
The control of upright standing is accomplished through the integration of different sources of sensory information and by providing an appropriate motor program to control both expected and unexpected perturbations imposed on the system. However, the dynamic characteristics of postural sway and its interplay with the regulation of Ia sensory information within the spinal cord are largely unknown. Here, using a stochastic technique for analyzing the dynamics of upright standing, we demonstrate that the changes in the dynamics of postural sway were accompanied by modulation of the soleus H-reflex during quiet standing. While the causality of this relation was not established, the results showed that these changes were independent of the sway of the center of pressure and were bidirectional and purposeful. With this novel perspective, the appropriate reflex gain, which is important for balance control, can be predicted from the dynamic characteristics of postural sway. Our current findings provide the first human behavioral evidence to suggest the contribution of the spinal cord in fulfilling the desired motor programming of a complex task. This contribution is, by conventional guess, carried out through interneuronal adjustments, which are under the control of different brain areas.

2. **Jansen ME, Begley CG, Himebaugh NH, Port NL.** Effect of contact lens wear and a near task on tear film break-up. *Optom Vis Sci.* 2010 May;87(5):350-7. PMID:20351601

**PURPOSE:** To study the effect of extrinsic controls on blinking by examining blink parameters and tear stability among adapted soft contact lens (CL) wearers performing tasks that require varying amounts of visual concentration.

**METHODS:** The Demographic Questionnaire, Contact Lens Dry Eye Questionnaire, and Current Symptoms Questionnaire were completed by 15 adapted soft CL wearers (nine females). Three 55 s simultaneous measurements of tear film stability via retroillumination and blinking were obtained with a slit-lamp biomicroscope and 200 Hz video camera while subjects listened to music and played a video game with and without their habitual CLs. Interblink interval (IBI) and blink amplitude (BA) were calculated. The area of break-up (AB) was calculated for the retroillumination image before each blink. The Current Symptoms Questionnaire was completed four times throughout testing.

**RESULTS:** With the game compared to music, IBI was significantly longer and BA significantly decreased without CLs (p < or = 0.001). With CLs, the IBI did not significantly change between tasks but the BA significantly decreased (p = 0.100). The AB significantly increased with CL and the game (paired t-test, p < or = 0.001). The BA was significantly correlated with self-reported severity of dry eye for all testing scenarios (Spearman r > or = 0.5579, p < 0.0001) and several symptom measures (Spearman r > or = 0.6262, p < 0.0001). The AB was significantly correlated with symptom measures including bothersome discomfort for the game with and without CLs (Spearman r > or = 0.5064, p < 0.0001).

**CONCLUSIONS:** During tasks requiring concentration, the IBI increased (blink rate decreased) and many blinks were incomplete without CLs. With CLs, tear film instability increased. Blinking frequency also increased, but it remained high when subjects played the game, and symptoms of ocular irritation increased. This suggests that wearing soft CLs, even when fully adapted, provides enough extrinsic ocular surface stimulation to override internal controls and affect blink parameters.


The superior colliculus (SC) of the monkey has been shown to be involved in not only initiation of saccades but in the selection of the target to which the saccade can be directed. The present
experiments examine whether SC neuronal activity related to target selection is also related to saccade generation. In an asynchronous target task, the monkey was required to make a saccade to the first of two spots of light to appear. Using choice probability analysis over multiple trials, we determined the earliest time at which neurons in the SC intermediate layers indicated target selection. We then determined how closely the neuronal selection was correlated to saccade onset by using our asynchronous reaction time task, which allowed the monkey to make a saccade to the target as soon as the selection had been made. We found that the selection became evident at widely differing times for different neurons. Some neurons indicated target selection just before the saccade (close to the presaccadic burst of activity), others did so at the time of the visual response, and some showed an increase in their activity even before the target appeared. A fraction of this pre-stimulus bias resulted from a priming effect of the previous trial; a saccade to the target in the movement field on the previous trial produced both a higher level of neuronal activity and a higher probability for a saccade to that target on the current trial. We found that most of the neurons (76%) showed a correlation between selection time and reaction time. Furthermore, within this 76% of neurons, many indicated a selection very early during the visual response. There was no evidence of a sequence from target selection first and saccade selection later, but rather that target selection and saccade initiation are intertwined and are probably inseparable.


The visual world presents multiple potential targets that can be brought to the fovea by saccadic eye movements. These targets produce activity at multiple sites on a movement map in the superior colliculus (SC), an area of the brain related to saccade generation. The saccade made must result from competition between the populations of neurons representing these many saccadic goals, and in the present experiments we used multiple moveable microelectrodes to follow this competition. We recorded simultaneously from two sites on the SC map where each site was related to a different saccade target. The two targets appeared in rapid sequence, and the monkey was rewarded for making a saccade toward the one appearing first. Our study concentrated on trials in which the monkey made strongly curved saccades that were directed first toward one target and then toward the other. These curved saccades activated both sites on the SC map as they veered from one target to the other. The major finding was that the strongly curved saccades were preceded by sequential activity in the two neurons as indicated by three observations: the firing rate for the neuron related to the first target reached its peak earlier than did the rate of the neuron for the second target; the timing of the peak activity of the two neurons was related to the beginning and end of the saccade curvature; a weighted vector-average model based on the activity of the two neurons predicted the timing of saccade curvature. Straight averaging saccades ended between the targets so that they did not go to either target, and they were accompanied by simultaneous rather than sequential activation of the two neurons. Thus when multiple populations of neurons are active on the SC movement map, the resulting saccade is determined by the relative timing of the activity in the populations as well as their magnitude. In contrast, SC activity at the two sites did not predict the final direction of the saccade, and several control experiments found insufficient activity at other sites on the SC map to account for that final direction. We conclude that the SC neuronal activity predicts the timing of the saccade curvature, but not the final direction of the trajectory. These observations are consistent with SC activity being critical in selecting the goal of the saccade, but not in determining the exact trajectory.

Animals control contact with surfaces when locomoting, catching prey, etc. This requires sensorily guiding the rate of closure of gaps between effectors such as the hands, feet or jaws and destinations such as a ball, the ground and a prey. Control is generally rapid, reliable and robust, even with small nervous systems: the sensorimotor processes are therefore probably rather simple. We tested a hypothesis, based on general tau theory, that closing two gaps simultaneously, as required in many actions, might be achieved simply by keeping the taus of the gaps coupled in constant ratio. Tau of a changing gap is defined as the time-to-closure of the gap at the current closure-rate. General tau theory shows that tau of a gap could, in principle, be directly sensed without needing to sense either the gap size or its rate of closure. In our experiment, subjects moved an effector (computer cursor) to a destination zone indicated on the computer monitor, to stop in the zone just as a moving target cursor reached it. The results indicated the subjects achieved the task by keeping tau of the gap between effector and target coupled to tau of the gap between the effector and the destination zone. Evidence of tau-coupling has also been found, for example, in bats guiding landing using echolocation. Thus, it appears that a sensorimotor process used by different species for coordinating the closure of two or more gaps between effectors and destinations entails constantly sensing the taus of the gaps and moving so as to keep the taus coupled in constant ratio.

Two rhesus monkeys were trained to intercept a moving target at a fixed location with a feedback cursor controlled by a 2-D manipulandum. The direction from which the target appeared, the time from the target onset to its arrival at the interception point, and the target acceleration were randomized for each trial, thus requiring the animal to adjust its movement according to the visual input on a trial-by-trial basis. The two animals adopted different strategies, similar to those identified previously in human subjects. Single-cell activity was recorded from the arm area of the primary motor cortex in these two animals, and the neurons were classified based on the temporal patterns in their activity, using a nonhierarchical cluster analysis. Results of this analysis revealed differences in the complexity and diversity of motor cortical activity between the two animals that paralleled those of behavioral strategies. Most clusters displayed activity closely related to the kinematics of hand movements. In addition, some clusters displayed patterns of activation that conveyed additional information necessary for successful performance of the task, such as the initial target velocity and the interval between successive submovements, suggesting that such information is represented in selective subpopulations of neurons in the primary motor cortex. These results also suggest that conversion of information about target motion into movement-related signals takes place in a broad network of cortical areas including the primary motor cortex.

The single-unit activity of 831 cells was recorded in the arm area of the motor cortex of two monkeys while the monkeys intercepted a moving visual stimulus (interception task) or remained immobile during presentation of the same moving stimulus (no-go task). The moving target traveled on an oblique path from either lower corner of a screen toward the vertical meridian, and its movement time (0.5, 1.0, or 1.5 sec) and velocity profile (accelerating, decelerating, or constant velocity) were pseudorandomly varied. The moving target had to be intercepted within 130 msec of target arrival at an interception point. By comparing motor cortical activity at the single-neuron and population levels between the interception and no-go tasks, we tested whether information about parameters of moving target is represented in the primary motor cortex to generate appropriate motor responses. A substantial
number of neurons displayed modulation of their activity during the no-go task, and this activity was often affected by the stimulus parameters. These results suggest a role of motor cortex in specifying the timing of movement initiation based on information about target motion. In addition, there was a lack of systematic relation between the onset times of neural activity in the interception and no-go tasks, suggesting that processing of information concerning target motion and generation of hand movement occurs in parallel. Finally, the activity in the most motor cortical neurons was modulated according to an estimate of the time-to-target interception, raising the possibility that time-to-interception may be coded in the motor cortical activity.


The monkey superior colliculus (SC) has maps for both visual input and movement output in the superficial and intermediate layers, respectively, and activity on these maps is generally related to visual stimuli only in one part of the visual field and/or to a restricted range of saccadic eye movements to those stimuli. For some neurons within these maps, however, activity has been reported to spread from the caudal SC to the rostral SC during the course of a saccade. This spread of activity was inferred from averages of recordings at different sites on the SC movement map during saccades of different amplitudes and even in different monkeys. In the present experiments, SC activity was recorded simultaneously in pairs of neurons to observe the spread of activity during individual saccades. Two electrodes were positioned along the rostral-caudal axis of the SC with one being more caudal than the other, and 60 neuron pairs whose movement fields were large enough to see a spread of activity were studied. During individual saccades, the relative time of discharge of the two neurons was compared using 1) the time difference between peak discharge of the two neurons, 2) the difference between the "median activation time" of the two neurons, and 3) the shift required to align the two discharge patterns using cross-correlation. All three analysis methods gave comparable results. Many pairs of neurons were activated in sequence during saccade generation, and the order of activation was most frequently caudal to rostral. Such a sequence of activation was not observed in every neuron pair, but over the sample of neuron pairs studied, the spread was statistically significant. When we compared the time of neuronal activity to the time of saccade onset, we found that the caudal neuronal activity was more likely to be before the saccade, whereas the rostral neuronal activity was more likely to be during the saccade. These results demonstrate that when individual pairs of neurons are examined during single saccades there is evidence of a caudal to rostral spread of activity within the monkey SC, and they confirm the previous inferences of a spread of activity drawn from observations on averaged neuronal activity during multiple saccades. The functional contribution of this spread of activity remains to be determined.


We analyzed the magnitude and interneuronal correlation of the variability in the activity of single neurons that were recorded simultaneously using a multielectrode array in the primary motor cortex and parietal areas 2/5 in rhesus monkeys. The animals were trained to move their arms in one of eight directions as instructed by a visual target. The relationship between variability (SD) and mean of the discharge rate was described by a power function with a similar exponent (~ approximately 0.57), regardless of the cortical area or the behavioral condition. We examined whether the deviation from mean activity between target onset and the end of the movement was correlated on a trial-by-trial basis with variability in activity during the hold period before target onset. In both cortical areas, for about a quarter of the neurons, the neuronal noise of these two periods was positively correlated,
significant negative correlations were seldom observed. Overall, neurons with higher signal correlation (i.e., similar directional pattern) showed higher noise correlation in both cortical areas. On the other hand, when the data were divided according to the distance between the electrode tips from which the neurons were recorded, a consistent relationship between the signal and noise correlations was found only for pairs of neurons recorded through the same electrode. These results suggest that nearby neurons with similar directional tuning carry primarily redundant messages, whereas neurons in separate cortical columns perform more independent processing.


We studied the kinematic characteristics of arm movements and their relation to a stimulus moving with a wide range of velocity and acceleration. The target traveled at constant acceleration, constant deceleration, or constant velocity for 0.5-2.0 s, until it arrived at a location where it was required to be intercepted. For fast moving targets, subjects produced single movements with symmetrical, bell-shaped velocity profiles. In contrast, for slowly moving targets, hand velocity profiles displayed multiple peaks, which suggests a control mechanism that produces a series of discrete submovements according to characteristics of target motion. To analyze how temporal and spatial aspects of these submovements are influenced by target motion, we decomposed the vertical hand velocity profiles into bell-shaped velocity pulses according to the minimum-jerk model. The number of submovements was roughly proportional to the movement time, resulting in a relatively constant submovement frequency (approximately 2.5 Hz). On the other hand, the submovement onset asynchrony showed significantly more variability than the intersubmovement interval, indicating that the submovement onset was delayed more following a submovement with a longer duration. Examination of submovement amplitude and its relation to target motion revealed that the subjects achieved interception mainly by producing a series of submovements that would keep the displacement of the hand proportional to the first-order estimate of target position at the end of each submovement along the axis of hand movement. Finally, we did not find any evidence that information regarding target acceleration is properly utilized in the production of submovements.


We investigated the capacities of human subjects to intercept moving targets in a two-dimensional (2D) space. Subjects were instructed to intercept moving targets on a computer screen using a cursor controlled by an articulated 2D manipulandum. A target was presented in 1 of 18 combinations of three acceleration types (constant acceleration, constant deceleration, and constant velocity) and six target motion times, from 0.5 to 2.0 s. First, subjects held the cursor in a start zone located at the bottom of the screen along the vertical meridian. After a pseudorandom hold period, the target appeared in the lower left or right corner of the screen and traveled at 45 degrees toward an interception zone located on the vertical meridian 12.5 cm above the start zone. For a trial to be considered successful, the subject's cursor had to enter the interception zone within 100 ms of the target's arrival at the center of the interception zone and stay inside a slightly larger hold zone. Trials in which the cursor arrived more than 100 ms before the target were classified as "early errors," whereas trials in which the cursor arrived more than 100 ms after the target were classified as "late errors." Given the criteria above, the task proved to be difficult for the subjects. Only 41.3% (1080 out of 2614) of the movements were successful, whereas the remaining 58.7% were temporal (i.e., early or late) errors. A large majority of the early errors occurred in trials with decelerating targets, and their percentage tended to increase with longer target motion times. In contrast, late errors occurred in relation to all three target acceleration types, and their percentage tended to decrease with longer target motion times. Three models of movement
initiation were investigated. First, the threshold-distance model, originally proposed for optokinetic eye movements to constant-velocity visual stimuli, maintains that response time is composed of two parts, a constant processing time and the time required for the stimulus to travel a threshold distance. This model only partially fit our data. Second, the threshold-tau model, originally proposed as a strategy for movement initiation, assumes that the subject uses the first-order estimate of time-to-contact (tau) to determine when to initiate the interception movement. Similar to the threshold distance model, the threshold-tau model only partially fit the data. Finally, a dual-strategy model was developed which allowed for the adoption of either of the two strategies for movement initiation; namely, a strategy based on the threshold-distance model ("reactive" strategy) and another based on the threshold-tau model ("predictive" strategy). This model provided a good fit to the data. In fact, individual subjects preferred to use one or the other strategy. This preference was allowed to be manifested at long target motion times, whereas shorter target motion times (i.e., 0.5 s and 0.8 s) forced the subjects to use only the reactive strategy.


Single-neuron responses in motor and premotor cortex were recorded during a movement-sequence delay task. On each trial the monkey viewed a randomly selected sequence of target lights arrayed in two-dimensional space, remembered the sequence during a delay period, and then generated a coordinated sequence of movements to the remembered targets. Of 307 neurons studied, 25% were tuned specifically for either the first or the second target, but not both. In particular, for neurons tuned during both target presentations, tuned activity related to a particular first target direction were maintained during the presentation of a second target in a different direction. During the delay period, 32% of the neurons were tuned for upcoming movement in a single direction. These delay period responses often reflected activity patterns that first developed during target presentations and may therefore act to maintain target period information during the delay. Neurons with tuned activity during both the delay and movement periods exhibited two patterns: the first exhibited tuned responses during the delay that were correlated with the tuning of first-movement responses, while the second pattern showed delay-period tuning that was better correlated with tuned responses during second movements. This indicates that, before movement, distinct neural populations are correlated with specific movements in a sequence. About half the neurons studied were not directionally tuned during the initiation, target, or delay periods, but did show systematic changes in activity during task performance. Some (34%) were exclusively tuned during movement and appear to be involved in the direct control of movement. Others (17%) showed changes in firing rate from period to period within a trial but showed no directional preference for a particular direction of movement. Population analyses of tuned activity during the target and delay periods indicated that accurate directional information about both first and second movements was available in the neuronal ensemble well before reaching began. These results extend the idea that both motor and premotor cortex play a role in reaching behavior other than the direct control of muscles. While some early neural responses resembled muscle activation patterns involved in maintaining fixed postures before movement, others probably relate to the sensory-to-motor transformations, information storage in short-term memory, and movement preparation required to generate accurate reaching to remembered locations in space.


Human subjects were instructed to intercept with a cursor real and apparent motion targets presented on a computer screen. Targets traveled counterclockwise (CCW) in a circle at one of five angular
velocities (180, 300, 420, 480 and 540 deg/s), either smoothly (real motion) or in path-guided apparent motion. Subjects operated a computer mouse and were instructed to intercept targets at the 12 o'clock position; there were no constraints on when to initiate the response, which was a movement from the center of the screen towards and past 12 o'clock. We found the following: (a) for both motion conditions and all target velocities, subjects were late in intercepting the target, especially at higher target velocities; (b) for both motion conditions, the directional variability of the response increased as a linear function of the target velocity; (c) the directional variability of the response was systematically higher for the apparent than the real motion condition; there was no significant interaction between target velocity and target motion type; (d) the response time did not vary significantly with velocity, but was consistently longer for apparent than real motion targets; (e) the movement time was very similar for different target velocities; and (f) the moment of initiation of the interception movement was delayed appreciably at higher target velocities, relative to that dictated for perfect interception at a given target velocity. This delay was greater for the apparent motion target. These results demonstrated the following: (a) for both target motion conditions, interception was not fully predictive but lagged the target in spite of the constant target velocity and the unconstrained time allowed for initiating the interception movement; (b) subjects can intercept an apparent motion target but, compared with real motion, the performance is somewhat degraded overall; (c) the similarities in performance between the two target motion conditions, and the fact that target velocity influenced performance in a similar fashion, suggest that the motor system can access the visual information provided by the moving target; and (d) since movement time was similar for different target velocities, the strategy for interception relied on controlling the moment of initiation of the interception movement. This was successful for low target velocities but became unsuccessful at higher target velocities.