From Eye to Hand: Planning Goal-directed Movements

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DESMURGET, M., D. PÉLISSON, Y. ROSSETTI AND C. PRABLANC. *From eye to hand: planning goal-directed movements.* NEUROSCI BIOBEHAV REV **22**(6) 761–788.—The nature of the neural mechanisms involved in movement planning still remains widely unknown. We review in the present paper the state of our knowledge of the mechanisms whereby a visual input is transformed into a motor command. For the sake of generality, we consider the main problems that the nervous system has to solve to generate a movement, that is: target localization, definition of the initial state of the motor apparatus, and hand trajectory formation. For each of these problems three questions are addressed. First, what are the main results presented in the literature? Second, are these results compatible with each other? Third, which factors may account for the existence of incompatibilities between experimental observations or between theoritical models? This approach allows the explanation of some of the contradictions existing within the movement-generation literature. It also suggests that the search for general theories may be in vain, the central nervous system being able to use different strategies both in encoding the target location with respect to the body and in planning hand displacement. In our view, this conclusion may advance the field by both opening new lines of research and bringing some sterile controversies to an end. © 1998 Elsevier Science Ltd. All rights reserved

Motor control   Vision   Proprioception   Target localization   Trajectory formation   Movement planning   Position sense   Pointing   Intersensory coordination

INTRODUCTION

DECADES AFTER the pioneering works of Woodworth (273) and Bernstein (12), the neural mechanisms involved in reaching movement generation are still, to a large extent, unknown. The present paper tries to take stock of this lack of knowledge. Our goal is to describe the state of our knowledge of the mechanisms whereby a visual input is transformed into a motor command. To this end, we consider the different problems that the nervous system has to solve to generate a movement; that is, target localization, definition of the initial state of the motor apparatus, and hand trajectory formation. For all these questions, we address three issues:

1. what are the main results presented in the literature;
2. are these results compatible with each other; and
3. which factors may account for the existence of possible incompatibilities between experimental observations or between theoretical models.

In our view, this triple level of investigation is essential in understanding how goal-directed movements are planned and in going beyond the limitations imposed by the classical approach of developing independent motor theories, in parallel. We believe that the original orientation given to the present review may be heuristic and helpful to improve our knowledge of the processes involved in the elaboration of motor commands. Before developing this idea in more detail we briefly introduce the main topics to be addressed.

First, this review pinpoints the key role of gaze information and retinal signals in building a sharp representation of the target location with respect to the body (Determination of the target location section). Three main topics are considered. The first one concerns the mechanisms whereby the position of a visual target is encoded in egocentric coordinates. The second one is related to the nature (afferent versus efferent) of the eye position signal used in egocentric coding. The third one investigates the possibility that target position encoding is improved by allocentric cues provided by structured visual scenes.

The second part of this review deals with the initial stage of movement planning. We investigate whether the ability to perform accurate reaching requires, in addition to a precise definition of target location, a knowledge of the initial configuration of the limb (Determination of the initial configuration of the arm section). This question is, in particular, crucial to evaluate the validity of the different models of trajectory formation.

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The last part of the present review concerns the puzzling problem of trajectory formation (Trajectory form anion section). For the sake of clarity, the main models proposed in the literature with respect to this topic, are grouped into three classes:

1. the positional models derived from the equilibrium-point hypothesis;
2. the vectorial models, which assume that the movement is programmed as a mismatch between an initial and a final state (the issue of whether this mismatch is defined in spatial or angular terms is addressed); and
3. the optimal control models, which presuppose that movement programming is constrained by energy minimization principles.

In the Trajectory formation section we emphasize that most of the theories presented in the literature to account for the spatio-temporal characteristics of goal-directed movements are supported by sound experimental facts. This leads us to propose the hypothesis that the nervous system is able to use different planning strategies depending upon context. From this point, it is suggested that the search for a global model of movement control, which appears as a watermark in several recent articles (179,16,85,76,201,220), may be in vain. Arguments favoring this view are presented.

INITIAL STAGES OF MOVEMENT PLANNING

The present section focuses on the initial programming stage of visually triggered movements. Both the nature of the information required to perform accurate reaching, and the way by which such information is acquired, are presented. We first describe the processes that encode visual target location and subsequently review arguments supporting the necessity of encoding the limb initial configuration to generate accurate responses. It is shown how these data have influenced theories of movement production.

Determination of the target location

It is self evident that planning a goal-directed arm movement requires implicit or explicit knowledge about the location to reach. Beyond this truism, however, it appears important to consider the ways by which this information is acquired. Knowledge about target localization processes is desirable in behavioral studies of motor control because it allows one to isolate within the global motor performance the features which are related to the motor system from those resulting from the target localization mechanisms. We first describe in the following the mechanisms whereby a visual target is encoded in egocentric coordinates (the first three subsections in the determination of the target location section). We then address the role of allocentric cues in target localization (The role of allocentric cues subsection).

The role of position signals derived from the eyes and head and their neuronal correlates

Whereas the spatial performance of a goal-directed hand movement obviously depends on an accurate representation of the target relative to the body, determining which sources of information are used to build this representation, and how they combine, is not trivial (see reviews in Refs (123,143,189)). Indeed, reaching at a visual target requires transformation of visual information about target position with respect to the line of sight, into a frame of reference suitable for the planning of hand movement, i.e. centered on the head, the trunk, the shoulder or the hand (see discussions about body-centered reference frames in the following sections). This problem is classically decomposed in analytic steps that respectively provide target position information in an eye, head, and ultimately body frame of reference (85). For the sake of clarity, we follow this progression to describe the mechanisms encoding retinal information and extra-retinal signals of eye-in-orbit and head-on-trunk positions.

The first information corresponds to the angle separating the target and the line of sight. The reliability of this retinal signal is constrained by the spatial anisotropy of the retina and visual system. Indeed, because of the gradient of visual acuity, the encoding of a target location with respect to the line of sight degrades when the stimulus falls in the peripheral visual field (192,269,191). This relative inaccuracy of signals from the peripheral retina can be illustrated by hand pointing errors observed when the movement is performed while the foveating saccade is prevented (26,29,208,219). Despite this limitation, which characterizes signals related to the position of gaze as well (see The optimal range of gaze direction cooling subsection), it is the peripheral part of the retina which is most often involved in the initial localization of a visual target (15).

In addition to the retinal signal, the position of the eye in the orbit is necessary to encode the location of the target in a body-centered frame of reference. Paradoxically, without retinal signal, orbital eye position appears to be only coarsely encoded by extra-ocular signals. Indeed, when subjects are required to point in darkness in the direction of their eyes, final hand position correlates to eye position but the scatter is much higher than when the target is a luminous spot (29). The possibility that retinal and extra-retinal signals do not simply add but also interact with each other has been raised in two behavioral studies. In the first one (206), subjects were asked to point at a peripheral visual target presented in a dark room. Whereas vision of the arm/limb was never available during the movement, testing conditions differed according to the duration of target presentation. In two of these conditions the target either disappeared 120 ms after the completion of the orienting saccade (interrupted target: IT) or remained illuminated for 2 s, a period of time far longer than necessary to complete both ocular and manual responses (permanent target: PT). It was found that the accuracy of the pointing movement was reduced in the IT condition as compared to PT. Since visual feedback from the limb was not available, this result indicated that visual signals from the target could update or refresh an internal representation of the goal which drives the pointing hand. There were two possibilities why this updating was not optimal in the IT condition: (a) extra-retinal signals were inaccurate because the eyes were not so closely aligned with the extinguished target or (b) extra-retinal signals were accurate but an optimal updating of target internal representation also required a permanent retinal signal. Although the methods did not allow quantitative analysis of absolute eye position, there are some reasons to believe that gaze was accurately anchored on the target in both IT and PT conditions. First, secondary

saccades were observed in both conditions. Second, previous quantitative analyses have shown that secondary saccades are truly corrective and fully eliminate any eye-to-target error when the target is extinguished 100 ms after completion of the primary saccade (210) or even during the deceleration phase of the primary saccade (209). Therefore, it was concluded that accurate encoding of target location requires concomitant foveal and extra-retinal signals. This may appear paradoxical as the foveal signals define a null information from an analytical point of view. This paradox may be explained by assuming that the biological association between an eye position signal and a retinal signal does not correspond to the analytical operation of addition. Compatible with this hypothesis is another study (23) that suggested that retinal signals can gate extra-retinal signals in target localization. In this study, subjects were asked to make a voluntary saccade in darkness and, after they had returned their eyes to the central fixation stimulus, to position a laser spot with a press-button device at the same location they thought they had reached after the initial saccade. This perceptual measure was compared between two conditions. In the first one, a laser spot was flashed for 200 ms after the saccade such that it stimulated the foveal region of the retina. In the second condition, the laser flash was replaced by a brief auditory signal coming from a fixed location relative to the subject. Using this procedure, the authors observed a significant improvement of the estimated post-saccadic eye position in the former condition (higher correlation with actual eye deviation and smaller constant error). Considering these two psychophysical studies together, it appears quite clearly that (a) the biological association between retinal and extra-retinal signals is not linear, and (b) retinal signals contribute more than expected based on a purely analytical basis. This conclusion will have important implications when considering the underlying neurophysiological basis as well as the capabilities of target encoding as studied in more natural and structured visual environnements (see subsection on The role of allocentric cues).

At the neurophysiological level, the search for interactions between retinal and extra-retinal information has stimulated many studies on the neural code of target internal representations. Two different conceptions have emerged: single-unit versus distributed coding.

The single-unit coding concept of integration hypothesizes the existence of individual neurons coding an information about target position, irrespective of eye position. In support of this hypothesis, individual neurons sensitive to elementary variables (retinal and eye eccentricities) and representing symbolic parameters such as target location in a head-centered or in any other reference system, have been described in several studies (232,103,89,96,97,121,71). Among these neuronal activities, those described by Graziano et al. (121) seem to code the position of a visual target in a hand-centered frame of reference. They might hypothetically result from an ultimate stage of coordinate transformation necessary to direct the hand toward a target.

By contrast to the single-unit conception, the distributed coding hypothesis assumes a statistical combination of elementary information about retinal eccentricity and eye position within large neuronal populations. In favor of this concept, there is a growing body of evidence for population-based interactions between retinal and extra-retinal

information. In particular, the visual or fixation-related activity of neurons in many cortical and sub-cortical areas conforms to retinotopically organized receptive fields but, at the same time, is modulated by extra-retinal signals of eye position (7,96,98,167,89,30,232,34,270). Interestingly, this multiplicative modulation of neuronal visual responses by eye position concurs with psychophysiological data that suggested a non-linear interaction between retinal and extra-retinal signals (23,206). Based on neural network modelling, Zipser and Andersen (275) showed that these characteristics of individual neuron discharges are compatible with the existence in the parietal cortex of a distributed code for egocentric target localization. This proposed role is consistent with classical views of parietal function (182,6,142,198). Note, however, that the mere presence of modulations of visual discharges by eye position does not for certain indicate a specific role of a given neural structure in target localization. Indeed, modulations of this sort have been found in many structures extending from the early stage of the visual system [down to V1 (270) and LGN (167) up to premotor centers (premotor cortex: (34,89), and superior colliculus: (194))]. It is at present difficult to conceive how such widely separated brain areas cooperate in a common function of visual target localization.

Looking at how head position signals are integrated to retinal and eye position signals has stimulated less neurophysiological investigation. Recently, Andersen and colleagues (42) have reported that the visual response of parietal cortex neurons is modulated by the direction of gaze (integrating both eye and head components). This result suggests that the distributed coding hypothesis of target relative to the head can be generalized to visual target encoding in trunk-centered coordinates. Thus, target-related information in a body reference system seems to be distributed in large neuronal populations.

Note that the single-unit and distributed concepts are not mutually exclusive. Indeed, symbolic information generated by distributed neuronal populations may ultimately converge at the output level to provide a single-unit representation. For example, the distributed model of Zipser and Andersen (275) yields an output signal of target position relative to the head which is represented at a single-unit level. In addition, a recent electrophysiological study of ventral intraparietal neurons in the monkey showed that the visual response of single units reveals a continuum between head-centered coding and retinotopic coding, leading to the hypothesis that ''space may be represented in the cortex both at the population level and at the single cell level'' [(71), see p. 847]. More generally, a perceptual or motor representation coded in a single-unit form has often been incorporated in conceptual models between sensory and motor-distributed representations, except for the simple case of non-redundant actuators (159).

The afferent and/or efferent nature of positional signals

Another problem raised by target coding processes is related to the nature of the positional signals. There has been a long debate about the sensory versus motor (efferent) nature of eye position extra-retinal signals [see, for review Refs (139,173)]. The emphasis has been put initially on efferent information derived from the oculomotor system. Three main lines of evidence were successively evoked.

First, some early studies have seriously questioned the

role of proprioceptive afferents in eye position sense. Indeed, it has been reported that passive movements of the eyes do not provide conscious perception of eye displacement in human subjects (41) and do not evoke any stretch reflex in the monkey (153).

Second, the role of the oculomotor efferent signals in target localization has been shown during perceptual and motor tasks in human subjects. In particular, it has been suggested to account for the past-pointing effect seen in patients with paralyzed eyes. When these patients attempted to look and point at a visual target, the hand overshot the target, suggesting a role of the oculomotor efferent signals in target localization (199). This hand motor effect is consistent with shifts in the perceptual estimate of target position (oscillopsia) that are observed when a subject with weakened eye muscles attempts to look at visual targets (174). Additional evidence for an efferent contribution to eye position sense comes from eye-press experiments in normal subjects. Pressing on one eye of an individual while the other eye is covered results in a shift in the perceived location of the target being fixated. This shift, which can be measured perceptually or by a hand pointing response, was interpreted as a change in the efferent signals related to the increased effort to maintain eye fixation (39,36,249).

Third, a large number of studies on the oculomotor saccadic system have provided compelling evidence for the existence of a non-sensory eye position signal. In their pioneering study, Hallett and Lightstone (127) demonstrated that the saccadic system did not only use retinal information about the location of a visual target. Subjects had to follow a visual target which was presented at two locations in rapid succession, in such a way that the second target flash had already disappeared when the subject made the first saccade. If the second saccade was encoded only on the basis of retinal signals evoked when the eyes were at their initial position, an error equivalent to the intervening eye displacement (i.e. saccade to first target) would be expected. In fact, the results showed that the second saccade landed close to the location of the second target flash, indicating that the saccadic system can take into account the intervening change in eye position without visual feedback. Based on these findings, which have been reproduced in several studies [reviewed in Refs (11,247)], the authors suggested that a saccade target is encoded in a head-centered frame of reference, which requires accurate monitoring of eye position and adding this signal to the retinal signal. This idea was supported by data from a series of animal experiments using intracerebral stimulation to perturb eye position. In a pioneering study, Mays and Sparks (176) electrically stimulated the motor layers of the superior colliculus during the latency period of a saccadic response toward a stimulus flashed in the dark. As in the double-step paradigm, the ocular perturbation evoked in darkness by the electrical stimulation allowed the testing of whether saccades rely only on the initial retinal signal. The results clearly showed that saccades compensated for the ocular perturbation and landed quite accurately on the location of the remembered target, which confirmed the original data and conclusions of Hallett and Lightstone (127). Moreover, the same group (124) reported that monkeys with deafferented eyes can still compensate for electrically induced ocular perturbations, which strongly suggested that the eye position signal involved in these compensations is not

proprioceptive in nature. Note that both these compensatory responses were also observed in the head-unrestrained condition for saccades of gaze (eye-in-space) (196) and that compensation can occur on-line when the on-going saccadic eye (or gaze) trajectory is perturbed in-flight [see, for reviews, Refs (195,152)].

The notion that an efferent signal of eye position is used by the saccadic system has been initially formalized in a model centered on an internal (or local) feedback loop that continuously monitors eye position by using a copy of the motor commands (217). More recently, a competing variation of this model proposed that the actual feedback signal does not code the absolute position of the eyes but their displacement achieved since the saccade onset (144). It is not within the scope of this paper to compare these models; more important in the present context is to stress that both models, as well as all their derivatives [reviewed in Ref. (264)], use eye-related (position or displacement) information derived from the oculomotor commands. At the neurophysiological level, many studies have described neuronal activity compatible with the use of an eye position signal by the saccadic system to encode targets. The first of these studies used Hallett and Lightstone's double stimulus paradigm while recording from SC deep layers (177). The authors first showed that monkeys can compensate for the intervening eye movement when programming the saccade toward the second target. Regarding the activity of deep SC neurons, they showed that one cell type (the quasi-visual or QV cells) signaled the separation between the current eye position and target-remembered location (motor error), rather than the retinal separation between the target flash image and the fovea (retinal error) [see also Ref. (248)]. These findings showed that the combination between retinal and extra-retinal signals, suggested by the behavioral data, occurred upstream from the QV neurons of the deep SC. Together with similar findings in cortex [see Refs (274,247) for reviews], these results suggested that visual activity in SC and cortical eye fields are remapped with each eye movement. Interestingly, a recent study suggested that a remapping of visual space can even precede the saccade in the parietal cortex (72). These authors showed that presenting a target when the monkey is preparing a saccade that will bring the neuron's receptive field toward the target location can elicit a neuronal discharge at a shorter latency than the visual feedback delay and for some neurons, even before the eyes start to move. The discharge that anticipated the actual visual stimulation was interpreted as a pre-saccadic shift of visual receptive field. For the present discussion, this finding indicates that eye position (or displacement) information involved in this anticipatory visual remapping cannot derive from oculomotor reafferent signals. Altogether, these electrophysiological studies suggest that non-proprioceptive eye position (or displacement) information is available to many brain areas and is likely used to encode target position independent of eye movements. When considered with the above observations on perceptual and hand pointing responses, these data on the saccadic system strongly suggest that efferent signals are used in eye position coding.

The idea of an exclusive contribution of efferent information in eye position encoding is difficult to reconcile both with the known widespread distribution of extra-ocular proprioceptive afferents in neural structures [see Ref. (43)
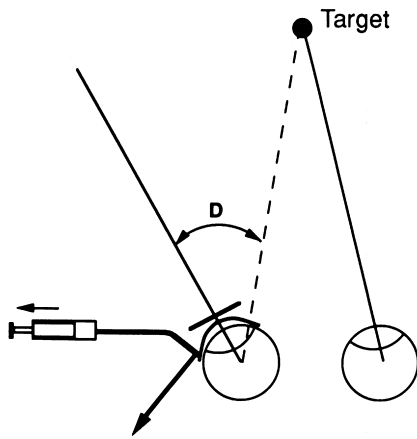
FIG. 1. Passive eye deviation technique to study visual target localization. The subject task is to manually point at a visual target viewed monocularly. The covered eye is displaced passively from its normal orientation (dashed line) using a contact lens secured to the cornea by an air vacuum produced by a syringe. Because of the law of equal innervation, this experimental strabismus does not affect the eye muscle activation of either eye and the resulting changes in localization are attributed to changes in ocular muscle proprioception. [Modified from Gauthier et al. (100).]

for a review), and with several experiments demonstrating the role of ocular proprioception in spatial perception. Concerning this latter point, Skavenski (239) used, for instance, a sensitive forced choice procedure to demonstrate that subjects could detect the direction of a passive eye deviation. He further showed that subjects could use this crude proprioceptive information to maintain gaze direction aligned with a previously lit target in darkness. Also, Stevens et al. (253) reported that attempts to make eye movements when both eyes were completely paralyzed did not induce oscillopsia, suggesting that oscillopsia in paralyzed subjects could result from proprioceptive inflow related to residual eye movements. Although the experiment of Stevens et al. seems to rule out the role of efference copy, another interpretation of their results can be proposed. Indeed, their measurements were performed in the presence of a structured visual background and subsequent studies showed that such visual environments can completely suppress the role of extra-retinal signals in target localization (see subsection on The role of allocentric cues). Other arguments for the role of extra-ocular proprioception come from studies in deafferented patients (252,251), from ocular muscle vibration experiments (218,265) and from passive eye deviation paradigms (36,100,101). Gauthier and coworkers (99–101) performed a quantitative evaluation of the contribution of proprioceptive signals to eye position by inducing in human subjects an experimental strabismus and testing manual pointing responses toward visual targets (Fig. 1). Graded deviation of the non-viewing eye led to a significant and proportional hand misreaching, corresponding to about one-sixth of the passive ocular deviation. Since this mechanical deviation of the covered eye is supposed not to alter muscle activation in either eye (law of equal innervation), hand misreaching was interpreted as the result of the effect of changing ocular muscle proprioception. Because proprioceptive signals from both eyes are normally involved (265), the net contribution of proprioceptive input to eye position sense was calculated to be about 30% (99–101). This lies close to the 25% contribution

estimated by manually pressing on the covered eye (36). In summary, it appears that both efferent and afferent signals can be used to encode static eye position when guiding a hand pointing response, with a larger contribution of the former.

Mechanisms presented so far are involved in encoding the egocentric direction of a visual target. Note that in a normal 3-D environment, reaching for an object also requires an evaluation of its absolute distance from the observer. This requirement of an accurate depth perception can be evidenced by the reduced pointing performance under monocular viewing condition relative to binocular viewing (237). Depth perception is achieved by combining signals extracted from visual cues (disparity and size of retinal images) with extra-retinal signals (vergence angle, lens accommodation). However, despite a growing number of behavioral studies [e.g. (90,92,54,75,94,261)] and of neurophysiological recordings (5,116,259,230), it appears that the mechanisms encoding the target location in depth are less understood than those involved in directional coding.

As seen above, the transformation of retinal signals into a body-centered representation must not only incorporate knowledge about eye position but also about head position. Although processes of head position coding have been less investigated than those of eye position coding, it is known that proprioceptive input is essential in providing head-to-trunk information. Indeed, misreaching of the limb has been reported after injection of local anesthetics in the vicinity of the dorsal roots at the C1–C3 level, in both monkeys (53,61) and humans (61). Vibration of neck muscles in man also impairs pointing responses toward a visual target, and is accompanied by an illusory sensation of movement of the visual target being fixated by the subject (13,218,256,148). Signals from the vestibular system may also contribute to head position sensing. In essence they provide information about the position of the head in space. In addition, they can assist proprioceptive information in sensing head-to-trunk position. Indeed, the perceptual estimate of passive head rotation on the stationary body has been shown to be better (lower threshold and more veridical sensation) than that of passive trunk rotation relative to the stationary head (256,178).

The optimal range of gaze direction coding

That the central part of the retina achieves the most detailed sampling of the visual scene is a natural consequence of its structure, and arguments for an optimal target localization in the central visual field have already been presented above (208,26,29). In contrast, it is not clear whether a most efficient coding of eye and head position in the central range of ocular and cephalic motility can be expected a priori. An answer to this question derives from behavioral studies suggesting that not only the retina, but the eye and the head each have a central optimal range in providing positional information (14,219,262,227). Altogether, these studies suggest that target encoding capabilities tend to degrade both when the visual target is presented at increasing eccentricities relative to the retina, and when the eyes and head are deviated too far from their normal resting position. Thus, some constraints seem to dictate a preferred configuration of the visual/gaze system to define target localization. This optimal condition would be achieved when gaze has captured the target (retinal image

centered on the fovea), head orientation has re-centered the eyes within their optimal range and, when initial target eccentricity is too large, the trunk has rotated to bring the head back within its optimal range. Under normal circumstances of simultaneous activation of gaze and limb motor responses, this condition is met only after the arm has started to move (15). Therefore, this gaze-related updating of target internal representation can potentially influence the on-going hand trajectory by feedback and feedforward mechanisms, the description of which is beyond the scope of this paper.

In summary, the above review reveals two main features of the target localization mechanisms. First, the neural implementation of the combination between retinal and extra-retinal signals does not correspond to a simple linear addition. Instead, these signals seem to combine synergistically to sharpen the accuracy of target location information, and this interaction occurs, at least in part, in parallel within large neuronal populations. The synergistic nature of this interaction explains that the overall accuracy in target localization sometimes exceeds that of the retinal or extra-retinal component studied in isolation. Second, the coding of target direction requires both extra-retinal information of conjugate eye position and head position information that derive from different sources. Eye position information is largely provided by efferent oculomotor signals with a smaller but significant contribution of extra-ocular proprioception; instead, sensory (proprioceptive and vestibular) inputs predominate for head position coding. It will be seen below (Determination of the initial configuration of the arm section) that proprioception also plays a major role regarding hand position coding. Thus, the predominance and reliability of efferent information in providing eye-related information can be explained by the simple geometrical and mechanical arrangments of the oculomotor apparatus as compared to those of the head and arm.

The role of allocentric cues

The discussion so far leads to the view that the localization of visual targets in body-centered coordinates is based on the combination of retinal signals and extra-retinal signals of eye/gaze position. We have pointed out that this interaction may be more complex than a simple analytical operation and, for instance, some observations suggest that visual information may gate input signals of eye position. It must be stressed that most of the studies reported in the previous sections were deliberately performed in an impoverished visual environment (generally using as visual target a small luminous spot in an otherwise dark field). It is thus worthwhile asking if a visual target can be encoded more accurately in natural environments. In particular, the presence of a structured visual background provides landmarks that could improve target localization. In the following, we review arguments for the use of such allocentric (or exocentric) cues in the production of accurate goal-directed hand movements.

The first indication that a structured visual field can improve target localization was provided by Conti and Beaubaton (55) who separately manipulated vision of the hand from vision of the background. They found moderately slow hand pointing to be more accurate when performed in a structured visual background than in the dark. This observation was further confirmed and expanded by Velay and Beaubaton (266) who demonstrated that movement final accuracy was improved when a visual context was provided during movement planning only. This significant contribution of environmental cues on target localization was reproduced in a recent study (50) but not in others (228,24,258). These discrepancies suggest that the implication of allocentric cues in target localization may depend on experimental conditions. Interestingly, in a recent study, Blouin et al. (24) tested the effect of visual background in a deafferented patient. In contrast to normal subjects, this patient made large errors in pointing toward a visual target in the absence of visual background, and these pointing inaccuracies were strongly attenuated, albeit not eliminated, in the presence of a structured visual field. The authors concluded that allocentric cues can be extracted from the visual environment to compensate for the patient's altered abilities to localize a visual target with respect to his or her body. This study therefore raises the possibility that the role of allocentric cues in target localization is particularly important when the normal operation of the sensori-motor system is perturbed.

Probably the most convincing argument for the use of allocentric cues, in the target localization phase of movement generation, was provided by studies dealing with the interaction between a complex retinal signal and extra-retinal signals of eye position. In these studies, the effect of various manipulations of eye position sense [attempt to move weakened eyes muscles (174), passive eye deviation (38), ocular muscle vibration (265)] was tested in the presence or absence of a structured visual field. Recall (The afferent and/or efferent nature of positional signals section) that in the absence of a structured visual field (darkness condition), these experimental changes in eye position sense lead to a profound modification in the perception of target position, as revealed by both perceptual and motor responses. Remarkably, mislocalization was much weaker or even completely absent when a structured visual background was provided (38,174,265). These observations indicated that the use of eye position signals was dependent upon the visual context and that retinal signals evoked by a complex visual scene can almost completely obliterate conflicting extra-retinal signals. They again stress the non-linear nature of the interaction between retinal and extra-retinal signals and suggest that the weight of visual information may be related to the richness of the visual scene. Recently, some evidence for the use of allocentric cues by the saccadic system was provided by Hayhoe et al. (130). In their study, two targets were presented simultaneously for a short period of time and after a short delay, one of the two was re-illuminated. Subjects were instructed to make a first saccade toward the re-illuminated location, and from there a second saccade to the second (remembered) location. In some trials, and unknown to the subjects, the first saccade target was actually re-illuminated in a slightly shifted location, rendering erroneous the allocentric cues about the second target location. In these trials, the second saccade endpoint also shifted in the same direction, but in a smaller proportion than the shift of the re-illuminated target. Thus, in this study the oculomotor system appeared to rely in part on allocentric cues provided by the simultaneous presentation of the two targets. Other recent studies also suggested that saccadic programming may benefit from allocentric cues provided by a visual background (137) or by two flashed visual targets presented

without temporal gap (59). Note that in all the above studies showing a consistent effect of allocentric cues, the experimental procedure introduced a discordance between these cues and the extra-retinal signal of eye position (either by perturbing this signal or by changing eye position itself). This suggests that the role of allocentric cues can be more clearly demonstrated when they conflict with extra-retinal information.

Interestingly, not only the availability of environmental cues can determine the way a visual target is encoded, but also some factors related to the requirements of the task. One of these factors is the timing of the motor response with respect to the visual stimulation [(37), for review, Ref. (222)]. As an illustration, we will present data by Bridgeman (37) which showed that the delay of a goal-directed hand pointing with respect to the extinction of the visual target interacted with the visual environment in which the target appeared. The experiments were as follows. Ten subjects were presented with a visual stimulus consisting of a spot enclosed within a visible rectangular frame. The target spot was randomly presented at one of five positions relative to the observer; the rectangular frame could be located straight ahead with respect to the observer, or located asymetrically to the left or to the right of the straight ahead direction. Both target and visual frame were presented for one second, after which subjects were asked either (1) to judge which target had been presented (perceptual response) or (2) to aim at the target with a pointer (motor response). Perceptual and motor responses were recorded in different trials that were randomly mixed within single experimental sessions. These responses were delivered immediately after the extinction of the visual stimulus or 4 s after stimulus offset, in two separate experiments. The results were different for perceptual and motor responses. Perceptual responses were systematically affected by the position of the frame such that the target was perceived closer to the nearest border of the frame (Roelofs effect). This effect was observed for all subjects in the immediate response experiment and for almost all (eight out of nine) subjects in the delayed response experiment. In contrast, motor responses were differentially affected depending upon their delay from target presentation. Responses delayed by 4 s were, in eight out of nine subjects, affected by the illusion induced by the position of the visual frame, suggesting that target localization was influenced by allocentric cues. In the case of immediate responses, five subjects relied on egocentric cues for locating the target such that their hand movements were not affected by frame position, while the remaining five subjects had a biased hand response which denoted an influence of allocentric information on target localization. These results clearly indicate that the use of allocentric cues in visuo-motor control depends on the delay of the motor response, with an increased propensity to use these cues when the motor response is delayed [see also (102)]. More recently, it has been shown that delayed pointing movements towards a visual or a proprioceptive target are influenced by the geometrical configuration of the target array used during the experimental session [review in Ref. (222)]. Specifically, the spatial distribution of delayed pointing endpoints to a given target, as measured by the main orientation of the confidence ellipse fitted to the scatter, varies according to the location of the other targets. Indeed, the confidence ellipses for movements directed toward a single target but recorded in two separate sessions can lie orthogonal to each other when only the orientation of the target array differs between these sessions (224,223). In contrast, no such difference in endpoint distribution is observed for immediate pointing movements. This result strongly suggests that delayed action is more likely to rely on a location information based on an allocentric representation of space, even though no external frame of reference was explicitly provided to the subject.

The results presented above (37,222) support the hypothesis of two separate representations of space: a ''cognitive'' one based on allocentric information and influencing the perceptual system and a ''motor'' one driving the sensorimotor system with a target position signal coded in egocentric space [(40,190); see also Refs (118,197) for further experimental evidence]. This hypothesis is compatible with the existence of dissociations, in brain-lesioned patients [e.g. Refs (257,44,213)] and monkeys [e.g. Ref. (203)], between the abilities to judge the position of a visual stimulus with respect to the body and to estimate its position with respect to other features of the visual scene (213). It agrees with suggestions that localization processes based on egocentric and allocentric cues are implemented in different neural structures (190,250).

Note that the existence of specific neural mechanisms using allocentric cues can be further illustrated by two examples. The first one is provided by patients suffering from left hemi-neglect [see for review Ref. (198)]. Owing to a right parietal lesion, these patients have lost any conscious awareness of stimuli situated in their left hemi-field, a deficit that cannot be explained by a pure sensory defect. Interestingly, some of these patients continue to neglect the left part of objects when presented in their right hemi-field (47,49). Without excluding the presence of deficits affecting the left hemi-field or hemi-space, this observation indicates that the lesion has impaired some mechanisms using allocentric cues to build a conscious representation of the environment. Another illustration of the presence of neural processes dealing with allocentric cues comes from a recent neurophysiological study in the primate (187). In this study, the neuronal activity was sampled in the frontal lobe (supplementary eye fields) of monkeys engaged in a saccade task designed to separate the oculocentric direction of the requested saccade from the object-centered direction (i.e. a rightward saccade could actually direct the eyes to the left of an object and vice versa). Surprisingly, a majority of neurons showed a higher specificity in their discharge to the object-centered direction of the saccade than to its oculocentric direction. This means that a typical neuron would discharge most when the animal intends to make a saccade toward one end of a horizontal bar (e.g. left), irrespective of the position of the bar with respect to the animal and thus of the oculocentric direction of the saccade. These unit recording data provide strong evidence that neuronal circuits involved in motor planning can extract allocentric cues from the visual environment.

In summary, the experimental data that convincingly support a role of allocentric cues in target localization are relatively limited to date. However, this may not be surprising as regards the few studies that have specifically addressed this question by using structured visual environments. Also, the use of allocentric cues seems to depend

upon specific requirements of the task, a possibility that may render a demonstration more difficult. From the present review, it appears that the clearest evidence for the use of allocentric cues are provided by experimental paradigms that either perturb the normal operation of the sensori-motor system (passive eye deviation or vibration, deafferentation, central lesions) or place it in more challenging situations (withheld the motor response during some delay). This last remark suggests that allocentric cues may be used to improve target localization when facing challenging conditions. However, a better understanding of the conditions that benefit from allocentric cues and of the interaction between allo-centric and extra-retinal information must await the development of behavioral and neurophysiological studies testing systematically the effect of different visual environments.

Determination of the initial configuration of the arm

In order to understand how goal-directed movements are generated, it is of prime importance to determine whether or not the nervous system needs to know the state of the motor apparatus prior to movement onset. As shown in this section, this question has remained controversial for years, and contrasting experimental data can be found in the literature. Initial experiments on monoarticular movements have suggested that accurate pointing can be performed without proprioception in certain conditions, whereas more recent studies provide evidence that manipulating the information available prior to movement significantly alters the action. This latter evidence will have important implications in The trajectory formation section when considering the putative ways in which multiarticular movements are programmed by the CNS. After reviewing the crucial issue of deafferentation, implication of information about the initial hand position in motor programming will be demonstrated by reviewing specific manipulations of this information.

Deafferentation studies

Since the end of the 19th century, deafferentation has provided a key means to investigate the role of initial hand position in motor control. Humans or animals deprived of proprioception were initially shown to be unable to locate their arm in the dark and thus to produce accurate movements [(238), for a review, see Ref. (143)]. However, later studies in deafferented patients and monkeys did not fully confirm these pioneering observations and suggested that accurate movements were possible in the absence of peripheral afferents [e.g. Ref. (170)]. In the 1960s, Lashley's idea was reformulated by Feldman who proposed that the limb configuration to be achieved could be determined irrespective of the starting configuration, by specifying only the intended end position [(80), review in Ref. (78)]. This influential view gave rise to several lines of research [review in Ref. (16)]. Experimental support for this theory was first obtained for head movements in deafferented monkeys (21,22), and then replicated for arm pointing (204). In the latter experiment three monkeys were trained to perform single joint pointing toward visual targets presented in a dark room, with their arm fixed in a manip-ulandum (only the elbow joint was allowed to move in the horizontal plane). The visual target, randomly chosen among a set of 17 LEDs distributed every 5° in front of the monkey, was randomly presented and the animal had to

point towards it with an accuracy of about 15°. Intrathecal deafferentation of the arm territory at the dorsal root level (C2–T3) was then performed and controlled by a stretch–reflex recording. After recovery from surgery, deaf-ferented monkeys were still able to reach the targets with relative accuracy. When the elbow angle position was unexpectedly modified by transiently loading the arm-splint about 150–200 ms prior to movement onset, neither normal nor deafferented monkeys displayed a significant decrease in accuracy or precision. The same was also true when the load was applied to the ongoing elbow movement. From these findings, Polit and Bizzi (204) concluded that joint movements depended mainly on neural patterns spe-cified before movement onset. They also suggested that, through the selection of a muscular equilibrium point, these preprogrammed patterns defined a mechanical attractor which could be reached without knowledge of the initial configuration of the motor apparatus (see The equilibrium-point hypothesis section for a more detailed discussion of this point).

The generality of this last conclusion was, however, chal-lenged by several experimental observations, among which three were particularly important. First, the deafferented monkeys trained by Polit and Bizzi (204) were unable to compensate for perturbations affecting the canonical pos-ture of their upper arm: when the center of rotation of the elbow joint was shifted forward by changing the canonical elbow angle, the monkeys were no longer able to accurately reach the targets. In addition, their pointing also became inaccurate when the arm-load was sustained throughout the movement. Second, the ability of deafferented patients to perform relatively accurate monoarticular movements in the dark (19,21,22,154,229,231) could never be generalized to multi-joint skills: subjects deprived of proprioception exhi-bit severe deficits when forced to perform multi-joint skills without vision of their limb (33,157,255,229,231,111,112). Third, manipulating finger starting position [e.g. Ref. (140)] and/or hand posture prior to reaching to grasp initiation (158) have been found to alter movement characteristics in normal subjects. This latter evidence will be addressed in more detail in the manipulating information on the static hand section.

When considered together, deafferentation studies suggest that the ability to perform accurate multi-joint movements requires the knowledge of the position of the limb segments with respect to the body.

Manipulating information on the static hand

The previous results provide only a partial demonstration that defining the initial state of the effector is a necessary step of movement planning. Indeed, the specification of the intended end-position may involve the proprioceptive sys-tem (77,76). In addition, complete deafferentation affects both the planning and the execution phase of the movement. Finally, as noted by Feldman (78), movement generation might involve different processes in intact and abnormal subjects. For these different reasons, deficits following complete deprivation of proprioceptive inputs cannot be unambiguously attributed to an altered coding of initial limb conditions.

To overcome these limitations, one may seek for a pos-sible relationship between the pointing accuracy in normal subjects and the available sensory information of the initial

state of the motor apparatus. For instance, vision of the hand prior to movement initiation has been shown to greatly improve the accuracy of movements performed by deafferented patients (111,112). A method to test the effect of visual information of the limb on movement accuracy consists of specifically allowing and disallowing the view of the hand prior to movement. This was initially done by Prablanc et al. (207) who compared the accuracy of visually directed movements performed under two different conditions. In the first one, vision of the hand was never allowed to the subjects (FOL: full open loop). In the second one, vision of the hand was allowed only in static position prior to movement onset (DOL: dynamic open loop). Results showed that movement accuracy was significantly better in the DOL than in the FOL condition. These data, which were subsequently reproduced by several authors (73,74,68,226,113), were interpreted in terms of optimization of the hand localization process when vision was available in addition to proprioception. The validity of this interpretation was, however, questioned by recent studies suggesting that the positive effect of viewing the arm at rest could be related, not to a better estimation of the initial state of the motor apparatus, but to the simultaneous vision of the hand and target during movement planning (211,24,226,214). In order to test this hypothesis, Desmurget et al. (66) analyzed whether viewing the right hand in static position prior to movement could affect the accuracy of pointing movements performed toward the unseen left hand. Results of this analysis showed that end-point accuracy was significantly better in the DOL than in the FOL condition. These data indicated that viewing the right hand prior to motion was sufficient to improve the subsequent movement, and hence suggested that accuracy of pointing to visual targets did not only depend on the simultaneous vision of the goal and the effector during movement planning. Such a finding confirmed that knowledge of the initial upper limb configuration (or hand position) was necessary to accurately plan multi-joint movements.

Another fruitful method to investigate the contribution of the knowledge of the initial state of the motor apparatus on performance is to alter the view of the limb prior to movement onset. For instance a sensory conflict can be introduced between the visual and proprioceptive cues related to the initial hand position. This was done by Rossetti et al. (225) [see also Ref. (141)] who asked human subjects to point toward visual targets without visual reafference from their moving hand in two conditions (Fig. 2). In the first condition, the pointing fingertip was viewed through prisms that created a visual displacement, while the target was presented outside the shifted field and thus was normally seen not only the lower part of the visual field. Presence of the proprioceptive–visual mismatch was not detected by most of the subjects. In the second condition, both the index fingertip and the target were seen normally, i.e. the relationship between the hand and the target was not altered. Comparison between these two conditions showed that the visual shift of the fingertip position prior to movement induced a systematic bias of the movement end-point, in a direction opposite to the visual shift. Note that a related method to manipulate the information about the initial hand position is to alter proprioceptive signals through tendon vibration. Human subjects were found to be inaccurate in reproducing a learned position of the elbow joint when a

vibration was applied to the biceps prior to movement onset (169). These two experiments demonstrated that accuracy of arm movements was linked to the sensory encoding of the initial state of the motor apparatus.

The interference between movement amplitude and location information, a well-known phenomenon in motor–short term memory research (268) provides further arguments for the crucial role played by the information about the finger starting position. It manifests itself in a characteristic pattern of response bias, such that, when the starting position for a reproduction movement is different from that of a criterion movement (without the subject being informed about this modification), the movement end-point reproduced by the subject is systematically biased in the direction of the change in initial position. One particularly important aspect of this phenomenon was that even when subjects are instructed to concentrate on the end-location of the criterion movement and to ignore its amplitude, the reproduction movement is unavoidably influenced by the actual starting position (140). Thus, this more cognitive line of research also demonstrates that initial hand position is a crucial parameter for programming a movement to a previously encoded location. Note that the result reported by Imanaka and Abernethy are congruent with the observation that end-point errors tend to accumulate during sequential pointing performed without vision of the limb (28,25).

Electrophysiological studies

As there is a convergence between psychophysics and electrophysiology in the study of target encoding (Determination of the target location section), it is interesting to seek electrophysiological evidence supporting the hypothesis that the initial arm position is used to plan the movement. Unfortunately, most emphasis has been put on the vectorial aspect of movement coding [(108); reviews in Refs (106,104)], and there are only a few studies in the literature that attempted to systematically investigate the coding of arm position by cortical neurons in the context of action. There is some evidence that static arm position is encoded in the parietal cortex [e.g. Ref. (107)] and in the motor cortex [e.g. Ref. (155)]. More specifically, the modulation of neuronal activity with arm position was shown to be contingent upon motor preparation in both the motor and premotor areas (10). In the posterior parietal cortex, some neurons in area 5 seem to discharge prior to and during the movement in accordance with initial position (81,162). In addition, the observation that the coding of target location can be affected by the arm position in space provides further arguments for the implication of initial hand position in the neuronal coding of action [Determination of the target location section (121)]. Taken as a whole, electrophysiological studies do not place much emphasis on the coding of initial hand position. However, the most recent results seem to follow the psychophysical evidence for a coding of initial hand position in the motor system.

In summary, the elimination or the alteration of visual and sensory information about the limb prior to movement clearly affects pointing accuracy. The data presented in this section provide converging evidence that defining the state of the effector prior to motion is a necessary step of movement planning. The question of knowing whether this definition is performed in angular (postural configuration of the upper limb), or spatial (position of final effector,
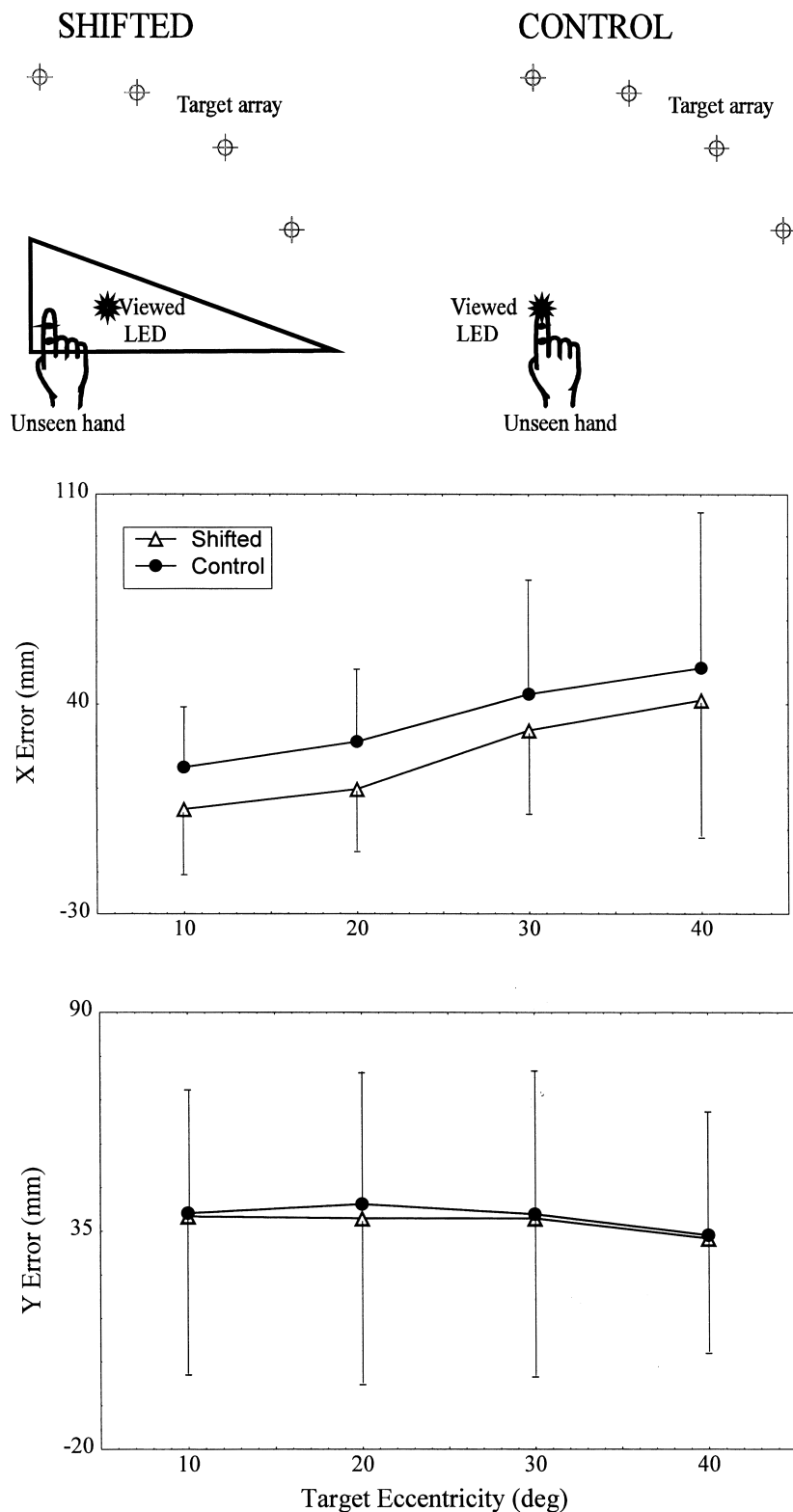
FIG. 2. Relationship between the movement end-point accuracy and the information available to estimate the initial state of the motor apparatus. Subjects were required to point in the dark toward visual targets presented in the right hemi-field. Two conditions were considered (upper panel). Control: the real and viewed position of the finger (LED on the fingertip) were the same. Shifted: the hand was viewed through prisms that created a visual displacement to the right (the targets were not displaced). Comparison of these two conditions showed that virtually shifting finger position before movement onset induced systematic bias along the x axis, in a direction opposite to the initial shift (middle panel). No significant bias was observed along the y axis (lower panel). This result is consistent with the hypothesis that visually directed movements are planned vectorially, that is as a mismatch between an initial and a final state. They also suggest that both visual and proprioceptive information, when available, are used to estimate the finger starting position. [From Rossetti et al. (225).]
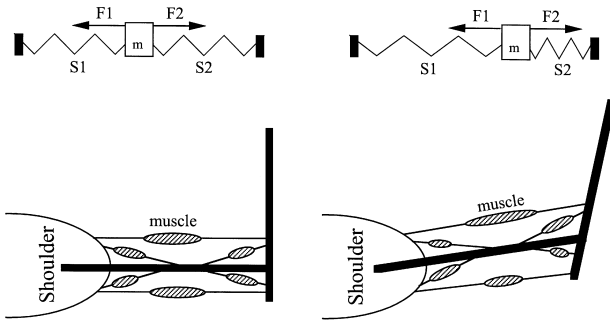
FIG. 3. Schematic diagram illustrating the theoretical foundations of the equilibrium-point hypothesis. When the forces (F_1, F_2) exerted by the springs (S1, S2) are equal, the mass m is in equilibrium. When the stiffnesses of S1 and/or S2 are modified the mass m moves to reach a new equilibrium state. If follows that a simple way to control the spatial location of m is to adjust the stiffnesses of the springs acting on it. Extrapolating from this observation one may suggest that an economical way to bring the hand at a given spatial position is to set the length–tension curves of all the muscles acting on the upper limb in such a way that the torques exerted by agonist and antagonist muscles nullify each other when the hand is at the desired position (see additional comments in the text).

e.g. the fingertip) coordinates, will be considered in the section on Trajectory formation.

TRAJECTORY FORMATION

Although widely addressed during the past decades, the problem of knowing how goal-directed movements are planned by the CNS still remains debatable. The main objective of the present section is to take stock of this issue. To this end, we review the main theories presented in the literature to account for the characteristics of goal-directed movements. For the sake of clarity, these theories are examined in three successive sections addressing the equilibrium-point hypothesis and its related models, the Cartesian and joint space coding hypotheses and the hypotheses related to the optimimal control theories. Beyond this survey we have a double goal: (1) identifying the factors which may account for differences between experimental observations or theoretical models; and (2) providing evidence that the CNS may use different strategies to plan arm movements depending on the constraints of the task. In our view, the examination of this latter hypothesis may advance the field by both opening new lines of research and bringing some sterile controversies to an end.

The equilibrium-point hypothesis

For the sake of clarity, let us introduce the theoretical foundations of the equilibrium-point hypothesis on the basis of a very simple example (Fig. 3). Consider a mass (m) subject to the influence of two springs (S1 and S2). The magnitude of the forces (F_1 and F_2) exerted on m depends of both the stiffness (k) and the length (l) of S1 and S2 ($F = kl$). When F_1 equals F_2, m is in equilibrium. If one modifies suddenly the stiffness of S2 the mass m moves to reach a new equilibrium state. This indicates that a simple way to control the position of m is to adjust the relative stiffnesses of the springs acting on it. The relation between this elementary observation and the general problem of motor

control appears if one considers that the muscles tend to behave like springs whose stiffness may be controlled by the CNS (175,79,212,184). Indeed, the spring-like properties of the biological actuators suggest that an economical way to move the hand to a given spatial position is to set the length–tension curves of all the muscles acting on the upper limb in such a way that the torques exerted by agonist and antagonist muscles nullify each other when the hand is at the desired position. Note, to avoid any ambiguity, the accomplishment of this apparently simple mapping is, in fact, far from trivial for complex systems such as the human arm. Due to muscular redundancy, the correct length–tension curve of the muscles cannot be unequivocally determined. That is, each position of the hand in space can be associated with an infinite number of muscle combinations (151).

As pointed out by Bizzi et al. (16) the equilibrium-point hypothesis is very attractive for, at least, three reasons:

1. no prior ''knowledge'' about the effector configuration is needed to program the movement;
2. when an unexpected external perturbation transiently causes the arm to deviate from its trajectory elastic restoring forces are automatically generated and the movement's final accuracy is not affected; and
3. because the hand driving torques result from the spring-like properties of the muscles, complex inverse dynamics computations are avoided.

A reformulation of each of these points in predictive terms generates three hypotheses: (P1), movement final accuracy should not depend on the ability to locate the limb prior to movement; (P2), movement final accuracy should not depend on the occurrence of transient perturbations during the hand displacement; and (P3), modifications of the inertial properties of the arm should consistently modify the path and trajectory of the movement. Let us briefly consider these three points.

P1: As pointed out in previously, several experimental arguments supporting P1 have been provided by Bizzi's group in the context of monoarticular movements performed by deafferented monkeys (cf. Deafferentation studies section). These arguments were, however, subsequently challenged in a large number of studies indicating that knowledge of the initial state of the upper limb was necessary to accurately plan multi-joint movements (see section on the Determination of the initial configuration of the arm for detail).

P2: Experimental observations favoring the hypothesis that transient perturbations did not affect movement accuracy were provided by Bizzi et al. (see the Deafferentation studies section). As for P1, however, the generality of these observations was strongly questionned in several subsequent studies involving deafferented subjects (60,229,231). Rothwell et al. (229) trained, for instance, a deafferented patient to make rapid flexions of the thumb to a fixed end-position. Whereas the subject was quite accurate in performing this task he was unable to compensate for transient disturbance applied during the movement. Interestingly, a congruent observation was reported in normal subjects by Coello et al. (51,52) and by Lackner and Dizio (161,70). These authors studied reaching movements performed in a room rotating at constant

velocity. The rotation, which was not perceived by the subjects, perturbed reaching movements by adding Coriolis forces to the displacement of the arm. Because these forces are proportional to limb velocity they can be considered as transient from a functional point of view (they are null at the begining and at the end of the movement). The first reaching movements performed by the subjects presented a consistent shift with respect to a control condition (no rotation). This indicates that transient perturbations strongly influenced the movement final accuracy.

P3: If visually directed movements are generated by changing an equilibrium position defined by elastic actuators, the inertial properties of the arm should consistently influence the charateristics of the hand displacement. As a consequence, the hand trajectory should vary both when the arm is loaded with a mass, and when the subject is required to perform the same movement (amplitude, direction) in different areas of the workspace [arm inertia varies with limb posture; (133)]. With respect to these predictions, Atkeson and Hollerbach (9) showed that adding a constant mass to the arm did not consistently affect the hand trajectory [see also Ref. (165)]. At the same time, Morasso (181) demonstrated that the hand path remained roughly invariant irrespective of the inital and final locations of the movements [see also Refs (1,88,120)]. None of these stabilities was predicted by the equilibrium-point model.

The observation that the hand followed invariant paths in the Cartesian space led several authors to hypothesize that the equilibrium configuration of the arm did not shift suddenly to its terminal state but moved gradually along a reference trajectory (20,19,133,134,76). Evidence supporting this view was initially provided by Bizzi et al. (19) in the context of single-joint movements. These authors trained three monkeys to perform forearm movements toward a visual target presented in a dark room. The performance of the animals was tested prior to and after a bilateral dorsal rhizotomy. Two conditions were considered: arm held in the intial position (H), arm displaced toward the target at movement onset (D). As would have been expected if the CNS had programmed a gradual shift of the arm equilibrium position, Bizzi et al. observed for both the intact and deafferented animals (a) that, in H condition, the hand initial acceleration increased gradually with the duration of the holding period; (b) that, in D condition, the forearm moved back in the direction of movement starting point when initially displaced to the target position. This backward displacement was followed by a forward movement allowing the animal to reach the target.

Evidence supporting a generalization of the ''equilibrium trajectory theory'' from single to multi-joint movements was mainly provided by modelling studies combining experimental observations and computer simulations (87,84,129,122). Among these studies, that presented by Flash (87) is indisputably the most classical. This author assumed that visually directed movements were planned by shifting the arm equilibrium point along a straight line. She also stressed that this planned path could be significantly different from the actual path because the elastic forces generating the movement interact with the arm dynamics during hand displacement. That is, even if the movement is

planned to follow a straight line path it can appear slightly curved due to the existence of uncompensated inertial and viscous forces. To test this hypothesis Flash simulated the arm dynamics and compared the trajectories predicted with those experimentally observed. She showed a very good agreement between her model and the behavioral observations. With respect to this result, however, two points must be stressed. First, Flash only considered movements performed at low velocity. Second, she used stiffness parameters defined from static postural measurements (184). These two points were shown to be critical by Kawato and colleagues (149,117). Indeed, these authors demonstrated (a) that muscular stiffness recorded during visually directed movements was much lower than those observed during postural maintenance. With adequate stiffness parameters, the curvature predicted by Flash's model would have been much larger than those experimentally observed; (b) that the ''equilibrium trajectory theory'' would require the implementation of biologically unrealistic stiffness values to account for the straightness of reaching movements performed at medium or fast velocities; and (c) that the only way to preserve the plausibility of the ''equilibrium trajectory theory'' was to postulate the existence of highly complex virtual trajectories which obviously obliterate the advocated computational advantage of this model (as pointed out by Katayama and Kawato defining these trajectories seems to be as complicated as performing inverse dynamic computations).

In addition to the computational evidence put forward by Kawato and colleagues, it is worth mentioning that the ''equilibrium trajectory theory'' is also challenged by several psychophysical arguments. These arguments are related to the large end-point errors observed during reaching movements transiently perturbed by the application of artificial inertial forces (51,52,161,70). They are also associated with the existence of modifications of the end-point accuracy when the initial hand location is misperceived [(28,113,225); cf the Determination of the initial configuration of the arm section]. It is important to clarify this last point since it is sometimes misunderstood (it might seem obvious that the nervous system cannot plan a virtual trajectory if it doesn't know the hand starting point). If movement is generated by shifting an equilibrium position defined by elastic actuators, a deviation from the intended path should result in restoring forces ''pulling'' the hand toward the planned trajectory (18,272). As a consequence, in case of discrepancy between the initial hand position, and the position from which the movement is planned, the hand should ''automatically'' return to the planned path (which behaves like a mechanical attractor), and the final accuracy should not be affected by the initial error.

Before concluding this section, it is worth noting that neurophysiological data provided by Bizzi's group (16,17,115) apparently support the equilibrium-point theory in the context of multi-joint movements. These authors microstimulated the spinal gray matter of spinal frogs and recorded the force generated by the leg. At the begining of each trial the frog's ankle was placed at one different location in the workspace. The results showed that the force vectors elicited by the stimulation varied as a function of the leg inital location. Remarkably, the distribution of these force vectors converged toward a single equilibrium point. That is, all the force vectors were

oriented to bring the frog's ankle to a given spatial location irrespective of the initial configuration of the limb. Although these results were not directly contested it must be stressed that their significance was vigorously questioned. As observed by Cavalerri [(48), p. 723; see also Ref. (172)], ''stimulation of any given point in the cord will almost necessarily activate several different pathways and exite many groups of motor neurons. The related muscle contraction will in turn generate a distributed pattern of elastic forces that will balance in a single equilibrium point''.

In summary, the previous observations suggest that the equilibrium-point hypothesis is mainly supported by psychophysical studies involving single-joint movements. The lack of direct behavioral confirmation in the context of multi-joint movements has led several authors to propose a revised theory through the concept of equilibrium trajectory. This revised theory raises two major problems. First, it abandons the simplicity of the initial model by forcing the CNS to define an entire (and potentially complex) virtual path instead of just an end-point to reach. Second, it is undermined by a wide range of experimental observations. In particular, it is challenged by the observations that the movement final accuracy depends on the ability to locate the limb prior to movement; that transient perturbations applied during the movements are not compensated in deafferented or normal subjects; that the modification of the inertial properties of the arm does not consistently influence the movement path; and that the muscular stiffness cannot reach a sufficiently high level to account for the small curvature observed during planar pointing movements performed at medium or high velocity. Although most of these problems have been acknowledged by Bizzi's group (16), they have not been satisfactorily addressed yet. This obviously cast some doubt on the credibility of the equilibrium-point models.

Task space and joint space hypotheses

As emphasized in the sections on Initial stages of movement planning and Trajectory formation, a large number of experiments dealing with multi-joint movements has demonstrated that both the initial and desired hand positions were essential parameters of motor programs. This observation led many authors to the conclusion that goal-directed movements were encoded as a displacement of the hand along a given pre-established trajectory (181,28,120,225,220,66,237). From a theoretical point of view, such a pre-established trajectory can be specified either in Cartesian or joint coordinates. Let us briefly examine these two possibilities.

Cartesian Coordinates: According to this view, the CNS first selects a given path in the task space. Then, it transforms this path into a pattern of joint covariation. With regard to this transformation it is worth noting that the relation beween the Cartesian and joint spaces is complex and non-linear. This point is important because it implies that the path curvature in the joint space presents consistent variations when the hand trajectory remains invariant in the Cartesian space. For instance, invariant straight paths in the task space are associated with joint paths whose curvature varies according to the absolute positions of the hand and target.

Joint Coordinates: According to this view, the CNS first transforms the spatial coordinates of the target into a set of arm and forearm orientations (i.e. a final posture to reach). Then, it defines the joint path required to move from the initial to the final posture. Because the relation linking cartesian and joint variables are non-linear, morphologically invariant paths in the joint space correspond to morphologically variable paths in the Cartesian space. For instance, invariant straight line paths in the joint space are associated with Cartesian paths whose curvature varies according to the absolute positions of the hand and target (the path followed by the hand in the external world is not directly defined. It is only the consequence of variations planned at the joint level).

The previous remarks indicate that hand displacement can be theoretically encoded in two different ways. They also suggest that a possible approach to decide between these two methods is to look for the existence of morphological regularities in either the task or the joint space. As will be shown in the following this privileged solution is not the only one.

Task space planning

The existence of an explicit specification of the hand path in the task space, prior to movement onset, is mainly supported by two lines of evidence showing (1) that the movement is invariant in the task space; and (2) that the CNS plans the hand displacement as a Cartesian vector, i.e. as an entity that has amplitude and direction. We shall take up these two issues in the following.

Movement path invariances in the task space. In a pioneering study, Morasso (181) required human subjects to perform planar point-to-point movements in different areas of the workspace. He observed that hand trajectories were extremely variable when expressed in joint coordinates, and remarkably stable when described in Cartesian coordinates. With regard to this latter observation, Morasso showed that hand displacements tended to follow a straight line path and a bell-shaped velocity profile irrespective of the initial and final locations of the hand. These results, which were subsequently faithfully reproduced in numerous studies [(1,136,88,120,271,113,126); see Fig. 4], supported the hypothesis: (a) that the hand trajectory in the task space is the primary variable computed during movement planning; and (b) that the joint covariation pattern constitutes a dependent variable computed secondarily in order to allow the hand to move along the planned trajectory. Note that this inverse computation is not trivial (56,8). It requires, because of joint redundancy, the existence of functional constraints that translate a Cartesian position of the hand into a unique angular configuration of the upper limb. As shown by Gielen et al. (114), the nature of these constraints remain widely unknown. We shall return to this issue later.

In contrast to the results initially presented by Morasso, several experiments have suggested that goal-directed movements were not invariant when expressed in a Cartesian frame of reference (9,163,205,67,65,220,125). Prablanc and Martin (205) observed, for example, during a pointing task that the hand path curvature tended to increase with the eccentricity of the target. Likewise,
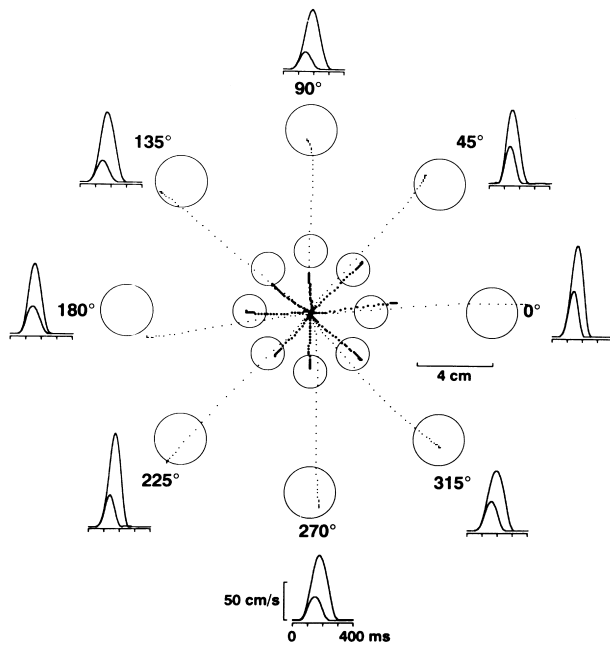
FIG. 4. Morphological invariances in the task space during visually directed movements. Subjects were required to point with a hand-held cursor (compliant movement) from a given starting position toward visual targets (circles) distributed within the workspace. In this situation one can observe invariant straight hand paths, and symmetric bell-shaped velocity profiles irrespective of the movement direction or amplitude. [From Gordon et al. (120); see additional comments in the text.]
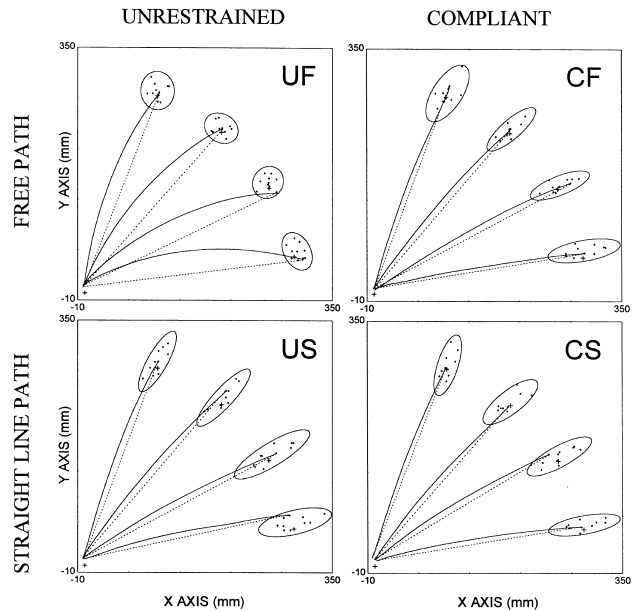

FIG. 5. Morphological invariances are not a general rule. This figure displays individual movements performed in four different conditions. UF: the hand was free to move, and the subjects did not receive any instruction about the path to follow. US: the hand was free to move, and the subjects were explicitly required to follow a straight line path. CF: the hand displacement was physically constrained in a plane, and the subjects did not receive any instruction about the path to follow. CS: the hand displacement was physically constrained in a plane, and the subjects were explicitly required to follow a straight line path. For the constrained (or compliant) movements, the paths were always straight, irrespective of both the instruction and the target eccentricity. In addition, the end-point distributions were elliptical and elongated in the movement direction. For the unconstrained free path movements, the hand trajectory presented a consistent curvature, the amount of which varied significantly as a function of the movement direction. Moreover, the end-point distribution was roughly circular. The straight hand paths and typically elongated end-point distributions observed for the US movements suggest that the difference observed between UF and the other conditions was not fully related to biomechanical factors. This result is consistent with the hypothesis that unconstrained movements are, by contrast to constrained movements, not planned to follow a straight line path. [From Desmurget et al. (64); see additional comments in the text.]

Atkeson and Hollerbach (9) showed that the amount of curvature of vertical reaching movements varied as a function of the initial and final location of the hand within the workspace. Three main hypotheses were proposed to account for these observations:

1. imperfect control processes causing the real motion to deviate from the centrally programmed trajectory [(87,133); see The equilibrium-point hypothesis section];
2. visual anisotropies inducing variations in the perception of the straightness in some part of the workspace (91,271); and
3. movement planning processes (260,220,65,188).

In order to distinguish experimentally between these different possibilities, Osu et al. (188) required human subjects to perform unconstrained visually directed movements between points set on a horizontal table. Two main conditions were considered: no-path instruction (NI) and instruction to move the hand along a straight line (SI). Results showed that subjects generated much straighter movements in SI than in NI. As shown by electromyograms, this difference could not be related to an increase in arm stiffness. On the basis of these findings, Osu et al. (188) concluded that path curvature was the result of the movement planning process.

As shown in the previous paragraphs, divergent results have been reported in the literature concerning the question of knowing whether or not visually directed movements are morphologically invariant in the external space. It may be worth noting that an important methodological difference generally exists between the experiments describing straight and curved motions: i.e. the presence or absence of an

''intermediate tool'' used to record the movement (hand-held cursor, pen, manipulanda…). Whereas the experiments showing consistently curved paths (9,163,205,188) involved unconstrained movements, the studies emphasizing the linearity of arm trajectory (181,88) involved compliant motions (i.e. motions constrained in a plane by external contact). This observation might suggest that the level of constraint imposed on the movement is critical with regard to the existence of spatial invariances in the external (or task) space. In order to address this hypothesis, Desmurget et al. (64) required human subjects to perform visually directed movements between points located in a horizontal plane. Two types of movement were compared: unconstrained (U; the hand was free to move along all the directions of the 3-D workspace), and compliant (C; a mouse constrained the hand movement in the pointing plane). Two different path instructions were considered: Free (F; the subjects were instructed to ''move the fingertip from the starting position to the target as quickly and accurately as possible''), and Straight (S; the subjects were instructed to ''move the fingertip from the starting position to the target as quickly and accurately as possible

following a straight line path''). The results revealed (Fig. 5) that the compliant movements were straight and invariant irrespective of the path instruction and that the unconstrained movements were much straighter in the S than in the F condition. On the basis of these findings, Desmurget et al. concluded that compliant and unconstrained movements involved different planning strategies. They also suggested that, under free path instruction, compliant motions were planned in the task space whereas unconstrained movements were not. Although Desmurget et al did not provide a clear explanation for this result in their original paper, several factors can be evoked to explain why compliant and unconstrained movements are planned differently. Among these factors, four seem to be particularly important. Let us briefly present these factors in the following.

Mechanical factors. It may be that the general solution used by the CNS to generate unconstrained movements can no longer be used when the hand displacement is constrained in a plane, i.e. when some of the degrees of freedom of the arm are frozen. As an illustration of this point, which is well documented in robotics (35,56,8), consider the recent work of Soechting et al. (240). These authors provided evidence that visually directed movements were planned to minimize the amount of work that must be done to reach the target. According to this hypothesis hand displacement should maximize the amount of rotation about the humeral axis (the moment of inertia of the arm is minimal for humeral rotations). Obviously, however, when the hand displacement is constrained in a particular plane the solution given by this maximization process is generally not acceptable. That is, the common strategy used by the CNS is no longer relevant to achieve the task.

Functional factors. For unconstrained movements the only objective requirement is to bring the final effector to the target. That is, a specification of the characteristics of the hand path in the Cartesian space is, although possible, not imposed by the task. It follows that a purely intrinsic coding is theoretically plausible for this type of movement. Such is not the case for compliant displacements. In this latter situation, indeed, the subject faces a double constraint: (1) bringing the final effector to the target; and (2) following a planar path in the task space. That is, the trajectory cannot be defined exclusively in an intrinsic space. It must conform to a standard specified in Cartesian coordinates: for compliant movements the acceleration of the end-point effector has to remain parallel to the pointing table. Considering this point, it is conceivable that the whole trajectory is defined in the task space for those movements. This solution presents the advantage of simplicity. It indeed allows the nervous system to define hand trajectory without switching between intrinsic and extrinsic constraints (see above).

Cognitive factors. All the compliant movements commonly performed by humans require a control of the hand displacement in the task space. This is obvious for drawing or hand writing. This is also the case for computer mouse manipulation. In this case, because there is no spatial compatibility between the motor (hand motion) and the visual coordinates (displacement of the pointer on the screen), the subject has to control the movement of the end-point effector (screen-pointer) in the external space. If one considers that situations perceived as similar by the CNS

tend to induce similar schemes of solution (200,215), it is possible to evoke transferential processes to explain why compliant motions are controlled in the task space. One may speculate that the requirement to move an object in a plane favors the emergence of a representation of the hand path in the task space by suggesting, as for a drawing or writing task, to ''trace a line'' between the hand starting point and the target location. This implicit representation may be absent for unconstrained movements which just impose to ''bring the final effector to a given spatial location''.

Economical factors. It is generally admitted that the CNS is an ''optimized'' system which tends to select the most economical solution to perform a given task (12,186,150). With respect to this assumption it is worth noting that the relations linking extrinsic and intrinsic variables are non-linear and very complex from a computational point of view (9,56). This suggests that a planning scheme which would transform an extrinsically specified trajectory into an intrinsically specified trajectory would be more ''costly'' than a planning scheme which would avoid this transformation. In other words, due to the complexity of the relationship linking extrinsic and intrinsic variables it seems to be reasonable to postulate that an extrinsic coding is more expensive than an intrinsic coding. This may explain why this latter strategy could be privileged by the CNS during unconstrained movements (163,220,65,240,188). Concerning the compliant movements we have already noticed that a purely intrinsic coding was not applicable. Indeed, for compliant movements the hand trajectory must satisfy a specific morphological requirement. This implies that the hand displacement cannot be defined without reference to Cartesian variables. Considering the complexity of the relations linking extrinsic and intrinsic variables it seems reasonnable to suppose that a planning scheme which would define hand trajectory by mixing intrinsic and extrinsic constraints would be more ''costly'' than a planning scheme which would consider only one of those variables at a time. This may explain why a task space coding is privileged by the CNS during compliant movements (181,88,120,271).

The previous observations indicate that compliant and unconstrained movements are not similar at all, as it is usually assumed, but fundamentally different in several aspects. This may explain why these categories of movements involve distinct planning processes.

The movement is planned as a spatial vector. From a descriptive point of view any Cartesian displacement can be represented as a vector, i.e. as an entity that can be characterized by its amplitude and its direction. Several authors have suggested that this analytic description may be an operational principle for the organization of the motor system (120,267). According to this view the CNS is assumed to plan the movement by specifying independently its amplitude and its direction in the Cartesian space. Arguments supporting this hypothesis will be presented in the following.

Visually directed movements are characterized by reaction times (RT) of about 200–500 ms (110,207). These RTs are supposed to reflect the time needed by the CNS to plan an adequate movement. Interestingly, several authors have noticed that a partial knowledge of either the amplitude or the direction of the upcoming movement
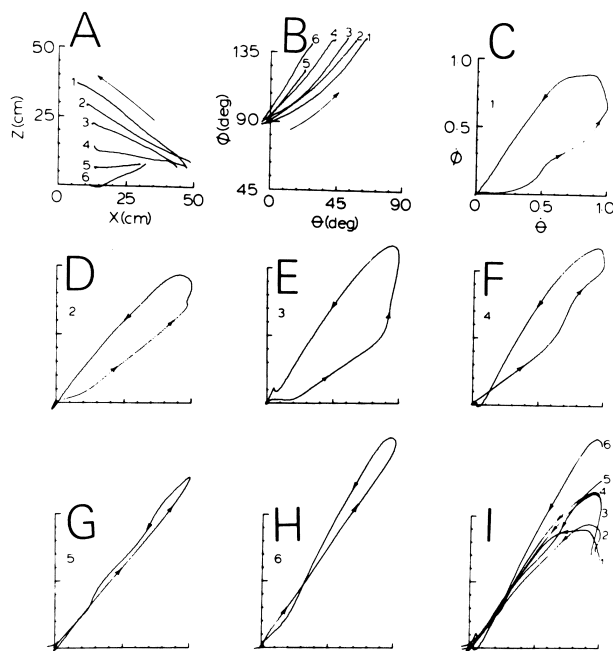
FIG. 6. Invariant pattern of joint covariation during visually directed movements. Subjects were required to point toward visual targets located in a vertical plane. Panel A shows individual hand paths in the Cartesian space for six different targets. Panel B displays the same curves in a joint space (θ: shoulder angle; ϕ: elbow angle). Panels C–H represent elbow velocity as a function of shoulder velocity (phase plane). The curves reported in panels A–C are superimposed in panel I (only the portion beginning after the peak velocity of the shoulder is reported). As shown in the panels C–I, the angular velocities of the shoulder and elbow reach their maximum roughly at the same time. In addition, the ratio of the elbow and shoulder velocities are constant and close to one during the movement deceleration phase. This invariant pattern of joint covariation is compatible with the hypothesis that movement is organized in an intrinsic frame of reference. [From Soechting and Lacquaniti (246); see additional comments in the text.]

significantly reduced RT (31,221). Consider as an illustration a recent experiment of Bock and Arnold (27). These authors required human subjects to perform pointing movements in a vertical plane. They observed that a specification (even partial) of the amplitude or direction of the upcoming movement significantly reduced RT. This result indicated that one component of the movement could be planned without information about the other. Such an autonomy strongly suggested that the amplitude and direction of goal-directed movements were planned independently. In order to address this hypothesis more deeply Bock and Arnold checked that the precues related to the direction or extent of the upcoming movement were not used in advance to select a small number of potentially relevant motor responses (119). To this end they presented the visual targets to reach to within ring-sectors whose angular opening was invariant but whose distance from the hand starting point was variable. In this situation the amplitude and direction uncertainty were kept constant whereas the pointing area (A) was modified. Results showed that RT was totally independent of A. This strongly reinforced the idea that movement preparation was a parametric process involving an independent specification of the amplitude and direction components of the upcoming displacement.

Additional evidence supporting the hypothesis that goal-directed movements are planned vectorially has been provided by behavioral studies examining the end-point error

distributions during planar movements (267,64). Consider as an illustration the pioneering study carried out by Gordon et al. (120). These authors analyzed pointing movements performed from a given starting location toward 16 visual targets presented on a screen. They observed for each target that the spatial distribution of the movement end-points were elliptical in shape (subjects were required to perform 24 movements toward each target). Remarkably, they also found that the major axis of the end-point ellipses was systematically oriented along the line (L) joining the movement starting point to the mean movement final error (see Fig. 5 for an illustration). This typical organization indicated, from a statistical point of view, that the variability observed along L was independent of the variability observed along an axis which was orthogonal to L. Since movement amplitude and direction are, by definition colinear and orthogonal to L, respectively, this result showed that variability observed in movement amplitude was statistically independent of variability observed in the movement direction. As pointed out by Gordon et al, such an independence would not have been expected if the movement amplitude and direction were not planned independently by the CNS. Further argument supporting this conclusion was provided by the fact that variable errors in direction and amplitude were differentially affected by the initial distance between the hand and target. Note that an independent specification of the extent and direction components of the movement were not observed by Desmurget et al. (64) for unconstrained movements. As shown by these authors, the movement end-point distributions tended to be roughly circular when the hand displacement was not constrained in a plane (Fig. 5). This reinforced the hypothesis that compliant and unconstrained movements involved different planning processes (see above).

A last major piece of evidence suggesting that visually directed movements are planned vectorially comes from electrophysiological studies showing a modulation of neuronal discharge with changes in movement amplitude or direction [for a review see Ref. (104)]. This observation is very attractive from a conceptual point of view. Indeed, the agreement between the neural signal variations and the modifications of the movement characteristics (direction or amplitude) might represent the neurophysiological underpinning of trajectory planning in spatial coordinates. As will be shown in the following, however, this interpretation still remains very controversial.

A modulation of the neuronal discharge with change in movement amplitude was observed in several cerebral areas including the globus pallidus and the subthalamic nuclei (108), the premotor cortex (216,160,95,82), and the motor cortex (95,82). From a conceptual point of view, this result suggests that the movement amplitude is represented as an independent parameter within the nervous system. This interpretation is, however, not totally unequivocal. As pointed out by Georgopoulos et al. (108) or Fu et al. (95), movement distance is tightly coupled with several parameters such as the hand initial acceleration, the force developed, the muscle activity, the movement duration, the hand initial acceleration or the amplitude of the joint motions. As a consequence, modulation of the neuronal discharge with change in movement amplitude may reflect the coding of an intrinsic parameter rather than an explicit specification of the movement extent.

In a pioneering study Georgopoulos et al. (109) recorded neuronal activity within the motor cortex of behaving monkeys performing a two-dimensional pointing task. They observed that the discharge of individual cells varied approximately as a cosine function of movement direction. This function was centered on one preferred direction that changed from cell to cell. Strikingly, however, the graded signal emitted by the individual cells was found to be rather broad and noisy. This led Georgopoulos et al. to suggest that movement direction was not encoded at the single-unit level but at the neuronal population level. In order to test this hypothesis the authors proposed a definition of a population vector representing the vectorial sum of the activity of all the individual neurons. The procedure used to transform cell discharge into a vectorial quantity was as follows: the ''cell-preferred direction'' was defined as the movement direction for which the cell presented the greatest activity; the ''cell amplitude'' was defined as the difference between the maximal firing rate of the cell and the firing rate observed for a particular movement. As shown by Georgopoulos et al., the direction of the population vector was in good agreement with the direction of the upcoming movement. This observation was subsequently reproduced in several studies involving tri-dimensional movements (105,46). It was also extended to a large number of cerebral areas including the premotor cortex (45), the parietal cortex (147,162), and the cerebellum (93). Finally, it was generalized to instantaneous movement variations by Schwartz (233,234) who showed that the neural signal of cell populations varied in real time with the direction and velocity of the end-point effector.

When considered together, all the previous results suggest the existence of a neuronal representation of the extrinsic features of the movement trajectories. This widely cited ''population coding vector hypothesis'' is, however, far from being totally unequivocal and several alternative interpretations can be proposed (145,146,171). In particular, as theoretically demonstrated by Mussa-Ivaldi (183), the transformation between hand path coordinates and muscle state variables involves a cosine function. This implies that the single-unit activity and the total population behavior initialy described by Georgopoulos et al. (109) would also be expected assuming that cortical cells encode muscle-related variables (e.g. the desired rate of muscle shortening). In agreement with this possibility Caminiti et al. (46) found that the preferred direction of individual motor cortex cells changed consistently when monkeys made parallel movements (same direction) from different starting points (different arm geometry). As pointed out by Georgopoulos (104), however, this evidence, based on analyses performed at the single-unit level, could not be considered as really decisive inasmuch as the population vector remained a ''good and unbiased'' predictor of movement direction. Interestingly, this objection was recently challenged by Scott and Kalaska (235,236) who observed significant differences in the direction of the cell population vectors in primary motor area (M1) when monkeys performed reaching movements with similar hand path but different arm postures.

Joint space planning

As previously observed, movement planning in joint space presupposes the existence of two sucessive stages.

First, the spatial coordinates of the target have to be converted into a set of arm and forearm angles. Second, a joint path allowing the arm to move from the current to the target posture has to be selected. Although this path can theoretically be curved, most of the authors have associated the concept of joint space planning with the existence of a straight line path in the intrinsic space (69,135,220). Mathematically, this straight displacement can be viewed as a multidimensional vector whose components represent the difference between the starting and target angles for each joint. Although difficult to figure at first glance this straight line displacement in the joint space has a simple functional meaning. It indicates that the movement is synchronized at each joint, or in other words that the rate of angular variation is the same for all the joints involved in the movement (if one assumes that there is no movement reversal, the movement starts, stops, and reaches its maximum velocity at the same time at all the joints).

If follows from the previous remark that the joint space planning hypothesis may be supported by two different lines of evidence suggesting: (1) that the movement is invariant in the joint space; and (2) that the final posture to reach is defined by the CNS before movement onset. We shall take up these two issues next.

Movement path invariances in the joint space. The first direct support of the joint coding hypothesis came from a series of psychophysical investigations carried out by Soechting and Lacquaniti at the begining of the 1980s (244–246,166). These authors required human subjects to perform two-joint pointing movements in a sagittal plane. They observed that the angular velocities of the shoulder and elbow joints reached their maximum at the same time, and that the ratio of the angular velocities of these two joints was constant during the last part of the movement (Fig. 6). Soechting and Lacquaniti interpreted these intrinsic regularities as evidence that movement was planned in the joint space. This conclusion was, however, subsequently challenged by Hollerbach and Atkeson (135) who pointed out that the movements studied by Soechting and Lacquaniti were also roughly invariant in the task space. In fact, the situation examined by Soechting and Lacquaniti represented one of the particular cases for which invariances could be expected at the same time in the intrinsic and extrinsic spaces. In order to abolish this indetermination Lacquaniti et al. (163) studied three-dimensional reaching movements performed from a given starting point toward visual targets located in different parts of the workspace. They observed that the shape of the hand path varied as a function of the movement direction. While some movements were approximately straight, others exhibited appreciable curvature (up to 4.5 cm deviation from the straight line). This extrinsic variability contrasted with the relative constantcy of the joint coactivation patterns. In particular, the elbow and shoulder joint variations were found to be linearly related for any given movement. This tight coupling strongly suggested that movement was planned in joint coordinates. Further arguments supporting this view were recently provided by Desmurget et al. (68,65) in the context of prehension movements. Subjects were required to reach and grasp a cylindrical object presented at a given spatial location with different orientations. During the movement,
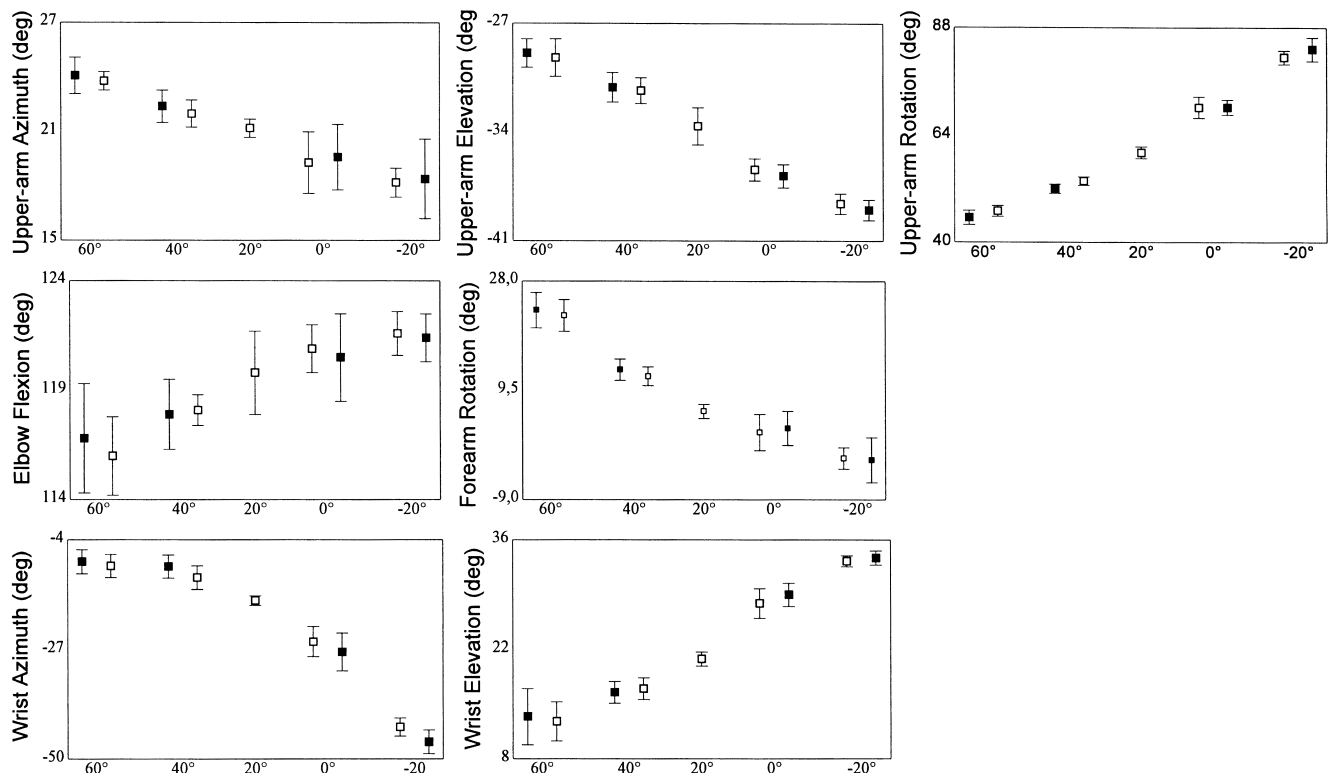
FIG. 7. Postural invariances during prehension movement. Subjects were required to reach and grasp a cylindrical object presented at a given spatial location with different orientations. During the movement, object orientation was either kept constant (unperturbed trials, □) or modified at movement onset (perturbed trials, ■). All the upper-limb angles were computed at hand–object contact (upper-arm azimuth, upper-arm elevation, upper-arm rotation; elbow flexion; forearm rotation; wrist azimuth, wrist elevation). For the unperturbed trials, statistically distinguishable posture could be identified. For the perturbed trials the upper-limb final posture was identical to that obtained when the object was initially presented at the orientation following the perturbation. This postural stability, which was particularly remarkable considering the large set of comfortable posture allowed by joint redundancy, was consistent with the hypothesis that upper-limb movements are initiated and controlled in the joint space via a mechanism comparing an estimate of the current postural state of the arm with a target value determined by converting the coordinates of the object to grasp into a set of arm, forearm, and wrist angles. [From Desmurget and Prablanc (65); see additional comments in the text.]

object orientation was either kept constant (unperturbed trials) or modified at movement onset (perturbed trials). Trajectory analyses showed for the unperturbed trials that the external hand path curvature changed significantly as a function of the object orientation. This ''extrinsic'' variability was concomitant with solid morphological regularities in the joint space. As shown by Desmurget et al. the joint path presented invariant charateristics during the unperturbed trials irrespective of the object orientation. In addition, the final posture reached by the arm was highly stereotyped for a given final orientation of the object to be grasped (Fig. 7). This latter observation was particularly remarkable for the perturbed movements considering joint redundancy. As pointed out by Desmurget and Prablanc (65), it strongly suggested that the final posture to reach constituted an internal reference to which the current posture was continuously compared.

Evidence supporting the existence of an early definition of the final postural state to reach. Because the number of degrees of freedom (df) of the upper limb exceeds those necessary to completely specify the position and orientation of an object in space, any configuration of the hand can be theoretically associated with an infinite number of joint combinations (12). Despite this fact, invariance in the final posture of the arm has been reported in numerous studies

dealing with both pointing and prehension movements. For instance, Hore et al. (138) [see also Refs (254,180)] observed for visually directed movements performed from different starting locations with an outstretched arm that the final joint configuration of the upper limb was invariant for a given position of the target to reach. Likewise, Helms-Tillery et al. (131) and Paulignan et al. (193) reported that the angular configuration reached by the arm during prehension movements was stereotyped for a given position and orientation of the object to grasp (note that these authors did not test the influence on the hand initial location). These observations were consistent with those of Desmurget et al. (69,65) who reported that the posture of the arm remained stable for a given final configuration of the object to grasp even if the orientation of this object was suddenly modified after movement onset (see above and Fig. 7). If one assumes that the representations used by the brain to plan and control goal-directed actions can be inferred from behavioral regularities (12), all the results reported in this section appear to be compatible with the hypothesis that the final posture to reach is one of the primary variables defined by the CNS during movement planning.

During the last decade the ''inverse mapping'' problem was tackled by Soechting et al. who undertook a series of experiments designed to identify the neural processes that

convert a visual input into a set of arm and forearm angles. In a first study (242) these authors required human subjects to point in the dark toward memorized targets. Two main conditions were tested: (1) pointing with the index finger (IF); and (2) pointing with a pointer held in the right hand (P). In the second condition, the movement involved mainly the wrist joint. Statistical analyses showed that the subjects were much more accurate in P than in IF. This strongly suggested that the errors noticed in IF were not related to an erroneous estimation of the target location but rather to the existence of approximations in sensori-motor transformations. In order to validate this hypothesis Soechting and Flanders (243) demonstrated that the motor behavior of the subjects was not random but, to a large extent, predictable. In addition, they showed, on the basis of complex, and contested [see Ref. (32)], analyses that the errors noticed in IF were compatible with the hypothesis that reaching movements involved a transformation from a representation of target location to a representation of intended arm orientation; and that the neural implementation of this transformation consisted of a linear approximation of the mathematically exact solution (243,86,241,132). The generality of this model, which predicted the existence of a unique correspondence between every location of the hand in space and a set of arm and forearm angles, was, however, recently challenged in a study involving three-dimensional visually directed movements. As shown by Soechting et al. (240), the posture of the arm observed for a given location of the target to reach did not remain invariant when the movement starting point was modified. This suggested that the unique mapping reported in several studies between the position of the hand in space and the arm posture depended mainly on the existence of specific experimental constraints such as pointing at distant targets with an outstretched arm (254,138). This also indicated that the strategies used by the CNS to transform the visual input into a set of arm and forearm orientations did not provide a single correspondence between the location of the hand in space and the posture of the arm. In agreement with this hypothesis several recent models have been found to be accurate in predicting systematic modifications of the configuration of the arm according to the movement starting point. For instance, Soechting et al. (240) showed that the variations of the angular configuration of the upper limb reported in their experiment could be predicted under the assumption that the subjects tried to expend as little energy as possible to achieve the movement (minimum work). Likewise, Rosenbaum et al. (220) noticed that consistent variations of the final configuration of the arm could be expected for a given target location assuming that the CNS evaluated stored postures prior to movement (Knowledge II model). According to this view, standard learned postures are supposed to be stored by the CNS. When a target appears a weight is assigned to each of these postures in the light of a double criterion:

1. the energetic cost necessary to reach the posture (this cost varies as a function of the initial location of the hand); and
2. the accuracy that would result from the selection of the posture.

The final posture is found by taking a weighted sum of all the stored postures (220). Note that the existence of

systematic variations of the arm configuration according to the movement starting location was recently confirmed by Desmurget et al. (63) in the context of a natural prehension task.

It appears that the task space and joint space coding hypotheses are each supported by a large number of experimental arguments. However, beyond this general remark, it is worth noting that a coherence can be found in the experimental observations if one distinguishes between unconstrained and compliant movements. A careful review of the literature indicates that a consistent methodological difference exists between the experiments describing Cartesian and joint invariances, i.e. the presence or absence of a constraining recording system (hand-held cursor, pen, manipulanda…). Whereas the experiments showing invariant paths in the joint space utilize unconstrained movements, the studies emphasizing the linearity of arm trajectories in the Cartesian space use compliant motions. This observation suggests that the level of constraint imposed on the movement is critical with regard to the existence of spatial invariances in the external (or task) space.

Models based on optimization principles

As indicated in the section on Task space and joint space hypotheses, goal-directed movements exhibit remarkable invariant properties despite the fact that a given point in space can be reached through an infinite number of spatial, articular, and muscle combinations. In order to account for this observation it is necessary to postulate the existence of a ''regularizer'' (202), i.e. a functional constraint, to reduce the number of degrees of freedom available to perform the task. Most of the regularizers proposed during the last decade [see Ref. (114) for a review] refer to the general hypothesis that the nervous system ''tries'' to minimize the energy expended to perform the movement. Nelson (186) first formulated this idea in an operative way by proposing to use mathematical cost functions to estimate the energy consumed during a movement. This approach was further developed by several investigators who proposed different criteria such as, for instance, the minimum muscular energy (58,4), the minimum effort (128,168), the minimum jerk (134,88), the minimum torque change (260), or the minimum work (240). Because the main goal of the present section is to assess the validity of the optimization procedure as a general tool for understanding movement control, we will not consider each of the cost functions in details. We will mainly articulate our dicussion around two models which are indisputably the most commonly evoked in the literature and which have proved to be very powerful in describing multi-joint movements, namely the minimum jerk and minimum torque change models.

On the basis of the observation that goal-directed movements tended to become smoother and smoother during learning, Flash and Hogan (88) suggested that smoothness was the primary variable controlled by the CNS. In order to formalize this assumption they proposed that movements were planned to be as smooth as possible in the task space, which implies in mathematical terms that the cost to be minimized over movement duration is the first derivative of the hand acceleration. As shown by Flash and Hogan (88),

this criterion predicts that goal-directed movements will exhibit straight hand paths and bell-shaped velocity profiles irrespective of their direction, amplitude, or velocity. As previously reported, these predictions are strongly supported by a large number of experiments dealing with two-dimensional pointing movements (cf. the section on Task space planning). At the same time, however, they are clearly challenged by most of the studies involving unconstrained movements. From a theoretical point of view, it is noteworthy that the minimum jerk model does not consider the charateristics of the biological actuators. This probably constitutes its most important limitation.

By contrast to Flash and Hogan (88), Uno et al. (260) suggested that movement planning must be related to arm dynamics. In order to make this assumption operative, they proposed the minimum torque change model according to which the objective cost function to be minimized is the sum of the square of the rate of change of torque integrated over the entire movement. This mathematical criterion predicts both asymmetrical bell-shaped velocity profiles, and slight (but nonetheless significant) variations of the hand path curvature as a function of the movement direction and amplitude. According to Uno et al. one of the main advantages of the minimum torque change model lies in its parsimony. Indeed, torques are supposed to be directly calculated from the respective positions of the hand and target. As a consequence, there is no necessity for (a) an explicit determination of the hand trajectory in the Cartesian space and (b) a transformation of the externally specified trajectory into joint angles. Note, however, with respect to this second point, that torque change minimization cannot be achieved if the CNS does not know the final postural state that the arm has to reach. This indicates, at least for nonproprioceptive tasks, that an inverse transformation that converts the Cartesian location of the target into joint angles cannot be avoided by the model. In fact, from a conceptual point of view, both the minimum torque change model and the joint space coding model, face the same major question of how the final position of a visual target is transformed into a set of arm and forearm angles.

Although very different from a conceptual point of view, the minimum jerk and minimum torque change models lead generally to very similar predictions, namely roughly straight hand paths with approximately bell-shaped velocity profiles (imperfect control may explain some variations from the straight line-planned path in the case of the minimum jerk model; see the Task space planning section). This convergence is problematical inasmuch as it makes it difficult to assess the respective validity of the minimum jerk and minimum torque change models. In order to overcome this uncertainty, Uno et al. (260) studied different situations for which the predictions of the minimum jerk and minimum torque change models diverged significantly. For instance, they considered movements performed from a point located in the fronto-parallel plane (arm outstretched to the right) to a point located in front of the subject. They observed in this situation (and in all the others), that a direct comparison between the experimental data and the model predictions supported the idea that hand trajectory was planned and controlled in accordance with the minimum torque change model. This conclusion was, however, challenged by several studies showing that neither the path nor the tangential velocity profile of the movement were altered

when the speed of the motion was changed, or when the hand carried a weight (9,165). It was also questioned by recent adaptation studies showing that artificially increasing the perceived curvature of the movement induced significant modifications of the shape of the hand path in the Cartesian space. Concerning this latter point, Wolpert et al. (271) required human subjects to point toward a visual target located in the sagittal plane [see also Ref. (83)]. During the movement the subjects could see the position of their fingertip on a semi-reflecting mirror. In a perturbed condition, the visual feedback was altered so as to increase the perceived curvature of the movement. The perturbation was null at both ends of the movement and maximal at the midpoint. Analyses showed that the subjects adapted to this perturbation so as to reduce the visually perceived curvature. This result would not have been expected if the movement trajectory was only planned by minimizing joint torque changes.

In the light of the previous remark, it appears that neither the minimum torque change nor minimum jerk model is totally successful in predicting the spatio-temporal chararacteristics of visually directed movements. Despite this fact, however, they both are able to capture the kinematic features of certain categories of movements. This indisputably suggests that the optimal control theory (156) can constistute a powerful approach to understanding how movements are planned and controlled by the CNS. Beyond this conclusion, however, one may wonder whether the various cost functions evoked in the literature really reflect the variables that the CNS represent. Let us briefly consider the minimum jerk model to illustrate this remark.

Flash and Hogan observed that point-to-point movements tended to follow a straight line path and a bell-shaped velocity profile irrespective of the initial and final locations of the hand. A possible explanation for this result is that the CNS only chooses the simplest path between any two points, that it begins by accelerating the hand and that it finally decelerates it to avoid overshooting the target. This ''trivial'' description may explain both why hand movements are roughly straight and why velocity profiles are approximately bell shaped. Another concurrent explanation may be, however, that the CNS cares mainly about movement smoothness and therefore tries to minimize jerk. Obviously, this explanation raises two main questions. First, how is the jerk sensed by the CNS? This problem is not trivial at all if one considers that smooth movements of the end-point effectors in the task space can be related to ''jerky'' movements of the different joints contributing to the motion (181). Second, how can we certify that the agreement observed between the predictions of the model and the experimental data is not incidental and contingent on the fact that the minimization of the jerk predicts straight line movements with bell-shaped velocity profiles? This interrogation seems to be all the more founded that it is generally difficult to distinguish between the predictions of very disparate cost functions underpinned by different assumptions (186,260,185). That is, divergent models are able to predict similar trajectories on the basis of totally different cost functions. Note that this absence of specificity becomes all the more marked if one considers, as recently proposed by several authors (57,62,220,263), that the CNS does not optimize one single variable but does incorporate several different constraints whose importance can be

modified as a function of the requirement of the task. Such an approach is indisputably very powerful in producing realistic movement trajectories. Nevertheless, it is questionable from a theoretical point of view. By mixing the constraints to be optimized it is possible to (re)produce a large range of trajectories and therefore to account, a posteriori, for almost every experimental observation. This absence of clear prediction makes it difficult to test the validity of ''mixed models''.

The optimal control procedures have proved to be potentially efficient at predicting the charateristics of goal-directed movements. Beyond this demonstration, however, it is worth noting that the exact relation between mathematical cost functions and the variables actually represented by the brain still remain unclear. An illustration of this remark can be found in the ability of totally divergent models to make similar predictions. The primary problem with optimization procedures seems to be that individual cost functions are generally very sensitive to external parameters [e.g. arm stiffness; see for an illustration Flash (87) versus Katayama and Kawato (149)]. As a consequence, by meticulously adjusting these parameters, it is usually possible to adequately fit the data. This ''adaptability'' is paradoxically, at the same time, the major strength but also the main weakness of the conceptual models based on the optimal control theory.

Synthesis

In summary, different exclusive models have been proposed during the last decade to account for the kinematic features of goal-directed movements. Since each of these models predicts specific levels of invariance, it should be easy to estimate their respective validity. As shown in the previous sections, however, such is not the case. Four main points may, in our view, explain this fact. Let us present them briefly.

Identifiability of a model
According to this concept, the parameters and structure of a model cannot always be identified unequivocally from a given set of data. This critical point is clearly illustrated by recent studies showing that the electrophysiological experiments favoring the ''task space coding'' hypothesis can also be interpreted in terms of muscle (183) or joint (162) planning. It is also illustrated by psychophysical studies demonstrating that the regularities of velocity profiles observed during drawing movements can be viewed as the result of movement planning processes (164), or as an emergent phenomenon related to the biomechanical properties of the human arm (122).

Sensitivity of a model
As pointed out by this concept, which is related to the question of knowing whether a statistically significant effect is obligatory and ''meaningful'', it may be perilous to establish a strict and unequivocal link between theoretical predicates and behavioral observations. To illustrate this point, consider the general problem of movement curvature in the task space. It is well established that planar pointing movements present a small, but systematic, curvature (87). Strictly, this result is in contradiction with the hypothesis that goal-directed movements are planned to follow a straight line path. No one, however, would take this conclusion for granted. Indeed, hand path curvature can be explained by ''perturbing'' factors such as an imperfect control or the anisotropy of the visual field (cf. the Task space planning section). Because the effect of these factors cannot be accurately quantified the exact origin of the hand path curvature cannot be firmly established. As a consequence, neither the models which predict a small path curvature in the task space nor the models which predict that the movement will be straight can be irrevocably rejected.

Objective validity of a model
As pointed out by this concept the validity of a model should be established on the basis of objective experimental observations. This assertion can appear trivial and almost provocative in the scientific field. It seems, however, that it is not. To illustrate this point consider the ''equilibrium-point hypothesis''. One can be struck by the discrepancy existing between the notoriety of this hypothesis and its objective support (2,172). As shown in the section on The equilibrium-point hypothesis, the main predictions of equilibrium-point models have been found to be systematically contradicted by experimental observations, at least in the context of multi-joint movements. Despite this fact, the influence of this model still remains strong.

Testability of a model
As pointed out in this concept, a model that can be adapted so as to be compatible with almost every experimental observation is virtually impossible to validate. Optimal control procedures are a good example of this problem. Because the exact biomechanical charateristics of the arm are not known, some parameters can be adjusted within a certain range. Inasmuch as these parameters have a strong influence on the characteristics of the trajectories predicted by the model it is possible, by adjusting them, to improve the general agreement between the predictions of the model and the experimental observations. Although this procedure is not theoretically reprehensible considering that real values are not known it nevertheless makes it difficult to really test the validity of the model. Note that the same uncertainty can occur when considering neural networks. As noticed by Gielen [(114), pp. 504–505], ''the main problem with models based on neural networks seems to be that neural networks can model almost anything. Therefore, the fact that a neural network can model inverse kinematics for a kinematically redundant manipulator, does not teach us much about the biological implementation of the solutions used by human beings''.

It appears from the previous observations that identifying the variables used by the central nervous system to plan goal-directed movements is a difficult exercise which must be performed with caution. Care must be taken, in particular, when making inferences from behavioral invariances, electrophysiological recording, or numerical fitting. Beyond this point, however, it remains clear that several divergent models, like the joint or task space coding hypotheses, are supported by a large amount of experimental observations. This might suggest that the failure to provide a unified and totally coherent theory for movement control is not only related to the theoretical traps previously evoked but also to the fact that the search for a general model constitutes an ''ill-posed'' problem. The wide

diversity of opinions on the question of motor control might, in fact, indicate that the nervous system is able to use different planning strategies, depending upon the experimental conditions. Sound experimental observations supporting this hypothesis are, in particular, reported in the Task space and joint space hypotheses section for compliant and unconstrained movements. Of course, further comparative studies to systematically test the effect of environmental constraints on the movement planning processes will be necessary to confirm and establish the degree of generality of this hypothesis.

CONCLUDING REMARKS

The purpose of this paper has been to describe the mechanisms whereby a visual input is transformed into a motor command. To address this question, we considered successively three main problems. First, how is the initially retinocentric representation of the target converted into a body-centered representation? Second, does the knowledge of the initial state of the motor apparatus constitute a prerequisite for movement planning? Third, what is the validity and the degree of generality of the different models which have been proposed during the last few decades to account for the characteristics of visually directed movements? Clearly, none of these questions has found a totally convincing answer. As shown throughout this review, the literature offers several divergent models to account for the human ability to localize a target, and to generate accurate hand movements. Strikingly, each of these models is supported and contradicted by sound experimental results. This might indicate that the approach consisting of developing independent motor theories within specific experimental and theoretical contexts is not relevant, alone, to permit a real understanding of the neural mechanisms involved in movement planning. Probably, our comprehension of the processes whereby a visual input is transformed into a motor command would be greatly improved by comparative studies allowing us to contrast various experimental situations and different paradigms. For instance, it would be interesting to test whether the preferential use of allocentric or egocentric information for target localization might be related to the motor distinction between task space and joint space coding. Likewise, it would be crucial to reconcile motor theories based on both psychophysical and electrophysiological approaches by trying to describe the neural mechanisms that might underlie the sequential operations which are supposed to occur during movement planning. Some recent studies showing the large benefit which can arise from a critical and constructive interaction between different theoretical models (162,214,64) and different fields of research (3) may support the pertinence of the comparative approach proposed in this conclusion as a future perspective of research.

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