Online visual control of the arm

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Abstract. The psychophysical and cerebrocortical mechanisms in visually guided reaching movements and isometric force pulses are discussed. The results of psychophysical studies of pointing movements have demonstrated a tight coupling between the visual information and the direction of the movement, and those of studies of directed isometric force pulses have documented the sensitive dependence of the motor system on the continuous availability of visual information for the ongoing correction of directional deviations from the instructed direction. Recordings of the activity of single cells in the motor cortex and parietal areas 2 and 5 have revealed the same tight, online coupling between visual information and cell discharge, and have partially elucidated the neural mechanisms underlying this function at the cortical level.

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Vision plays a major role in the motor repertoire of primates. Commonly, purposeful arm and hand movements are directed towards, and adapted for the use of, objects of interest within the visual field. The visual aspects of this problem are dealt with in other chapters of this symposium (e.g. this volume: Goodale 1998, Jeannerod et al 1998). In this chapter I review the results of psychophysical and neural studies pertaining to arm movements and isometric forces that are instructed, controlled and/or guided by visual information. Altogether, these results show that the arm motor output is tightly coupled to, and sensitive to changes of, ongoing visual information. This results in an efficient and effective visuomotor control function which apparently involves the cooperation of several brain areas and which is reflected in the neural activity of motor cortical and parietal cells.

Visual control of arm movements

Discrete movements to stationary visual targets

Reaching movements to stationary visual targets have been studied extensively (for a review see Georgopoulos 1986). Typically, such movements are learned during infancy, and their trajectories are fairly stereotyped and show invariant properties (Soechting & Lacquaniti 1981). With respect to the neural mechanisms involved, many studies have been performed by recording the impulse activity of single cells in several brain areas of behaving monkeys trained to reach towards visual targets (for a review see Georgopoulos 1990a).

Basically, two kinds of analyses have been carried out. In one, the average firing rate during reaching has been analysed with respect to motor variables; this provides a robust estimate of the intensity of activation and of its relation to movement but destroys the fine time-course of cell activity. Those studies have revealed that the activity of single cells in several brain areas, including cerebrocortical and cerebellar areas (see Georgopoulos 1990a), varies in an orderly fashion with the direction of reaching so that cells are directionally tuned: cell discharge is highest for reaching in a particular direction (the cell's 'preferred direction') and decreases progressively with reaching in directions farther and farther away from the preferred one. The directional tuning is generally broad and can be expressed as a cosine function (Georgopoulos et al 1982, Schwartz et al 1988). Preferred directions differ for different cells and are distributed throughout the directional continuum in 3D space (Schwartz et al 1988). A neuronal population vector code provides accurate information concerning the direction of movement under various experimental conditions (see Georgopoulos et al 1993 for a review).

Finally, cell discharge also varies with the amplitude of the movement but the preferred direction remains the same for movements of different amplitudes (Fu et al 1993). Directional tuning is observed during both the reaction and movement time whereas the variation with movement amplitude is observed during the movement time (Fu et al 1995).

In a different study (Ashe & Georgopoulos 1994) the fine time-course of single-cell activity (e.g. every 20 ms) was analysed with respect to the direction of the visual target as well as with respect to time-varying motor parameters, including position, velocity and acceleration. It was found that cell activity was related to all of these parameters, but that target direction and movement velocity were the most important determinants of the time-varying cell activity. The importance of the ongoing movement velocity signal was also indicated by neural studies of tracing movements (Schwartz 1993) and of simultaneous recordings from several cells (Humphrey et al 1970). It is reasonable to suppose that these effects reflect motor control signals as well as the effects of peripheral inputs. A contribution of feedback is supported by the known inputs to the motor cortex from the somatic periphery. A feedforward signal could relate to the length-tension state of the muscles (Fromm 1983), in which case this signal could be tailored to the current states of the muscles to be controlled. This combination of afferent and efferent signals could be quite complex, given the appreciable divergence of corticospinal axons at the spinal level, the wide distribution of motor cortical output signals to various cortical and subcortical structures, and the convergence of peripheral inputs to cortical areas (e.g. areas 2 and 5) which provide major inputs to the motor cortex. If one adds the known inputs from subcortical structures (basal ganglia, cerebellum) and considers the large divergence (Shinoda & Kakei 1989) and convergence (Darian-Smith et al 1990) of the thalamic projections to the motor cortex, then a picture emerges in which the motor cortex occupies a nodal point at the cross-section of many interacting sensorimotor circuits.

Reaching in a target shift task

Many times the object of interest towards which the hand is directed changes location, and therefore it is interesting to know whether the motor system can follow the target and change the movement in mid-flight. We studied this problem in monkeys (Georgopoulos et al 1981) and human subjects (Massey et al 1986) who moved an articulated manipulandum on a planar working surface. Two peripheral lights in opposite locations were used (e.g. at 12 and 6 o'clock). The subject held the handle in the centre for a variable period of time after which one of the two peripheral targets was turned on; it remained on for 50, 100, 150, 200, 250, 300 or 400 ms and then was turned off and the other target was turned on. The animal was rewarded after holding at the second light for 0.5 s. Trials in which the first light stayed on without changing location were interspersed among those in which the target location changed so that the subject could not predict whether the target would change location in a certain trial; moreover, the subject could not predict for how long the first target would stay on in the trials in which it changed location. The effect of the change in target location on the movement trajectory is shown in Fig. 1A. The first target was at 12 o'clock and the second target at 6 o'clock. Single trajectories of arm movements are shown in the lower trace. It can be seen that the arm moved initially towards the first target, then changed direction and moved towards the second target. Therefore, the arm movement could change online depending on the target instructed.

There are several aspects of these experiments that are noteworthy. First of all, how consistently is a movement made towards the first target? This question was examined by varying systematically the duration of the first target and observing the arm movement towards it. It was found that the occurrence of a movement towards the first target depends on how long the first light stays on. This is illustrated in Fig. 1B which plots the probability of occurrence of a movement towards the first target versus the duration of presentation of the first target. It can be seen that this probability increases steeply and becomes one when the first light stays on for at least 100 ms.

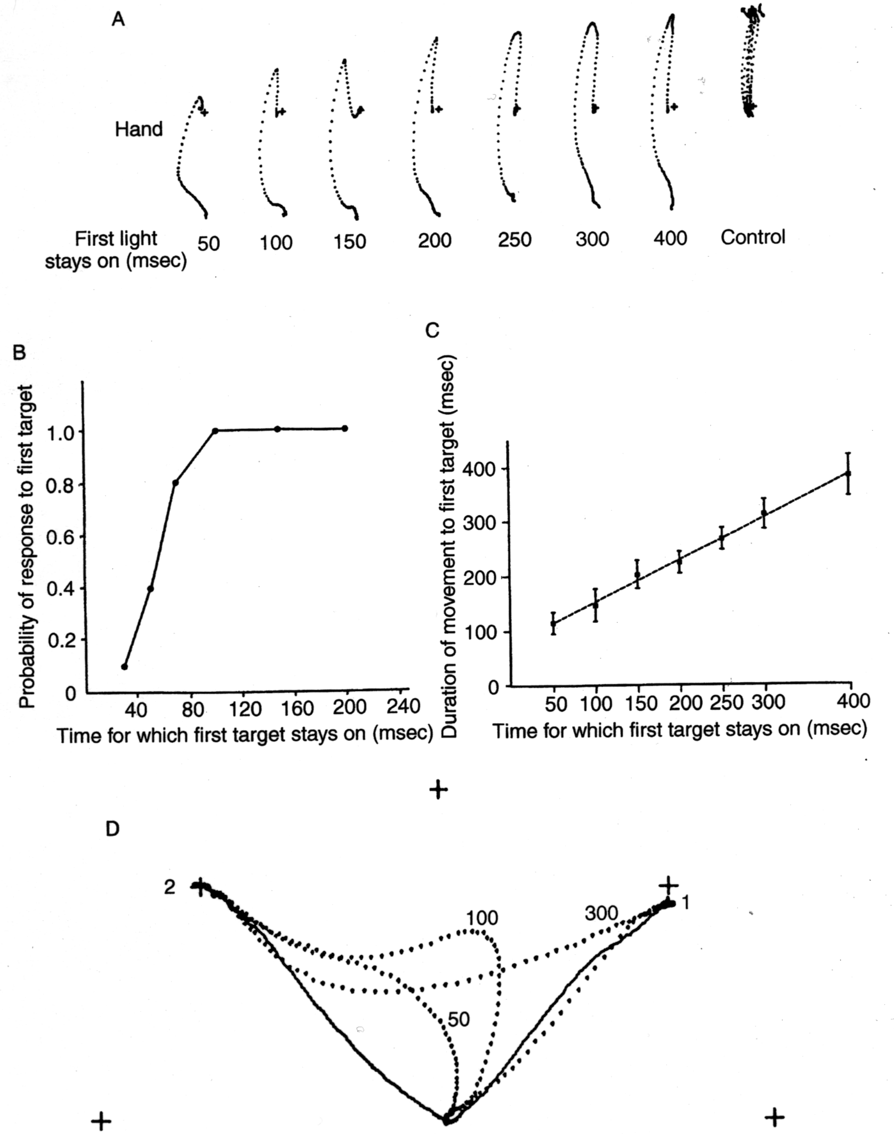


FIG. 1. (A) Modification of hand movement trajectories in the target shift task. The first target light was at 12 o'clock; it stayed on for the time indicated and then changed location to 6 o'clock. Single trajectories are shown (X–Y data points were recorded every 10 ms). At the far right (control), seven trajectories to the target at 12 o'clock are superimposed. (B) Probability of response to first of two targets presented in quick succession. (C) Duration of movement towards the first of two targets (ordinate) presented in succession at specified interstimulus intervals (abscissa). Data from one monkey. (D) Modification of the direction of movement elicited by the first target (#1) when the second target (#2) was at an angle of 90°. Solid lines indicate control trajectories of movements made directly to targets A and B. Dotted lines are trajectories of movements made at the stated interstimulus interval (X–Y data points were sampled every 10 ms). (Adapted from Georgopoulos et al 1981 and Georgopoulos 1990b.)

The second question concerns the temporal relations between the direction of the target and the duration of the movement. Figure 1C illustrates the finding that the duration of the arm movement towards the first target is a linear function of the time for which the first target stayed on.

The third question concerns the spatial characteristics of the trajectory of the first movement. In most cases tested, the two target lights were located along the same line, so that the first and second movements were in opposite directions. However, when the two target lights were arranged in such a way that the corresponding movements were not in opposite directions, a modification of the direction of the trajectory of the first movement was observed in some trials. An example is shown in Fig. 1D. The first light (#1) was at approximately 2 o'clock, and the second light (#2) was at 90° angle from it. The two continuous lines in Fig. 1D show examples of trajectories made directly to each of the lights in control trials. The dotted lines plot trajectories obtained at the interstimulus interval indicated in the plot (50, 100 and 300 ms). It can be seen that the trajectory deviated towards the direction of the second target, the more so the shorter the interstimulus interval was. These results indicate that the motor command for the direction of movement generated after the appearance of the first target can be modified by the second target when the targets shift early in time.

The fourth question concerns the velocity characteristics of the trajectories of the movements towards the second target, after their reversal. It can be seen in Fig. 1A that these movements were faster than those made towards the first target. In fact, the peak velocity of the movements towards the second target was approximately three times that of the movement towards the first target. This was true even for the interstimulus interval of 50 ms, in which case the movement towards the first light was small and, therefore, the amplitude of the second movement was very similar to that of the movement made directly to the second target in control trials. These results can be explained by the strategy that monkeys and human subjects used to solve the problems posed by this target-shift task. This strategy was revealed by an analysis of the forces exerted on the manipulandum during performance of the task (Massey et al 1986).

The problem is that if the trajectory is to be interrupted at different points along its extent, the dynamics of the hand and the manipulandum will differ in these points reflecting different velocities and accelerations; therefore, the braking forces will have to be precalculated in accordance with the anticipated kinematic and dynamic conditions. However, the subjects ignored the differences between the mechanical conditions associated with different interruption points and, instead, produced a large braking force in the opposite direction in response to the second target that stopped the limb and moved it to the second target. These braking forces were excessive for the short movements towards the first target but were effective for all cases and did not require individual adjustments for particular trials. Therefore, the computational load was reduced at the expense of increased spending of mechanical energy; in other words, a simple and mechanically effective but energy-inefficient strategy underlay the efficient eye–hand coordination in this task.

A correlate of this increased efficiency in information processing might lie in the observation by Soechting & Lacquaniti (1983) that under similar conditions of rapid response 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.

Neural mechanisms of visuomotor coupling

When the location of visual stimuli is changed in quick succession, the patterns of cell activity in motor (Georgopoulos et al 1983) and parietal (Kalaska et al 1981) cortex follow these changes with remarkable temporal fidelity and attest to the efficient engagement of those areas during eye–hand coordination. An example is shown in Fig. 2A. The location of the first and second target, and the required movement direction, are shown in the top of the figure. The pattern of cell activity associated with movements directly to these targets consisted of an increase in cell activity when moving to target A and of a decrease in activity when moving to target B. When the first target was target A, the pattern of cell activity was that associated with movement to that target; this pattern lasted for a time proportional to the time for which the first target stayed on, and then became like the pattern of activity associated with movement to target B. These results indicate that when a sequence of hand movements is generated towards targets that change location, the motor cortical activity follows the changes in visual information well and generates the appropriate motor commands without temporal smearing. This apparently underlies, at least in part, the efficient eye–hand coordination observed at the behavioural level.

Visual control of isometric force pulses: an information-theoretical analysis

In these experiments we investigated the effects of an external constant force bias and of various manipulations of the visual information on the information transmitted (T_i) by the direction of isometric force exerted in a two-dimensional space by human subjects. For that purpose we used an isometric manipulandum and random dot stereograms generated in a colour display (Massey et al 1991a,b). Human subjects viewed the display through appropriate colour filters and perceived the image of a disk rotated about a horizontal axis on the frontal plane; the top of the disk was rotated around that axis by 45° away from the subject. Subjects were instructed to exert force pulses of >200 g force intensity in the direction of a visual target ($n = 20$ targets) presented on the disk in a reaction time task. The instantaneous force exerted by the subjects on the manipulandum was shown on the disk in the form of a feedback cursor. The T_i was calculated as described previously (Georgopoulos & Massey 1988). The time course of force development and the gain of directional information transmitted (i.e. the rate of increase of T_i) during force development were studied under three experimental conditions; namely, (a) in the absence and presence of a constant force bias, (b) when the force feedback cursor was frozen or (c) turned off when the force developed exceeded 100 g force. Each one of these experimental manipulations probed different aspects of the specification and generation of net force in a visually specified direction.

Online gain of directional information

In order to determine the gain of directional information during force development, we calculated the T_i at various levels of force intensity, ranging from ~ 50 g force to >200 g force. There was a gain of information (i.e. the T_i increased) with force intensity for all experimental conditions studied (i.e. stereoscopic depth, absence of visual force feedback and presence of force bias). This suggests that the specification of the direction of force improves as the force intensity increases, which could be due to a continuous comparison and correction of the force produced so that it is in the visually defined direction, as was suggested by the results of other studies (Cordo 1987, Gordon & Ghez 1987).

Quantitatively, the curves of T_i vs. force intensity, F, were negatively accelerating. The relation between T_i and F was a power function of the form:

$$T_i = kF^m \tag{1}$$

where k and m are constants. Equation (1) is linear in a log–log scale:

$$\ln T_i = A + m \ln F \tag{2}$$

where $A = \ln k$ ('ln' refers to the natural logarithms, that is to base e).

Effects of force bias

Subjects exerted force pulses so that the force feedback cursor moved in the display past the target cursor. In the absence of force bias, the force exerted by the subject (Fig. 3A) increased from near zero to >200 g force at the end of a trial and was close to the visually defined direction. When a constant bias force of 110 g force was applied in various directions in blocks of trials, the force exerted by the subject increased in time, as above; however, its direction also changed in time (Fig. 3B) so that the instantaneous vector sum of the bias force and the force exerted by the subject pointed close to the visually defined direction. The T_i calculated at 200 g force and the reaction time did not differ significantly in the two experimental conditions (Massey et al 1991b). Figure 3C is a log–log plot of the T_i against force in the absence (open circles, interrupted line) and presence (filled circles, solid line) of force bias. (The lines are fitted regression lines.) It can be seen that the lines are very similar; the slopes did not differ statistically at the 5% level of significance. (The values of the constants k and m are given in Table 2 in Massey et al 1991b.) Altogether, these results demonstrated that presence of a constant force bias did not degrade performance: subjects were able to specify accurately (i.e. at a high T_i) the net force output of the manipulandum to be in the visually defined direction by changing continuously the direction and magnitude of the

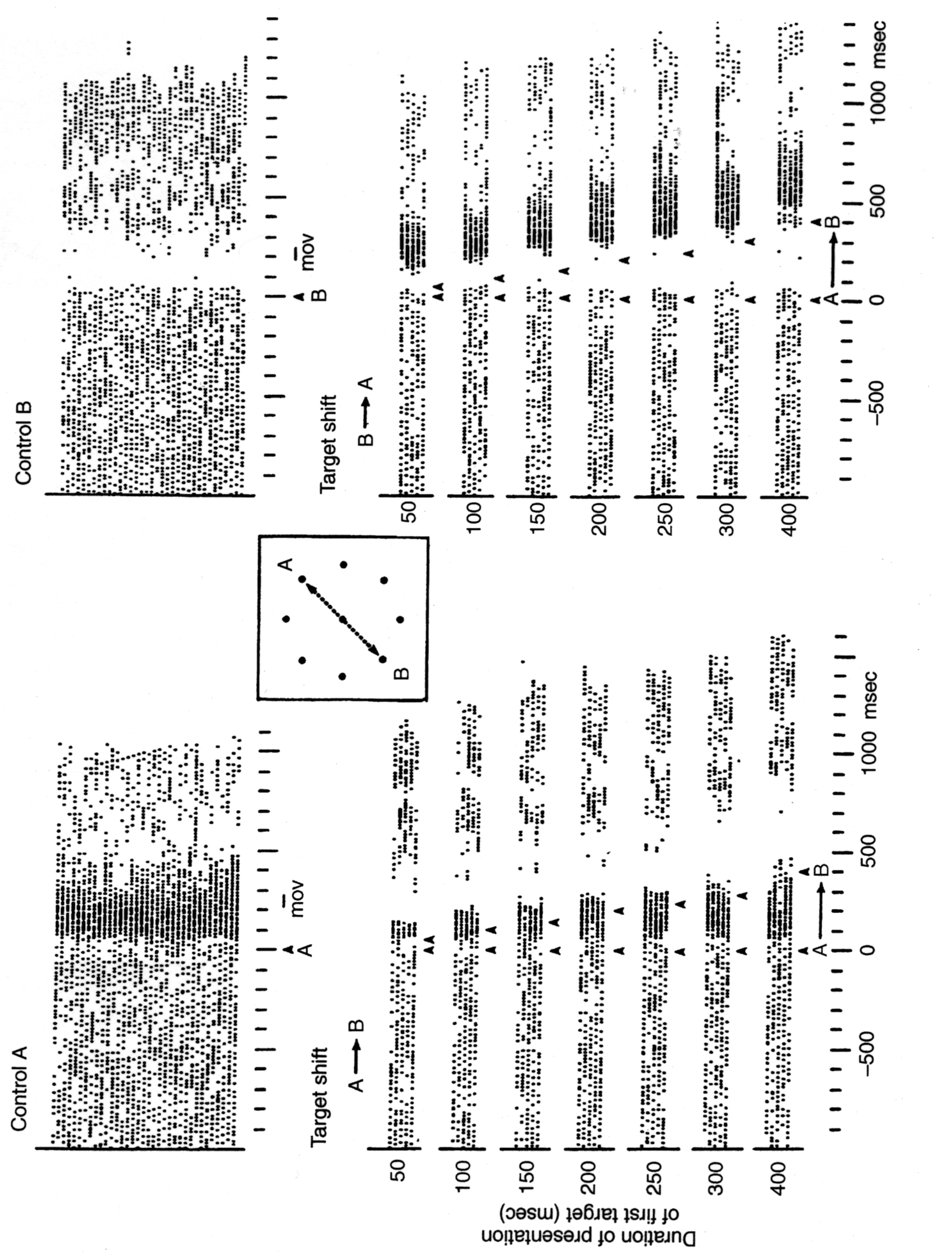
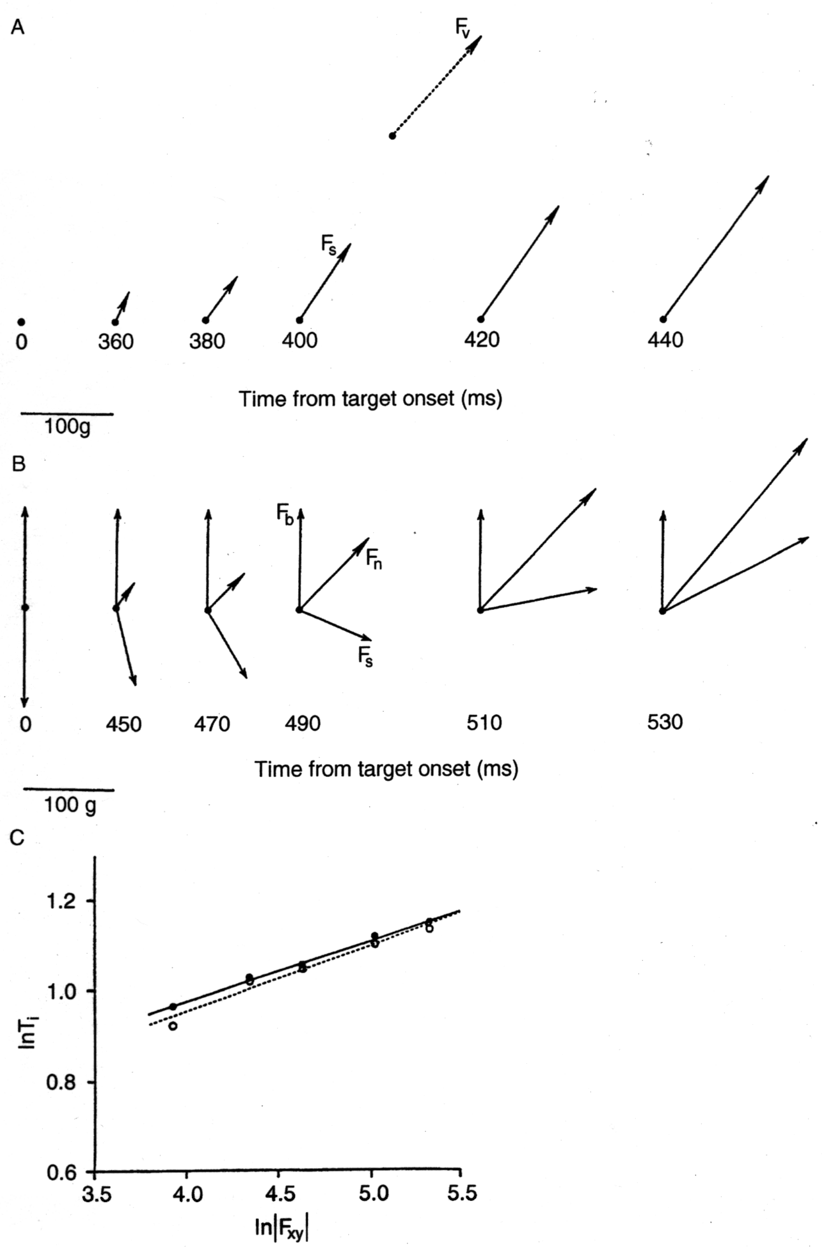


FIG. 2. Changes in discharge of a motor cortical cell in the target shift task. Beneath each control raster are seven rasters of trials during which the target changed location after 50–400 ms, as indicated; the first target to appear in each trial was the same as that for the control trials plotted above it. The initial change of activity seen in the target shift trials was of the same sign as that during the corresponding control trials, i.e. an increase in cell activity on the left and a decrease on the right. The initial pattern of activity did not continue as long as in control trials, however, for a short while after the target changed it was replaced by a pattern of activity similar to that recorded during movement to the other target. Thus, the initial increase in activity during movements to target A was truncated by a complete suppression of activity similar to that seen in control trials during movements to target B, while the decrease in activity on the right side was terminated by a brisk increase in activity like that seen for movements to target A. This was true for all interstimulus intervals tested. The time at which the switch in the pattern of activity occurred was related to the time of the target shift (second arrows). The horizontal bar labelled MOV indicates the range of the times of movement onset. The first and second arrows indicate the time of presentation of the first target and of the target shift, respectively. (From Georgopoulos et al 1983; reproduced with permission.)



active force they exerted at no extra time (i.e. without a longer reaction time). Thus external loads are processed very efficiently even under dynamic conditions.

Effects of manipulations of visual information

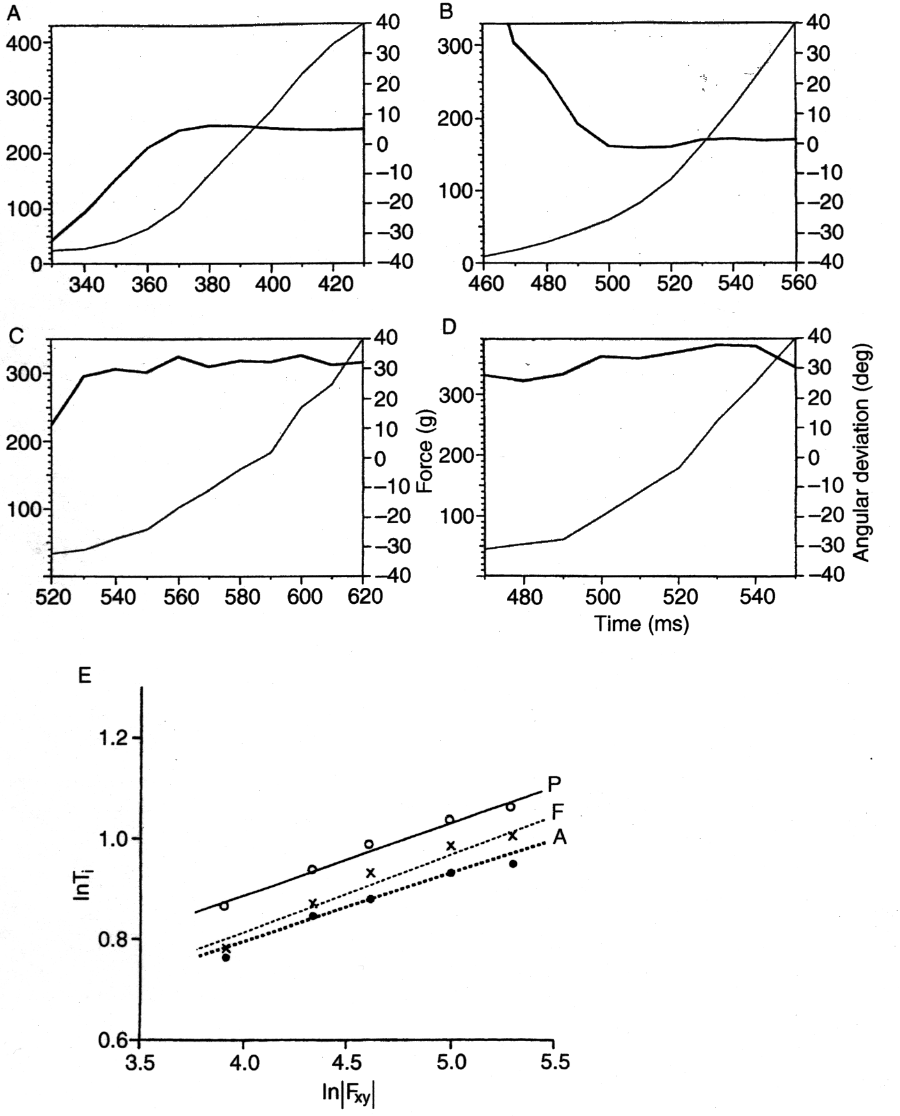
Figure 4 A–D illustrates individual trials of force development and angular deviations of the force from the stimulus direction in the presence (Fig. 4A) and absence (Fig. 4 B–D) of force-feedback cursor. It can appreciated qualitatively from the plots in Fig. 4 A–D and quantitatively from the plots in Fig. 4E that manipulation of the visual force-feedback had a significant effect on the gain of information. The plots of the gain of information for the three conditions used (force feedback cursor intact, frozen or absent) are shown in Fig. 4E. It can be seen that the absence of the force feedback cursor resulted in lowering of the line (Fig. 4E, line labelled A), whereas freezing the cursor at the centre of the disk resulted in an intermediate positioning of the line (line labelled F), between those obtained in the presence (line P) and absence (line A) of the force feedback cursor. The gradients *m* did not differ statistically at the 5% level of significance.

Discussion

In the present experiments, subjects exerted forces on an immobile manipulandum so that a cursor reflecting the net X–Y forces exerted on the manipulandum moved in a direction defined by a target in the display. Enough force had to be exerted to exceed a 200 g force threshold but an upper limit was not defined. Indeed, subjects performed accordingly and generated force pulses; the intensity of force kept increasing even after the 200 g force threshold was exceeded. Therefore, the data can be regarded as reflecting specification and/or control of force direction but not its termination.

Inspection of individual trials indicated that the direction of force was not specified accurately from the beginning of force change; instead, there was a period of gain of directional information as the force intensity increased (Fig. 4).

FIG. 3. (A) Force vectors (F_s) generated in the absence of force bias. Data are from a single trial. The visually defined direction (F_v) is indicated at the top of the figure. Numbers indicate the time (in ms) from the target onset. (B) Force vectors generated in the presence of force bias (F_b) for the same visually defined direction (F_v) as in *A*. The force bias vector was towards 12 o'clock. The subject's force vector (F_s) was initially equal and opposite (towards 6 o'clock) to the force bias vector. With the development of more force, the force exerted by the subject changes in direction and magnitude so that the net force (F_n), that is the resultant of F_b and F_s, is in the visually defined direction (F_v). Numbers indicate the time (in ms) from the target onset. (C) T_i is plotted against force intensity in a log–log scale. Open and filled circles correspond to absence and presence of force bias (at 90°), respectively. Interrupted and solid lines are fitted regression lines for absence and presence of force bias data, respectively. (Adapted from Massey et al 1991b.)



The gain of directional information during increasing force intensity was observed under all experimental conditions. This suggests that there may be a process by which the direction of force is continuously corrected with respect to the visually specified direction. A continuous effect of visual information on the direction of an upcoming movement was shown previously (Georgopoulos et al 1981, van Sonderen et al 1988). It is remarkable that the rate of gain of information was very similar for the different conditions but the whole curve was transposed to lower levels in the cases in which the visual definition of direction was degraded. These findings suggest that the process of gain of directional information is fundamentally the same for a variety of conditions but that it operates at various levels depending on the actual information available. This information was reduced when the force-feedback cursor was absent or fixed in the centre.

It is noteworthy that, in contrast to the effect of visual manipulations, the presence of a constant force bias had no adverse effect on information gain. This indicates that the motor system is very efficient in controlling the direction of force. It is possible that when a constant force bias is present, this is offset actively by an opposite force vector, and then the required force is exerted in the visually specified direction. The results of neurophysiological studies in the motor cortex of behaving monkeys (Georgopoulos et al 1992) supported this hypothesis as discussed below.

Neural mechanisms of visually instructed isometric force pulses

The exertion of an isometric force pulse involves the production of a rapid change in force in the absence of limb motion. When such a force pulse is instructed by a

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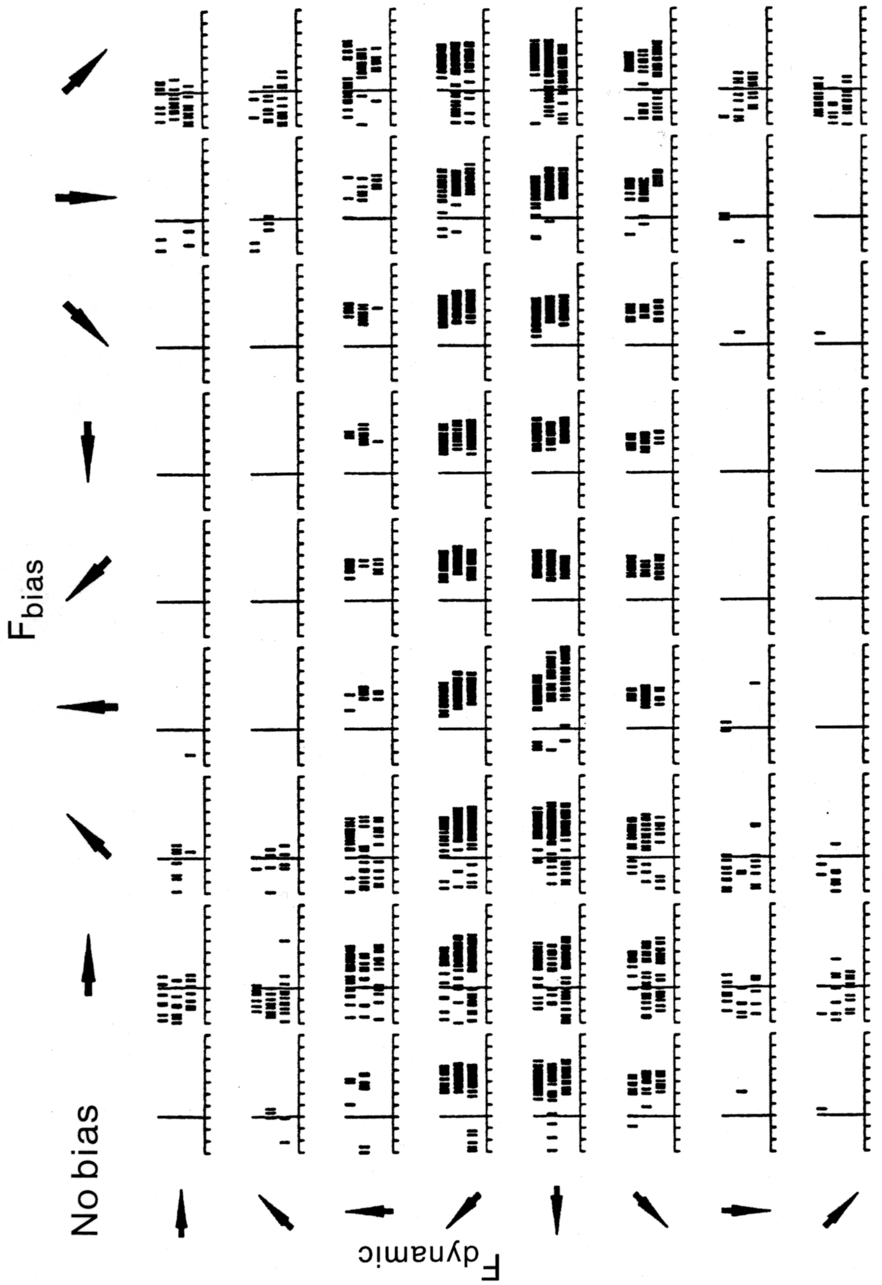
FIG. 4. *A–D* are plots of force development (thin line, left Y-axis) and angular deviations of that force from the stimulus direction (thick line, right Y-axis) at the time from stimulus onset indicated in the abscissa. All four plots are from single trials. For the angular deviations, positive and negative values are counterclockwise (CCW) and clockwise (CW), respectively, from the stimulus direction (0 value). (A) A trial in which the force-feedback cursor was present throughout the trial. When a direction of force was attained close to the stimulus direction (approximately 5° CCW) at approximately 370 ms after stimulus onset, it was maintained for the rest of the trial. Stimulus direction was at 113°. Plots *B–D* are all from trials in which the force-feedback cursor was eliminated at the onset of the RT. In (B) the subject attained and maintained the correct direction of force. Stimulus direction was at 353°. In (C) the subject attained and maintained a force that was approximately 32° CCW from the stimulus direction. Stimulus direction was at 137°. Finally, in (D) the subject maintained from the beginning a force that was more than 30° CCW from the stimulus direction. Stimulus direction was at 99°. (E) log–log plots and regression lines of T_i vs. force intensity for three conditions in which the visual force-feedback was manipulated. Visual force-feedback cursor was present throughout the trial (P), was absent from the beginning of the reaction time (A), or was frozen at the centre of the disk from the beginning of the reaction time (F). Data points are means of 12 subjects. (Adapted from Massey et al 1991b.)



visual signal, it allows the study of the relations of neural activity to visuomotor parameters at the isometric force domain, as was done in recent studies (Georgopoulos et al 1992). The following experimental arrangement allowed the dissociation between dynamic and static components of the force exerted. Monkeys produced pure force pulses on an isometric handle in the presence of a constant force bias so that the net force (i.e. the vector sum of the monkey's force and the bias force) was in a visually specified direction. The net force developed over time had to stay in the specified direction and to increase in magnitude in order to exceed a required intensity threshold. Now consider the case in which the directions of the net and bias forces differ, by being, for example, orthogonal. In order for the task to be performed successfully under these conditions, the animal's force has to change continuously in direction and magnitude, so that, at any moment during force development, the vector sum of this force and the bias force is in the visually specified direction. Thus this experimental arrangement effectively dissociated the animal's force vector, the direction of which changed continuously in a trial, from the net force vector, the direction of which remained invariant. Eight net force directions and eight bias force directions were employed. Recordings of neuronal activity in the motor cortex revealed that the activity of single cells was directionally tuned in the absence of bias force, and that this tuning remained invariant when the same net forces were produced in the presence of different directions of bias force (Fig. 5). These results show that, during the generation of the force pulse, cell activity does not relate to the direction of the animal's force *per se* but to its dynamic component. In fact, in this experimental design, three vectors possess the same direction but different time-varying magnitudes, namely the dynamic component of the force, the first time-derivative of the force, and the visually instructed target direction. The magnitude of the first two vectors varies over time but in different ways, whereas the magnitude of the last one remains constant. The potentially different relations between these parameters and the time-varying cell activity was investigated recently using a pulse-and-step isometric force task (Ashe & Boline 1997). A time-course analysis (as described in Ashe & Georgopoulos 1994) revealed that the visual target direction and the first time-derivative of force had the most substantial effects on the time-varying cell activity (J. Boline & J. Ashe, personal communication 1998). This finding is formally similar to the result obtained for

FIG. 5. Force directional tuning and its invariance across force biases are illustrated for the impulse activity (three repetitions) of one motor cortical cell. The directions of $\mathbf{F}_{dynamic}$ and $\mathbf{F}_{bias}$ are shown in the rows and columns, respectively, including the case of no force bias (first column). Rasters are aligned to the onset of the peripheral stimulus (0 time); the time scale is 100 ms per division. (From Georgopoulos et al 1992; reproduced with permission. Copyright AAAS 1992.)

movement, in which the direction of the target and movement velocity (i.e. the first time derivative of position) had the strongest effects on cell activity (Ashe & Georgopoulos 1994). These findings underscore the importance of the visual information and the change in the motor output for the ongoing cell discharge.

Concluding remarks

The results of the studies reviewed above attest to the remarkably efficient and effective eye–hand coordination in primates. They also document the involvement of the motor cortex in this function, obviously as part of a dynamically interconnected, widespread brain network. Recent studies of the neural mechanisms underlying manual interception of moving targets (e.g. Port et al 1994, 1996, Lee et al 1997) have provided additional support for the involvement of the motor cortex in processing visual information for the initiation and online control of arm movements aimed at catching accurately moving visual targets. A major challenge for future research is the elucidation of the interplay of the various areas participating in online control of arm movements.

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