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Spatiotemporal Motor Processing[a]

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INTRODUCTION

Many studies of motor function deal with essentially static aspects of motor control; for example, the representation of motor output in maps,[1] the encoding of motor parameters in the discharge of single cells,[2,3] and the effect of behavioral context on neuronal activity.[4] These questions do not encompass time as a crucial variable. However, actual motor performance always evolves in time. Moreover, daily activities, from eating to playing, depend critically on efficient processing of sensorimotor information. The devastating effect of a general slowness of this processing can be seen in patients with Parkinson's disease who, without medication, are quite incapacitated in practically all everyday activities. In this paper we focus on the spatiotemporal processing of sensory–motor information in the motor cortex and the basal ganglia within the context of simple motor acts, such as movements to a target, as well as in more complicated tasks, such as mental rotation. Moreover, we treat the temporal processing of movements more formally within the context of information theory.

BASAL GANGLIA

Perhaps the most striking example of abnormality in temporal sensory motor processing is seen in the clinical syndrome exhibited by patients with Parkinson's disease. Simple movements of the limb take much longer than normal, while simultaneous or sequential movements are particularly impaired.

Simple Limb Movements

A reduction in speed, of even the most simple movements, is one of the most consistent findings in Parkinson's disease.[5–8] Although movements of small amplitude are often completed within a time comparable to normal subjects, those of larger amplitude take significantly longer. Normal subjects tend to take the same amount of time to perform small- and large-amplitude movements, and achieve this by

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increasing the speed proportionately to the amplitude of the movement.[9] There are a number of possible explanations why this strategy is not used in Parkinson's disease.

(1) Patients with Parkinson's disease rely substantially on visual information, and when making movements to a visual target they perform "closed-loop," continually comparing the progress of the movement to the position of the target, thus reducing the speed.[7] In tasks where the movements are to be performed as quickly as possible, thus not allowing time for modification of motor output based on sensory feedback, Parkinson's disease patients are very inaccurate, particularly in larger movements. When there are no temporal restrictions, the large movements are performed as accurately as those of controls. In Parkinson's disease the speed–accuracy tradeoff is exaggerated, with the result that movements of a given accuracy take a longer time, and, conversely, attempted fast movements are very inaccurate.[7,10] In terms of the formulation of this question by Fitts,[11] Parkinson's disease patients show very low rates of information transmitted by their movements (see below).

(2) The initial burst of electromyographic (EMG) activity in agonist muscles is reduced, thus requiring a number of additional bursts of activity in order to reach the target.[9] Some scaling of initial agonist EMG activity does occur for movements of increasing amplitude, but the overall amount consistently falls short of that required to execute the movement at normal speed.[12] The temporal sequence and the duration of activation of agonist and antagonist muscles is normal.

(3) There is perhaps an impairment in planning or predicting upcoming motor behavior in Parkinson's disease. When given a set of visual and other sensory cues, normal subjects are able to predict or plan a movement in advance, so that it can then be generated quickly and accurately. Is it perhaps the inability to predict in this fashion in Parkinson's disease that leads to continuous monitoring of movement during its execution, with the inevitable slow or inaccurate result? This possibility has been tested in Parkinson's disease by assessing the ability to predict movement or motion in the external world. Patients were asked to follow a target that moved across a screen at a constant speed and changed directions in a predictable fashion. The target disappeared from the screen at certain points and the subjects had to move the cursor as if the target were still visible. Patients with Parkinson's disease had difficulty in accurately predicting the rate of target movement and the changes in direction.[13] However, it was found in other studies that Parkinson's disease patients were similar to controls in the continuous tracking of predictable or unpredictable target movement.[14,15]

The studies just reviewed have examined simple movements, usually across a single joint, and that they do not accurately reflect the disability experienced by patients is perhaps no surprise. We normally perform unconstrained movements using multiple joints in three-dimensional space. Abnormalities in the performance of simultaneous and sequential movements more closely reflect the degree of disability experienced by patients with Parkinson's disease, and underline the fact that deficits in the temporal processing of motor output is a major feature of the disease.

Simultaneous Movements

We normally perform simultaneous movements effectively and efficiently: indeed this is a normal part of our everyday motor repertoire. When driving a car, for example, it is vital to be able to engage the clutch with the left leg while moving the gear stick with the right hand. This ability to perform simultaneous movements is impaired in Parkinson's disease, and can lead to interference between two simultaneous tasks, so that the time taken to perform each task increases compared to the time for each task performed separately. In some cases the interference is such that one task stops completely. Schwab *et al.*[16] had patients draw with the nondominant hand while squeezing a bulb with the other hand, and found that the patients resisted doing the tasks simultaneously. In another study[17] patients were asked to press a counter with one hand while using a tweezers to pick up beads with the other; in this case, the patients avoided the counter press and concentrated on the beads. More recently Benecke *et al.*[18] have studied patients with Parkinson's disease, using tasks of equal complexity (elbow flexion, squeezing of an isometric force transducer, and finger flexion) executed by the same or different arms. There was an increase in movement time during the simultaneous performance of any two tasks, and this was most marked when the two tasks were combined in the same arm.

Sequential Movements

Many of our movements are part of a movement sequence, such as the sequential movements required to rise from a sitting position. In fact very few of our movements occur in isolation. These movement sequences, which are performed "automatically" by most people, cause great difficulty for patients with Parkinson's disease. The possible reasons for this were examined by Benecke *et al.*[19] in an experiment where patients with Parkinson's disease were required to perform three simple movements sequentially in various combinations. The interval between movements in the sequence was twice that seen in controls. The separate movements within a sequence were executed more slowly than when performed in isolation. The problem with sequential movements in Parkinson's disease is threefold: (1) the component movements are slower than normal when performed in isolation, (2) within a movement sequence the time taken to perform each component is increased, and (3) the time interval between each component in the sequence is also increased.

Neural Studies

Most neurons in the basal ganglia neurons change activity after the onset of EMG activity,[3,20–22] and have probably little to do with the initiation of movement in reaction-time (RT) tasks. Georgopoulos *et al.*[3] studied the relations between neural activity in the globus pallidus and the subthalamic nucleus, and parameters of movement in a task constrained to one dimension but allowing movements of different amplitudes in two directions. Significant relations were found for the direction, amplitude, and peak velocity of the movement. For movements in a particular direction, the discharge of many cells was related in a linear fashion to the amplitude of the movement. In these cases, given the rate of cell discharge, it would be possible to predict the amplitude of the movement. This relation was most significant during the movement, but was also evident in the discharge rate of the cells during 100 ms immediately prior to the movement. It appears that there was a gain in information after the beginning of the movement, resulting in a greater number of cells having a relation to movement amplitude. This relation of neuronal activity in the basal ganglia to the amplitude of movement is somehow the positive image of the negative condition in Parkinson's disease, namely the inability to produce large movements in a single step.

MOTOR CORTEX

Cells in the motor cortex typically change activity well before the beginning of the movement. Therefore, this structure, together with the cerebellum,[23] is involved in the initiation of movement in RT tasks. Studies of motor cortical cell activity during two- or three-dimensional reaching movements have shown a clear relation to the direction of movement in space,[2,24] and less so to its amplitude.[25–29]

Coding of Directional Information

The investigation of the relations of neural activity to direction is complicated by the fact that direction is not a linear variable but a closed circular (or spherical) variable. There are basically two ways to represent direction: one is to allocate specific cells to represent specific directions, and the other is to represent direction in an ensemble of cells. In the first case, reaching in the intended direction would be initiated by recruiting cells possessing the appropriate directionality, whereas in the second case the whole ensemble would be engaged in such a way that direction would be represented unambiguously in the ensemble. The results of experimental studies[2,24] proved the second idea to be correct. Indeed, most cells are active with movements in different directions, which means that for a movement in a particular direction a whole neuronal population is engaged; therefore, the direction of an intended movement is represented in the population. The question then is what is the nature of this representation and whether it is unambiguous and operationally useful.

A clue for the solution of this problem came from the directional tuning function of single-cell activity. This function has three basic characteristics: (a) it is broad, which means that cell activity varies throughout the range of directions, in both two-dimensional and three-dimensional space; (b) it is orderly and can be described well by a cosine function,[2,24] and (c) it is symmetric and unimodal, which means that there is a direction for which cell activity will be highest (the cell's "preferred direction"); the preferred directions differ for different cells and range throughout the whole directional continuum.[24] It follows from these characteristics of the directional tuning curve that, except at the peak, the directional information provided by cell activity is ambiguous, for the same discharge rate can correspond to two different directions.

The broad directional tuning of single-cell activity indicates that a given cell participates in movements of various directions and that, conversely, a movement in a particular direction will involve the activation of a whole population of cells: how, then, is the direction of reaching represented in a unique fashion in a population of neurons each of which is directionally broadly tuned? An unambiguous population code was proposed[30–32] that regarded the motor cortical command for the direction of reaching as an ensemble of vectors. Each vector represents the contribution of a directionally tuned cell. A particular vector points in the cell's preferred direction and has length proportional to the change in cell activity associated with a particular movement direction: then the vector sum of these weighted cell vectors (the "neuronal population vector") points at or near the direction of the movement.[30–32] Therefore, information concerning the direction of movement can be unambiguously obtained from the neuronal ensemble. This provides a tool with which to monitor the processing of directional information in time, that is, while the movement is intended.

Temporal Processing of Directional Information

There are several aspects of intending a movement: (a) The commonest case is when a movement is produced as soon as a stimulus appears. Under these circumstances there is a time interval between the occurrence of the stimulus and the beginning of the movement that is the traditional RT. The RT then can be regarded as a time during which the movement is *intended.* (b) In other cases a delay can be imposed so that the movement will be initiated after a period of waiting, while the stimulus is still present. These *instructed delay paradigms* probe further the representation of intended movements, in the sense that there is not an immediate motor output while the representation is being kept active. (c) In some cases of delayed movement tasks, the movements are produced on the basis of information kept in *memory.* The difference between these and the instructed delay task is that now the stimulus defining the direction of the movement is turned off after a short period of presentation and the movement is triggered after a delay by a separate "go" signal. Thus information concerning the intended movement has to be retained during the memorized delay.

In all three cases the representation of information about the intended movement can be studied under different conditions that impose different constraints on the system. It would be interesting to know whether this representation could be identified and visualized during the RT, the instructed delay, and the memorized delay periods. Since the information assumed to be represented is about direction, the neuronal population vector could be a useful tool by which to identify this representation. For that purpose we computed the population vector every 20 ms (a) during the RT,[32,33] (b) during an instructed delay period,[34] and (c) during a memorized delay period.[35] The results were clear: in all these cases the population vector pointed in the direction of the intended movement during the cited time periods. These findings (a) underscore the usefulness of the population vector analysis as a tool for visualizing representations of the intended movement, and (b) show that in the presence or absence of an immediate motor output, as well as when the directional information has to be kept in memory, the direction of the intended movement is represented in a dynamic form at the ensemble level. These results also document the involvement of the motor cortex in the representation of intended movements under various behavioral conditions.

Spatiotemporal Processing in a Directional Transformation

In the delayed-movement tasks previously described, the movement to be made is unequivocally defined in the sense that its direction is determined by the location of a stimulus relative to the starting point. In that situation the visual information concerning direction is used to generate the appropriate motor command to implement a movement in that direction; truly, this movement direction has to be generated and kept available during the delay period, but it is defined from the beginning; therefore, the direction of the intended movement is the same throughout the various times previously considered. A very different situation was created in an experiment[36] in which the direction of the movement to be made had to be determined freshly at every trial according to a certain rule, namely that the movement direction be at a clockwise (CW) angle from the stimulus direction. This experiment takes us away from the idea of a *fixed* motor intention: instead, this intention has now to be derived as the solution to the problem. Subjects performed eight sets of twenty consecutive trials each; one set for moving in the stimulus direction and seven for moving in directions at an angle from it. The angles were 5°, 10°, 15°, 35°, 70°, 105°, and 140°. The direction of the movement in two-dimensional space and the RT were measured. The major finding was that the RT increased as a linear function of the amplitude of the angle; the slope of the line was (2.37 ms/degree). This finding suggested that performance in the task may involve a mental rotation of the imagined movement vector about its origin. The rotation would begin from the stimulus direction and end when the required angle was judged to have been reached; in addition, corrections of this angle at the end of the rotation could be made; the slope of 2.37 ms/degree observed then would correspond to a rotation rate of 422 degrees/s.

The neural mechanisms underlying the process of mental rotation in the movement domain were investigated by training monkeys to perform a task in which they made a movement in a direction 90° counterclockwise (CCW) from a stimulus direction. We supposed that if a mental rotation of an imagined vector was taking place, the neuronal population vector could reveal it. Indeed, the population vector rotated during the RT from the stimulus to the movement direction through the 90° CCW angle.[37,38] Interestingly, the rotation rates (direction of population vector versus time) observed[38] were very similar to the rates (increase in RT versus angle) observed in the human studies.[36] Thus, the dynamic processing of a directional transformation was successfully visualized using the neuronal population vector analysis. The crucial aspect of this analysis is the consideration of neuronal populations as the meaningful level of synthesis of motor cortical events.

INFORMATION THEORETICAL ANALYSIS OF TEMPORAL MOTOR PROCESSING

When a pointing movement to a target has to be made, there usually intervenes a RT of approximately one-third of a second during which the movement is planned and its initiation implemented. The time from the onset until the end of the movement is the movement time that varies with the amplitude of the movement and the accuracy of the target.[11] Both of these times, then, reflect processing loads and can be used to derive rates of processing, given that these loads can be quantified. An accurate and convenient way is to quantify processing loads within the context of information theory. For targeted movements, Fitts[11] defined the processing load (I_d, index of difficulty) in bits, as

$$I_d = \log_2 \frac{2A}{W}, \tag{1}$$

where W is the diameter of the target window (target accuracy) and A is the amplitude of the movement. The *rate* of information processing (I_p, index of performance) is in bits/second:

$$I_p = \frac{1}{T}\log_2\frac{2A}{W}, \tag{2}$$

where T is the movement time.

Rate of Information Processing in Reaching Tasks

Reaching movements have been studied in various tasks. With respect to the movement itself, these tasks can be distinguished between those that allowed unconstrained, free reaching in three dimensions, and those in which the reaching movement was constrained in one or two dimensions. Since constraining the movement is likely to have an effect on information processing, we discuss these tasks separately below.

Unconstrained Three-dimensional Reaching Movements

In a three-dimensional free-reaching task[24] monkeys made movements of amplitude $A = 12.5$ cm to visual targets of width $W = 1.6$ cm. Under these conditions the I_d was 3.97 bits, obtained by substitution of the preceding values in (1). The average movement time was 431 ms, which yields an I_p of 9.2 bits/s [from (2)]. It is noteworthy that this value is the same as that obtained in a previous three-dimensional reaching experiment (unpublished observations from Mountcastle *et al.*[39]). In that experiment monkeys had to reach to a target in front of them; first they depressed a key and when the target dimmed, they released the key and hit the target. The target was stationary or was moving at 12 or 21°/s when it dimmed. The I_p calculated from that experiment was 9.2 bits/s for the stationary target, and 8.3 and 8.4 bits/s for the 12 and 21°/s target motion, respectively. Thus these values of 8–9 bits/s are well established for three-dimensional reaching tasks.

In a different experiment, Sanes[10] studied normal human subjects and subjects with Parkinson's disease during repetitive movements between two targets. There was a consistent reduction in the rate of information processing in the parkinsonian group. In the case with the most pronounced difference in which movements of 32 cm were made between targets of 0.5 cm width, the I_d was 7 bits. The average movement time for this condition was 764 and 1118 ms, for the normal and parkinsonian subjects, respectively (estimated from data in [10, fig. 3]). This yields an I_p of 9.2 bits/s in the normal group and 6.3 bits/s in the parkinsonian group. The normal I_p is again the same as that obtained from monkeys in three-dimensional reaching tasks, but the parkinsonian I_p is much lower, by almost 3 bits. This attests in a formal way to the major defect in Parkinson's disease, namely the reduction in the rate of spatiotemporal motor processing.

Constrained Reaching Movements

Two-dimensional Movements: In a two-dimensional reaching task[40] monkeys and normal human subjects moved an articulated manipulandum in various directions to visual targets on a planar working surface. They first held the manipulandum in the center of the plane and then moved to radially arranged targets in a reaction-time task. The average I_p was 7.25 bits/s and was very similar in monkeys and human subjects.[40] This value is lower than that of 9.2 bits/s obtained for unconstrained movements (see earlier). This reduction probably reflects the constraint imposed on the two-dimensional movements.

One-dimensional Movements: Monkeys were trained to move a very low friction manipulandum along one dimension in response to a visual target.[3] The display consisted of two rows of 128 light-emitting diodes (LEDs). The two rows were placed one below the other, and the distance between adjacent LEDs in a row was 2.54 mm. The upper row indicated the target of the movement, whereas the lower indicated the current position of the manipulandum. The monkey had to move the manipulandum so that the lower (feedback) LED would be aligned to the upper (target) LED in a reaction-time task. Movements of three amplitudes (2.5, 6.25, and 10 cm) were performed. We calculated the I_p for the largest movements that were also the fastest. For these data (unpublished observations from Georgopoulos *et al.*[3]), A and W were 10 cm and 0.676 cm, respectively, and the average movement time was 770 ms; therefore, $I_d = 4.89$ bits and $I_p = 6.99$ bits/s.

This task was performed during recordings of single-cell activity in the basal ganglia of behaving monkeys.[3] The neural rate of movement information processing was estimated as follows: (a) For a given cell, the mean and standard deviation (SD) of the discharge rate during the movement time was calculated from 15 trials of movements made for each of the three amplitudes, as mentioned earlier. (b) A linear regression analysis was performed to determine the relations between the discharge rate and the amplitude of movement. It was found that for a number of cells a statistically significant relation existed of the following form:

$$D = K + Ba, \tag{3}$$

from which

$$A = \frac{D - K}{b}, \tag{4}$$

where D is the frequency of discharge, K is a constant, b is a regression coefficient, and A is the movement amplitude. (c) The W' predicted by a single cell's discharge was estimated for the 10-cm movement from the difference

$$W' = A_{\text{high}} - A_{\text{low}}, \tag{5}$$

where A_{high} and A_{low} are the predicted movement amplitudes obtained from (4) when D is substituted by the corresponding mean ±SD; that is, by a high and low discharge rate. Then, the I_d and I_p were calculated from those values; the average movement time was also available. Ten cases of cells recorded in the internal segment of the globus pallidus were analyzed; these cells had statistically significant relations to movement amplitude [(3)]. The mean (±SD) I_p was 1.57 ± 0.83 bits/s. This value is appreciably lower than the I_p of 6.99 bits/s transmitted behaviorally by the movement (see earlier). Similarly low values were obtained for cells recorded in the external segment of the globus pallidus and the subthalamic nucleus. These results indicate that single cells do not carry enough information to fully account for the behavioral performance. This is not surprising, for the motor performance is the result of processing by the whole neuronal ensemble that should carry, as an ensemble, the requisite information. Indeed, this has been shown to be the case for the ensemble coding of the direction of movement (see below).

Rate of Information Processing in a Movement Sequence

In this task two-dimensional reaching movements were made in quick succession in response to a target shift.[40] Subjects were instructed to point with their hand to a visual target as soon and as quickly as possible. During various times following the appearance of the first target (50–400 ms) the target shifted, and the subject had to move to the new target. It was found that the rate of information processing increased substantially (by as much as twofold) during the second movement. The highest rate (14.4 bits/s) was attained when the target shifted 150 ms after its first appearance. These results show that it is possible to increase the rate of information processing of the motor system, that is, to increase the speed of the movement without degrading its accuracy. In a way, of course, this characterizes skilled motor performance. For example, a good tennis player is frequently both fast and accurate, especially so if one considers that the accuracy required under these circumstances extends to several aspects of movement, that is, orientation of the hand, force of hitting the ball, precise timing, and so forth. How is that increase in information processing being accomplished? We suggest that a key factor responsible for the improved performance in motor skills that involve a sequence of movements may be a parallel motor processing. It seems that, under certain conditions, generating a movement while another one is evolving or being generated "primes" the perceptual–motor system so that, instead of being constrained, it actually processes information more efficiently and emits movements that are faster than, and as accurate as, movements produced in isolation. A correlate of this increased efficiency in information processing was described by Soechting and Lacquaniti,[41] namely that when responding to a target change there is a reduction in the degrees of freedom of the movement; this is achieved by imposing constraints on the kinematic variables (angular deceleration at the shoulder and elbow joints), and by generating more stereotyped patterns of activity in the muscles acting on these two joints.

Rate of Motor Information Processing in Mental Rotation

The studies discussed previously concerned information processing during actual movements. We wish now to consider this question for a case that seemed to involve a mental movement, namely a mental rotation of movement direction. Some of the results of these studies were summarized earlier; we provide below the results of an information–theoretical analysis. In these experiments[36] human subjects were asked to make movements in directions at various angles from a stimulus direction that varied in two-dimensional space from trial to trial in a pseudorandom fashion. Under these conditions, the RT increased as a linear function of the angle; this suggested that subjects rotated mentally an imagined movement direction. Assuming this model of internal motion, we analyzed the amplitude-accuracy relations using Fitts's[11] approach described previously: for this case, we considered the RT as a mental movement time during which the imagined movement vector rotated. Indeed, we found that the increase in RT was a linear function of task difficulty that was calculated from the angle achieved and its variability. This indicates that Fitts's law holds for the hypothesized rotary motion of the imagined movement vector, and suggests that both real and imagined movements might be governed by similar amplitude–accuracy relations. The average I_p in this task was 4.21 bits/s, which is almost one-half the information processing rate for straight movements ($I_p = 7.25$ bits/s). This is probably due to the cognitive load in this task and also to the fact that rotation involves operating on direction, which is known to be a time-consuming process.[42]

The neural mechanisms underlying this mental rotation were studied by recording single-cell activity in the motor cortex of two monkeys who made movements at an angle 90° CCW from a stimulus direction.[37,38] The neuronal population vector (see earlier) was calculated as a measure of the directional tendency of the neuronal ensemble. It was found that during the RT it rotated CCW from the direction of the stimulus to the direction of the movement. These results provided a direct visualization of the mental rotation hypothesized previously in this task on the basis of the results obtained from human subjects, summarized in the preceding section. There were eight stimulus directions available, and therefore eight time-series of population vectors rotating during the RT; summary data are shown in [38, tables 4 and 5]. From these data, the estimated I_p was 4.785 bits/s. This is the estimate of the rate of processing of directional information by the neuronal ensemble during the mental rotation. The I_p of the behavioral performance in the same monkeys was also calculated as follows. The rotation angle required was 90°, with an allowance of ±30°, and therefore, the angular "target" width was 60°; the average RT was 413.7 ms. From these data, $I_p = 3.832$ bits/s. There are two noteworthy points here. First, this last behavioral I_p by the monkeys is close to the value of 4.21 bits/s calculated from the human data given earlier. And second, the neural I_p of 4.785 bits/s was approximately 1 bit higher than the behavioral one of 3.832 bits/s calculated for the same conditions in the same animals. This validates further this analysis and suggests, as probably was expected, that there is some loss of information from motor cortical processing to behavior, as suggested previously.[43]

CONCLUSIONS

We have reviewed the general features of temporal sensory–motor processing in the basal ganglia and motor cortex. We have further quantified this processing within the context of formal information theory and evaluated the rate of information processing in various types of reaching movements. An important result of this analysis is that the highest processing rate (9.2 bits/s) is observed in unconstrained three-dimensional movements, and that this rate is appreciably reduced to about 7 bits/s in movements constrained to one or two dimensions. This shows that higher degrees of freedom in movement are processed more efficiently, and that the processing of "simpler," that is, constrained, movements is more difficult. One explanation for this could be the fact that three-dimensional movements are very practiced, which could result in more efficient information processing. This efficient processing of complex, multidimensional movements is reflected in their control by the central nervous system, as evidenced by the orderly variation of cell activity with movement parameters and the preferential disruption of multi- but not single-joint movements by reversible inactivation of central motor structures.[44]

Finally, the importance of considering neural information processing at the neuronal population level was discussed within the context of temporal processing of directional information and its transformation in a mental rotation task.

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