion flowing toward its movement field and poorly or not at all to motion in the opposite direction [9,10]. In contrast, previous studies have established that the visual receptive fields (RFs) of SC neurons are spatially coincident with movement fields [17,20] and poorly tuned for direction [5,15,16]. The current experiments address the discrepancy between the unusual visual RFs we

observed and the well-established, retinotopically-organized visual RFs that are described in the literature.

Direction-selective visual responses were present in three monkeys, all of whom had been trained to perform a standard direction discrimination task, illustrated in Fig. 1A [11]. In this task, monkeys discriminated between two opposed directions of motion in a random dot stimulus that was usually presented within the central 4° of the visual field. To report its perceptual judgment, the monkey made a saccadic eye movement to one of two visual targets aligned with the axis of motion. A saccade to the target in the direction of motion was counted as a correct response and triggered a reward. A saccade to the other target did not trigger a reward. Thus, the direction of the operant saccade was similar to the direction of visual motion in the random dot stimulus.

During performance of the discrimination task, the stimulus selectively excited SC neurons whose movement fields lay in the direction of stimulus motion, as expected from the logic of our task. Such “prelude” or “build-up” activity has been documented in previous studies and has been interpreted as representing the monkey’s saccade plan or motor set. We were surprised to discover, however, that this response was present in some neurons during blocks

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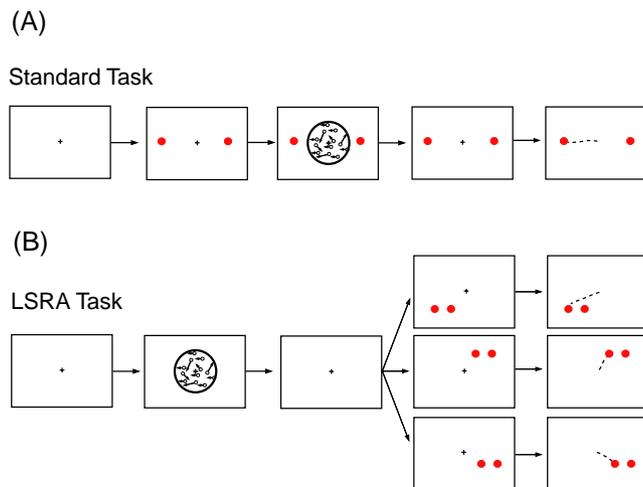


Fig. 1. (A) The standard direction discrimination task. Three hundred milliseconds after the monkey acquired the fixation point (panel 1), a pair of saccade targets appeared (panel 2). After a variable delay of 500–900 ms, a 7° diameter random dot motion stimulus appeared (panel 3), usually centered on the fixation point. Coherent motion flowed toward one of the two targets. The stimulus movie lasted 2 s and was followed by an additional 1–1.5 s delay period (panel 4). Once the fixation point was extinguished, the monkey made a saccade (dashed line in panel 5) to that target which lay in the remembered direction of motion. (B) The loose stimulus-response association task. Three hundred milliseconds after the monkey acquired the fixation point (panel 1) the random dot motion stimulus appeared (panel 2) for 1 s. After a 1–2 s delay period (panel 3), a pair of targets appeared in a random location (panel 4). The fixation point disappeared 1–1.5 s later (panel 5), whereupon the monkey made a saccade to that target which lay in the direction of motion relative to the location of the other target. Target positions were balanced so that any given operant saccade was equally likely to be associated with either direction of stimulus motion. Thus, the direction of stimulus motion (panel 2) provided no information about the metrics of the correct operant saccade.

of passive fixation trials in which no saccades were necessary. The monkey was rewarded in these trials only for maintaining accurate fixation on the central fixation point; no saccade targets appeared and fixation breaks resulted in brief time-out periods. In the passive fixation blocks, therefore, the direction-selective responses are unlikely to result from a saccade plan or motor set. In addition, we conducted a series of control experiments to rule out the possibility that the direction-selective responses resulted from “covert” saccade planning in the absence of an overt eye movement [10]. Thus, the direction selectivity of these neurons appears to be due to visual inputs originating from the random dot motion stimulus.

We hypothesized that the direction-selective visual responses reflect a learned sensorimotor link dictated by the logic of our direction discrimination task. Because the monkeys learned through extensive training that visual motion in a particular direction required a saccadic eye movement in the same direction, we suggest that neural circuits were modified during learning so as to facilitate this stereotyped visuomotor transformation. To test this hypothesis, we searched for direction-selective visual responses in two other monkeys

that had been trained to perform a loose stimulus-response association (LSRA) task, illustrated in Fig. 1B [8]. This task is similar to the standard direction discrimination task in that it requires monkeys to discriminate the direction of motion in a random dot stimulus and to report the judgment by making a saccade to one of two targets. Importantly, however, in the LSRA task the direction of the operant saccade was dissociated from the direction of motion in the visual stimulus. Thus, the monkey could not predict the metrics of the operant saccade during the presentation of the motion stimulus and could not plan the correct operant saccade.

In both tasks the geometry of the display was arranged so that the axis of motion was aligned with the cell’s movement field, and the motion direction varied pseudorandomly from trial to trial. The stimulus subtended 7° of visual angle and had a density of 15 dots/ $^\circ^2$ per s. On each frame of the stimulus movie, a specified percentage of dots moved in a particular direction, comprising a “coherent” motion signal. The remaining dots were flashed at random locations, creating a masking motion noise. The monkey’s task was to discriminate the direction of the coherent motion signal. In the standard task, the percentage of dots carrying the coherent motion signal varied from 0 to 51.2%, spanning psychophysical threshold. In the LSRA task, the percentage of coherent dots was fixed at 51.2%. To measure visual responses during passive fixation trials, we presented 51.2% coherent stimuli for 1–2 s at the center of gaze. We obtained at least six repetitions each of motion toward and away from the movement field for each neuron tested. Experimental procedures conformed to standards established by the National Institutes for Health and were approved by the Institutional Animal Care and Use Committee of Stanford University. Eye position was monitored by the scleral search coil technique [14], and was required to be within an electronically-defined $3^\circ \times 3^\circ$ window during fixation.

We used slightly different procedures to select neurons for study in the standard and LSRA direction discrimination tasks. For monkeys that performed the standard task, we qualitatively assessed each neuron’s activity as the monkey performed the discrimination task. If the firing rate during the stimulus presentation and subsequent delay period varied systematically with the monkey’s choice (if the activity was “choice-predictive”), we collected direction-tuning data in a separate block of passive fixation trials. Roughly one-third of the neurons we encountered in the intermediate and deep layers of the SC responded this way.

We could not use precisely the same criterion to select cells in the LSRA task monkeys, because these monkeys did not perform the standard task. Instead we selected neurons on the basis of choice-predictive activity in the LSRA task. Choice predictive neurons in the LSRA task, however, accounted for only $\sim 10\%$ of the SC neurons we encountered, raising the unsettling possibility that they were a fundamentally different population from those we had studied in the standard task. We, therefore, used a memory-guided saccade task as a supplemental criterion for selecting neurons in

the LSRA monkeys. Neurons with choice-predictive activity in the standard task also tended to have sustained activity during the delay period of a memory-guided saccade task (Horwitz and Newsome, unpublished observations). Thus, we could study an equivalent population in the LSRA monkeys by selecting neurons that yielded sustained delay period activity in the memory-guided saccade task, whether or not they had choice-predictive activity in the LSRA task. Approximately one-third of the SC neurons we encountered satisfied one or both of these criteria (choice-predictive activity in the LSRA task or delay period activity in the memory-guided saccade task), and as we will show, our results did not depend critically on which of these criteria we used.

Fig. 2A shows the responses of a single neuron from a monkey trained on the standard version of our direction discrimination task. Trials on the left are those in which motion flowed toward the movement field; trials on the right are those in which motion flowed in the opposite direction. This cell responded to the stimulus in a highly direction-selective manner: motion toward the movement field excited the cell strongly whereas motion in the opposite direction suppressed it.

Fig. 2B shows the responses of a single neuron from a monkey trained on the LSRA task. As in Fig. 2A, firing rates were higher when motion flowed toward the movement field than away from it. However, direction selectivity was much weaker in this cell than in the one shown in Fig. 2A.

To quantify direction selectivity, we computed an ROC curve from neural responses to the two directions of mo-

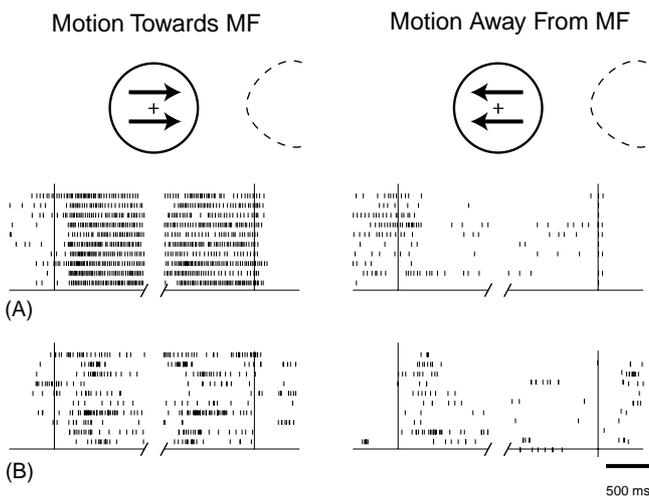


Fig. 2. Visual responses during the passive fixation task. The visual motion stimulus (circle with arrows) appeared at the fixation point (cross) and flowed either toward (left column) or away from (right column) the movement field (dashed curve) on pseudorandomly interleaved trials. (A) Visual responses from an SC cell recorded from a monkey trained on the standard task. (B) Visual responses from an SC cell recorded from a monkey trained on the LSRA task. Within each panel, responses are aligned on stimulus onset (left) and stimulus offset (right), with small gaps in the rasters to permit simultaneous alignment of trials with unequal stimulus durations.

tion [3]. The area under the ROC curve was defined as the direction-tuning index for the cell. This direction-tuning index assumes a value of “1” if motion toward the movement field always elicited a stronger response than motion in the opposite direction, “0” if the reverse is true, and “0.5” if the two directions of motion elicited similar firing rates. The cell in Fig. 2A had an index of 1.00 and the cell in Fig. 2B had an index of 0.88, which were among the largest we recorded for monkeys trained on the standard task and the LSRA task, respectively.

Direction-tuning indices were consistently higher in monkeys trained on the standard task (Fig. 3A) than in monkeys trained on the LSRA task (Fig. 3B). The difference in direction-tuning indices between tasks was highly significant (Mann–Whitney U -test: $P < 0.0001$). Furthermore, this difference was largely maintained when we restricted our attention to individual pairs of monkeys, indicating that no single animal was responsible for the observed effect (four Mann–Whitney U -tests, $P < 0.05$, two Mann–Whitney tests

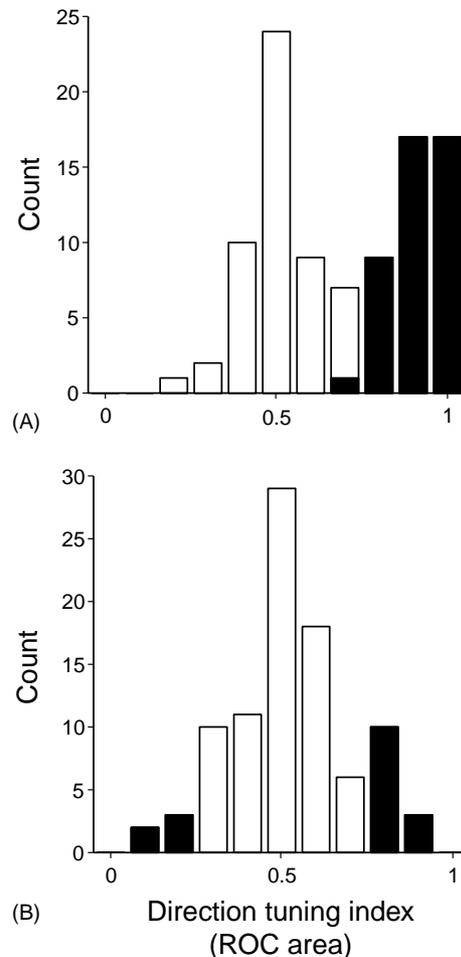


Fig. 3. Distribution of direction-tuning indices for (A) standard task monkeys and (B) LSRA task monkeys. Individual cells with statistically significant direction-tuning are represented by filled bars (randomization test: $P < 0.05$). The mean index for the standard task monkeys, 0.70, was significantly greater than the mean index for the LSRA monkeys, 0.53 (Mann–Whitney U -test: $P < 0.0001$).

$P < 0.1$). Similarly, this difference was maintained if we considered only cells with choice predictive activity in the LSRA task ($P < 0.05$) or only cells with delay period activity in the memory-guided saccade task ($P < 0.01$). We conclude that strongly direction-selective visual responses in intermediate and deep layer SC neurons occur in monkeys trained on the standard direction discrimination task, but not in monkeys trained on the LSRA task.

Direction-tuning indices for LSRA monkeys, although small, were significantly greater than “0.5”, the value expected by chance (one-tailed Wilcoxon test: $P < 0.05$). Thus, these cells, like those recorded from standard task monkeys, preferred visual motion flowing towards the movement field than away from it, but the directional bias was very weak in the LSRA monkeys. One possibility is that this weak directional response reflects the allocation of visual attention in the direction of visual motion.

The difference in direction selectivity between the two groups of monkeys likely arises from the difference in the stimulus-response associations in the standard and LSRA tasks. In the standard task, the correct saccade was always in the direction of motion, and the monkey could plan the operant saccade immediately upon making the direction discrimination. In the LSRA task, the direction of the correct saccade was independent of the motion direction, and the monkey did not know the metrics of the required saccade until well after the stimulus had disappeared. Thus, standard task monkeys were trained to associate visual motion near the center of gaze with a saccade in the direction of motion, but LSRA monkeys were not. The direction-selective visual responses we observed in the standard task monkeys appear to be a neural manifestation of the behavioral association that these monkeys had learned.

The superior colliculus is closely involved in orienting movements of the eyes and head, but it carries a variety of sensory signals as well as motor signals (for a review see [19]). These sensory signals appear to be those that are important for guiding orienting movements. Outside the laboratory, flashes of light, sudden noises, and tactile vibrations attract saccades, and such stimuli are potent for many intermediate and deep layer SC neurons [6,13,20]. Inside our laboratory, saccade metrics were instructed by the direction of motion in a random dot motion stimulus. One possibility is that neurons that were direction-selective in our hands may integrate a variety of inputs each of which contributes to the likelihood that a saccade into movement field will occur. For instance, such neurons might be expected to become color-selective in a task in which the metrics of the operant saccade are given by the stimulus color, texture-sensitive in tasks in which stimulus texture is the key variable, etc. These neurons may also carry non-sensory signals that contribute to saccade preparation such as signals relating to bias, recent reward history, etc. [1,9,12].

Our results contribute to a growing body of evidence that consistent association between stimulus and response induces sensory signals in motor areas. Neurons in the lat-

eral intraparietal area (LIP), the frontal eye fields (FEF), and the supplementary eye fields (SEF) are involved in saccade planning and execution, and they can carry sensory signals that depend on the training that the animal has received [2,4,7,18]. Task training thus appears to be a key determinant of sensory response properties in motor areas of the brain. This observation provides important constraints for models of how sensory signals are processed into motor commands, and suggests that task training be considered when interpreting responses to sensory stimuli.

Acknowledgements

We thank J. Stein, J. Riehl, C. Doane, and A. Millous for technical assistance during the course of this study. W.T. Newsome is an Investigator at the Howard Hughes Medical Institute. G.D. Horwitz was supported by a graduate research fellowship from the Office of Naval Research and by the National Institute of Mental Health (grant no. MH-17047). Research in this laboratory is also supported by the National Institute of Health (grant no. EY-05603).

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