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## The Roles of Vision and Proprioception in the Planning of Reaching Movements

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### Abstract

While vision and proprioception can both provide information about arm configuration prior to movement, substantial evidence suggests that each modality is used for different stages of the planning process. In this chapter, we provide support for the idea that vision is mainly used to define the trajectory and the kinematics of reaching movements. Proprioception appears to be critical in the transformation of this plan into the motor commands sent to the arm muscles.

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The idea that information about hand position is critical for accurately reaching to targets has been supported by many studies over the past few decades. However, which sensory modalities provide this information, and how information from these modalities is combined to provide a single estimate of hand position remains largely unknown. The goal of this chapter is to give an overview of the research that has addressed how vision and proprioception might be combined to plan goal-directed arm movements.

It has been well established that a motor plan is prepared in advance of movement initiation. However, exactly what features of the movement are explicitly planned remains controversial. It has been suggested that only the final position of the movement needs to be planned in advance (Feldman and Latash 2005; Feldman et al. 1998; Polit and Bizzi 1979). However, other studies have provided evidence that information about the position of the hand prior to movement is critical to movement accuracy (for a review, Desmurget et al. 1998). For example, Gielen et al. (1985) showed that the peak in movement acceleration, which occurs so early that it must be specified prior to movement, scales with intended movement distance. This finding suggests that the central nervous system estimates movement distance between the starting hand position and the target position to plan the movement. In support of this idea, Ghez and colleagues (Ghez and Vicario 1978; Gordon and Ghez 1987a), Gottlieb and colleagues (Gottlieb et al. 1990, 1996) and Brown and Cooke (1981, 1984, 1986) showed that various measures of amplitude specification, that arise in the first 50 milliseconds of movement, scale with target amplitude. These include force amplitude in isometric tasks, and agonist electromyographic amplitude, acceleration amplitude, and torque slope during motor tasks. In addition, Gordon and Ghez (1987b) provided evidence that errors in specification of these variables can be compensated during the course of movement by extending initial agonist burst duration, which extends the duration of initial acceleration, or the time to peak force or torque. This process reflects the use of on-line sensory information in correcting errors in initial planning. Even though the online control of movement is deferred by sensory motor loop delays, it is essential if an

unexpected perturbation occurs during the movement (Cordo et al. 1995; Lestienne 1979; Sainburg et al. 1999; Sarlegna et al. 2004, 2006; Shapiro et al. 2004). For example, if you are going to shake the hand of a friend but he/she unexpectedly moves his/her hand in a different position, you will, nonetheless, reach the displaced target, as demonstrated by double-step experiments (e.g., Flash and Henis 1991; Goodale et al. 1986; Prablanc and Martin 1992; Sarlegna 2006; Soechting and Lacquaniti 1983). Nevertheless, in this chapter, we will focus on the planning stage of goal-directed arm movements.

## **Proprioception Plays a Critical Role in the Planning of Goal-Directed Movements**

Proprioception refers to the component of somatosensation that provides information about the orientation and motion of body segments and the state of the muscles. This information is conveyed largely through muscle spindles and Golgi tendon organs. To investigate the role that proprioception plays in planning and controlling movements, proprioception has been removed through either surgery or by studying rare sensory neuropathy conditions, or has been distorted by the use of vibration. Following the pioneering findings of Mott and Sherrington (1895), many studies have examined the role of proprioception in movement control by examining movements in non-human primates who have undergone partial dorsal rhizotomy surgery, including the studies of Gilman et al. (1976), Taub et al. (1975), Polit and Bizzi (1979) and Gauthier and Mussa Ivaldi (1988), among others. It has been well established that animals proprioceptively deafferented in this way show substantial impairments in accuracy and coordination during multijoint reaching and natural unrestricted movements. Nevertheless, Polit and Bizzi (1979) demonstrated that performance of single joint targeted elbow movements remained relatively unimpaired, following deafferentation. This brought into question whether proprioception is necessary to plan and execute movements. In this study (Polit and Bizzi 1979), monkeys were well trained in the task prior to surgery, suggesting that they might have been able to recall, but not necessarily plan the learned movement patterns following deafferentation. Thus, proprioception may have been crucial for the planning and learning of new movements, but not for recall of learned patterns. In fact, Polit and Bizzi (1979) also reported that when the shoulder configuration was altered by rotating the trunk prior to movements, the movements became grossly inaccurate and uncoordinated. This supports the idea that the animals recalled a learned plan that was only appropriate to the perceptual and mechanical conditions experienced during learning. The monkeys were apparently unable to adapt that plan to changes in limb configuration. These findings support the idea that proprioception is essential for providing information about the initial state of the motor apparatus.

Deafferentation in humans has been studied in the rare condition of large-fiber sensory neuropathy, in which damage occurs only to the large diameter sensory neurons that carry proprioceptive information. Quantitative analyses of the motor behavior of these patients have emphasized the importance of proprioception in performing coordinated, accurate movements (Cooke et al. 1985; Forget and Lamarre 1987; Ghez et al. 1995; Gordon et al. 1995; Messier et al. 2003; Rothwell et al. 1982; Sanes et al. 1985; Sainburg et al. 1993, 1995; Sarlegna et al. 2006). While deafferented patients can perform many activities of daily living, given intense concentration and effort (Cole 1995), the quality and efficiency of performance is severely impaired and patients are often substantially disabled because of this sensory deficit.

Similar to the effects of surgical deafferentation in monkeys, these patients are able to perform constrained single joint movements without substantial errors, even in the absence of vision (e.g., Nougier et al. 1996; Sainburg et al. 1995). However, they show severe limitations in the performance of unconstrained activities of daily living, suggesting that

proprioception might be critical for the intersegmental coordination requirements of more complex movements. Sainburg, Poizner and Ghez (1993) tested this hypothesis by analyzing the performance of the unconstrained pantomimed gesture of slicing a loaf of bread, which required sequential out-and-back motion of the hand within a single plane. Kinematic analysis revealed that even with eyes closed, healthy subjects performed straight, planar hand movements in the inward and outward phases, such that the hand paths nicely overlapped. In contrast, movements of deafferented patients were spatially disordered, and severely non-planar. Analysis of segment kinematics showed that, at the movement reversals, the elbow and shoulder joint motions were temporally decoupled, causing a systematic deviation of the movement trajectory. Because intersegmental interaction torques that occur between the moving segments of the limb are maximized at movement reversals (Hoy and Zernicke 1986; Schneider et al. 1989), it seemed plausible that patients without proprioception were unable to control these interactions. This might explain the relative accuracy with which patients could perform single joint motions that do not involve these interactions.

In order to test this idea, Sainburg et al. (1995) designed a multijoint reaching task that required variations in intersegmental interaction torques. The task consisted of out-and-back movements made in the horizontal plane between a fixed starting position and peripheral visual targets. As shown in Fig. 1, control subjects had no difficulty making straight and overlapping out-and-back movements. However, the deafferented patients movements were substantially more curved and most significantly, showed large errors at movement reversals that depended on the direction of movement. Inverse dynamics analysis revealed that these errors resulted from the direction dependent variation of interaction torques, which was accounted for by control subjects but not patients. Sainburg et al. (1995) thus suggested that proprioceptive information during movement was used to update an internal model of limb mechanics, used to anticipate impending mechanical interactions during the course of movement.

Proprioception appears critical for controlling other aspects of limb mechanics, in addition to the effects of intersegmental dynamics. For example, Ghez et al. (1995) showed that deafferented patients were unable to account for direction dependent variations in limb inertia during reaching movements, which resulted in substantial errors in movement distance and direction. Because direction dependent variations in limb inertia vary with limb configuration, this finding underscored the importance of proprioception in providing configuration information.

The critical role of proprioception in providing initial information of the postural state of the motor apparatus for movement planning is also supported by a study of Larish et al. (1984) in healthy subjects. This study showed that when the limb was vibrated in the absence of visual feedback prior to the movement, final position was systematically altered. The muscle vibration presumably biased subjects' perception of the arm position as the arm would be perceived as being displaced (DiZio et al. 1993; Lackner and Taublieb 1984). Larish et al. (1984) therefore suggested that terminal errors increased because the initial limb configuration was not correctly determined.

## **Vision is Used to Enhance the Planning of Reaching Movements**

Whereas proprioception appears critical for controlling many aspects of targeted movements, vision can also provide information about the body segments, as well as essential information about target location. In order to assess the role of vision to the control of movements, early studies simply removed visual feedback. One century ago, Woodworth (1899) showed that movements toward visual targets are more accurate with vision than

without vision. However, whether information about the starting limb position, the moving limb, or the target was most critical in assuring movement accuracy was not assessed. More recently, the roles of these different parameters have been more clearly differentiated (Bagesteiro et al. 2006; Brenner and Smeets 2003; Paillard 1996; Prablanc et al. 1979a; Proteau et al. 2000; Rossetti et al. 1995; Sarlegna et al. 2003, 2006). Vision of the starting hand position has been specifically manipulated to determine its role in the planning of arm movements. Several studies showed that reaching movements made in the absence of visual feedback of the moving limb are more accurate when vision of the starting hand position is available, compared to when such information is removed (Desmurget et al. 1997; Elliott et al. 1991; Ghez et al. 1995; Prablanc et al. 1979b; Vindras et al. 1998; for a review, Desmurget et al. 1998). In fact, when visual feedback of initial position is distorted, systematic errors in movement endpoint are produced (Bagesteiro et al. 2006; Holmes and Spence 2005; Rossetti et al. 1995; Sainburg et al. 2003; Sarlegna and Sainburg, 2006; Sober and Sabes 2003). However, these studies have underscored the role of proprioception in contributing to initial position information, by showing that subjects do not rely completely on visual information about hand position to plan movements. These findings introduce the question of how vision and proprioception might be integrated to provide a single perception of limb position.

Recent findings from our laboratory have suggested that each modality might provide a distinct and independent estimate of limb position, each employed for different features of movement planning. Some studies have suggested that visual information is critical in determining static limb position because, when vision is removed, judgements about limb position have been shown to “drift” over time (Paillard and Brouchon 1968; Wann and Ibrahim 1992). Brown, Rosenbaum and Sainburg (2003a, b) directly investigated whether the tendency of actual limb position to drift during repetitive movements results from a drift in proprioceptive position sense. A schematic of the experimental set-up is shown in Fig. 2. Subjects are comfortably seated and are asked to point to visual targets. These targets are presented on a horizontal screen that prevents direct view of the limb. The recorded coordinates of the index fingertip are used to project on this screen a cursor that reflects the position of the hand.

In the experiment of Brown et al. (2003a), subjects were asked to perform a series of continuous out-and-back movements of the hand between two visual targets, always visible on the screen. The repetitive movements were paced with a regular audible tone, so that movement speed was similar throughout the experiment. Subjects had continuous visual feedback of hand position for 5 out-and-back cycles, and on the 6th cycle, visual feedback was turned off until the end of the two minute trial. Subjects were instructed to continue on-pace as accurately as possible.

Over the 75 movements made during a two-minute repetitive forward-and backward-cyclic movement trial, the start location of each forward movement was quantified in order to measure potential drift in limb configuration. This position drifted an average of 8 centimeters from the initial start location, as shown in Fig. 3A. This drift increased sharply when visual feedback was removed, then reached a plateau after approximately 40 trials. The drift was associated with substantial changes in limb configuration, i.e., elbow and shoulder joint angles varied substantially. During this drift, the distance and direction of each cycle of movement remained fairly constant (Fig. 3C). Inverse dynamics analysis, which yields joint torque estimates from kinematic data, revealed that the torques required to produce each cycle of movement changed significantly throughout the session. These changes implied that the neural commands to the muscles took account of the changes in limb position associated with the drift, in order to maintain constant movement direction and distance. In fact, forward dynamic simulations (Fig. 3B) showed that if subjects had not

altered their torque strategies to accommodate changes in limb configuration during the course of the drift, movement directions would have systematically shifted as much as 308 over the course of the trial.

These findings point out an interesting paradox: Subjects drifted their limb positions during the course of motion, but apparently accounted for the associated changes in limb configuration in order to maintain movement direction and distance. This surprising result was confirmed in several conditions, as the series of movements were produced from three start locations, in two movement directions and at three different speeds (Brown et al. 2003a, b). Participants were able to maintain accurate reproduction of each cycle of the movement trajectory, even though they failed to maintain their limb position. Thus, proprioceptive information about limb configuration must have been accurate, indicating that position drift cannot result from changes in proprioceptive position sense.

These findings lead to the question of why subjects allowed their limbs to drift if they had the necessary configuration information to generate joint torques that compensated the associated changes in limb position. The answer to this question may be that different modalities are employed for regulating different features of movement. Vision is likely to be the main sensory source of information to generate a spatial plan for movements directed toward visual targets. Proprioception, on the other hand, appears to be crucial for transforming this kinematic plan into the variables that correspond to the forces required to produce the desired kinematics. Thus, both modalities provide information about initial limb configuration, as required to plan motion, but each modality appears to inform different features of the control process.

## **The Relative Contributions of Vision and Proprioception to the Control of Goal-Directed Arm Movements**

The separation of visual and proprioceptive contributions to different features of control appears to reflect the type of coordinate system in which the information is represented. Vision provides extrinsic, world based coordinate information and is used to plan spatial features of movements toward visual targets. Proprioception provides intrinsic information about limb configuration and movement, as well as muscle state, and predominates in transforming a spatial plan into commands that result in muscle forces and joint torques. Nevertheless, information from both modalities is likely to be combined for each of these processes, to some extent (Graziano et al. 2000; Ramachandran et al. 1995; van Beers et al. 1999). It remains unclear exactly how information represented in disparate coordinates might be combined to yield integrated percepts.

It is interesting to note that Lackner and Taublieb (1984) observed that the illusory effects of arm muscle vibration (i.e., perceived motion of the arm) decreased as a function of the amount of visual information (finger only, hand only or complete vision). This suggests that vision might trump proprioception in providing configuration information, as proposed initially by Hay et al. (1965). However, Lackner and Taublieb (1984) emphasized that the vibration-induced illusion of motion is still observed in full vision conditions, even though it is attenuated. In fact, DiZio et al. (1993) showed that when a light-emitting diode (LED) is attached to the finger of subjects in complete darkness, muscle vibration not only induces illusory motion of the finger but also produces an illusory motion in vision of the LED. This demonstrates that proprioception can also trump vision in certain task contexts.

It is plausible that when vision and proprioception are both available, proprioception provides information about the status of the limb, while vision provides information about the extrapersonal environment. Prablanc and Martin (1992) examined the role of the visual

feedback about hand position in making online corrections to target position changes. The visual target was randomly shifted at movement onset, requiring subjects to modify the *direction* of movement. Subjects were able to make rapid adjustments in order to correct toward the “new” target, highlighting the importance of visual information of target position. However, the timing or efficacy of these responses was the same, whether or not subjects had feedback about hand position. (see also Goodale et al. 1986). However, in a similar target-shift paradigm, Sarlegna et al. (2003) recently reported that visual feedback of the hand induced a 70 millisecond advantage over the no-vision condition. In this experiment, the target-shift required changes in movement distance, rather than direction. This brings into question whether the role of vision in making on-line movement corrections varies depending on the nature of the required response. Whereas direction corrections in the Prablanc and Martin (1992) study occurred in the initial acceleration phase of motion, distance corrections in the Sarlegna et al. (2003) study occurred substantially later, in the deceleration phase. These results indicate that corrections in distance might evoke longer preparation times than corrections in direction. It is possible that visual feedback might not yet be available for the early, direction corrections, due to visual-motor loop delays. However, recent studies have shown visual-motor latencies of under 200 milliseconds (Day and Lyon 2000; Desmurget et al. 1999; Sarlegna et al. 2004; Saunders and Knill 2004), which renders visual motor loop delay as a poor candidate to explain the differences in visual contributions between responses to distance and direction shifts in the visual target. More research is necessary to distinguish whether visual feedback differentially mediates corrections in movement direction and distance, or whether the observed differences in visual contributions to movement corrections might result from limitations in visual-motor loop delays.

It should be stressed that completely removing information from a given modality may not provide accurate information about the relative contribution of that modality to the control process. For example, when vision is removed, our ability to reach for objects accurately should not be interpreted as a *uselessness* of visual feedback in controlling movements but rather as an *adequacy* of proprioception to mediate the coordination of volitional movements. As Cruse et al. (1990) pointed out, it is remarkable that elimination of visual input can have minor effects on motor behavior, while distortion of the very same signal can have drastic effects. In line with this idea, we will present how visual distortion techniques have helped us to better understand its relative contribution to the control of purposeful actions. In a seminal study using such techniques, Hay et al. (1965) dissociated visual and proprioceptive information by using prismatic goggles, which rotated a subject’s visual field by a few degrees. This dissociated the “seen” position of the hand from its “felt” position. Interestingly, subjects indicated that they did not notice any mismatch, and that they felt their hand where they saw it. More recently, Rossetti, Desmurget and Prablanc (1995) used prisms to displace the location of an LED, representing hand position prior to movements. The LED was turned off at movement onset, and movements were performed in the dark, eliminating visual feedback about hand motion during the course of movement. The results indicated that the direction of movement was biased toward the distorted visual information of the starting hand position, and that proprioception also played a significant role in determining movement direction. In short, subjects reached as though their hand was located between its seen and actual start location. The authors concluded that visual and proprioceptive information are fused together to provide a single estimate of hand location. However, recent research from our laboratory, as well as others, has suggested that both modalities provide independent information to different components of motor planning, a hypothesis that we detail in the next section of this chapter.

## Visual and Proprioceptive Contributions to Two Serial Stages of Motor Planning

Visual perception appears to influence the way movements are planned. For example, Morasso has shown in several studies that during goal-directed arm movements, the hand tends to move fairly straight, even though the joint displacement patterns associated with such movements can be quite complex and even change direction (e.g., Morasso 1981). In fact, Flanagan and Rao (1995) and Wolpert et al. (1995) showed that when visual feedback of apparent hand position was displayed in a non-linear joint angle-based coordinate system, subjects arm movements became very curved in order to make straight cursor motions. Together, these findings support the idea that hand movements are planned as vectors, defined in extrinsic, world based coordinates. In fact, several studies have indicated that movement distance and direction, defined in extrinsic coordinates, are separately planned prior to targeted movement (Ghez et al. 1997; Rosenbaum 1980). Supporting the idea that movements are initially planned in extrinsic, visual space, studies of reaching in non-human primates have shown that motor cortex neuron firing patterns correlate well with hand direction, defined in extrinsic coordinates (Georgopoulos et al. 1986; for a review, Georgopoulos 1998; see also Alexander and Crutcher 1990; Fu et al. 1995; Kakei et al. 1999; Sergio and Kalaska 2003). However it should be emphasized that other studies have shown that intrinsic variables, such as joint torque, might show as good or better correlations with motor cortex neuron activities (Scott and Kalaska 1995).

While goal directed arm movements toward visual targets appear to be planned according to an extrinsic coordinate system, as sampled by vision, ultimately this plan must be transformed into variables that correspond to the forces required to produce motion. Thus, a plan to move the hand toward a target must be transformed into the motor commands that ultimately result in muscle activations, a transformation akin to the computational process of inverse dynamics. Interestingly, Atkeson and Hollerbach (1985) showed that unconstrained movements, performed at different target speeds and with different loads, exhibit similar shaped, unimodal hand tangential velocity profiles (i.e., the same kinematics). The joint coordination patterns associated with these simple hand velocities were often quite complex and varied across movements. This suggests that the movement kinetics were modified so that a reliable kinematic plan could be executed under varied dynamic conditions. Flash and Hogan (1985) presented a model for the organization of arm movements that attempted to explain the aforementioned characteristic features of kinematic profiles. They suggested that subjects might be constraining the kinematic plan to the smoothest possible movement. Smooth movements are characterized by low jerk, the 4th derivative of displacement. When Flash and Hogan performed optimizations for a large variety of two segment arm movements, the solutions were straight hand paths and unimodal, bell shaped velocity profiles, similar to the profiles characterized in human subjects (Papaxanthis et al. 2005). Thus, limb segment kinetics appear to be modified in order to make smooth and efficient movements of the hand as it is transported to the target.

These studies suggested that movement planning might take place in two major phases: First, in the initial stage, initial limb configuration, target position and the environmental conditions would be taken into account to determine a kinematic plan for the desired movement (e.g., at a very high speed, with a curved trajectory to avoid an obstacle). Then, a second stage of planning might correspond to the transformation of that plan into the motor commands that result in the forces producing motion. Supporting evidence for this view comes from a study (Sainburg et al. 2003) in which subjects pointed to visual targets using a similar set-up as the one shown in Fig. 1. A virtual-reality system was used to introduce a mismatch between the actual fingertip position and its seen position (the cursor representing hand position) prior to reaching movements.

In this manner, it was possible to dissociate visual from proprioceptive information about starting position. Cursor start position and finger start position differed by as much as 5 cm across nine different fingertip positions that corresponded to a single cursor start position (see Fig. 4). The analysis of movement trajectories showed that movements from all fingertip start locations were matched in terms of direction to the vector defined by the cursor start location and the target. Movement direction was thus planned on the basis of visual information of starting position while proprioceptive information did not appear to contribute to the directional planning. Inverse dynamics analysis revealed that muscle torques changed substantially between the different starting arm configurations. Thus, subjects adjusted their muscle torques so that movement direction matched the direction of the vector between the cursor start location and the target. This compensation suggested that proprioception provided accurate information about arm configuration, supporting the findings of Brown et al. (2003a). We thus concluded that the direction of movement was planned in accord with visual start location, while the dynamic strategy employed to execute this plan was based on proprioceptive information.

The fact that movement direction appeared to be planned in visual coordinates (on the basis of vision of the cursor and the target) was confirmed in a subsequent study from our laboratory (Lateiner and Sainburg 2003). In this study, a single hand position was used but the cursor could be initially presented either at a location corresponding to the veridical hand position or at a location differing by a few centimeters. Using such a visuo-proprioceptive mismatch confirmed that visual information of hand and target positions was used to plan movement direction. Sober and Sabes (2003) used a similar experimental protocol to examine the relative contributions of vision and proprioception to the planning of movement direction toward visual targets. However, they assessed the findings using a computational model in which each modality could contribute to each of two different stages of the planning process: Direction planning in extrinsic coordinates, and the transformation of this plan into intrinsic, dynamic related variables. The model included coefficients that provided a weighted contribution of each modality. According to this model, the first stage of direction planning relied predominantly on visual information (~80%), whereas the second stage of processing, the transformation of the direction plan into joint-based coordinates, relied mostly on proprioceptive information (~70%). This result was consistent with those of Sainburg et al. (2003) and Lateiner and Sainburg (2003) indicating that the extrinsic planning stage of movement direction appears to rely mainly on visual information of starting hand location.

Whereas the studies reviewed above investigated the processes underlying direction planning, the planning of movement distances might employ processes quite distinct from those employed in planning movement directions (Fu et al. 1995; Ghez et al. 1991, 1997; Paillard 1996; Riehle and Requin 1989; Rosenbaum 1980; Soechting and Flanders 1989). In a series of studies, (Bagesteiro, Sarlegna and Sainburg 2006; Sarlegna and Sainburg 2007), we investigated the relative roles of proprioception and vision to the control of movement distance, in a single joint task that has no requirements for directional planning. A visuo-proprioceptive mismatch of initial hand position was introduced prior to the reaching movements, performed without visual feedback of the limb once the movement started. Figure 5 shows sample hand paths (5A) under three randomly presented conditions: The left column shows movements performed under veridical conditions, in which the initial positions of the cursor and hand were the same. In all cases the target (large open circle) was the same. However, either the cursor (small closed circle) or the hand position (beginning of hand path) was different. The conditions were presented randomly, and subjects reported that they were not aware of any dissociations or odd conditions in during the course of the study. As can be readily determined from the figure, when the initial positions of cursor and finger were the same (Fig. 5A, left column), movements were adjusted, such that start



position 3 elicited longer movements than start position 1. This finding was consistent across subjects, as reflected by the bar graph in figure 5B, left column. When the finger started from the same location, but the cursor was shown in the varied start positions (Fig. 5A, center column), subjects also varied movement distance, such that the finger substantially overshoot the target, when the starting cursor location was shown in position 3, farthest from the target. In other words, subjects appeared to plan target distance, based predominantly on the seen location of the cursor, rather than on the felt location of the hand. Nevertheless, the location of the hand did contribute, though less substantially, to distance planning. This is reflected by the hand paths in the right column of Fig. 5A. While the initial cursor location was the same between the three conditions, the finger location varied. The distance of the movements did vary slightly across conditions, as though the cursor position, and not the finger position, was the major determinant of movement distance. These findings are quantified across subjects in Fig. 5B, which shows the greatest change in distance under veridical conditions (left: 9.9 centimeters), followed by the condition in which the cursor but not the hand changed its initial location (center: 5.5 cm). Finally, the least variation in distance occurred for the conditions in which the initial cursor location was constant, while the initial finger location varied (right: 3.4 cm). Interestingly, the summed variation in movement distance produced by varying cursor location and hand location (8.9 cm) was very similar to that produced by varying both hand and cursor location, veridically (9.2 cm), as though the two modalities contributed independently to distance planning.

These findings indicated that movement distance was planned predominantly on the basis of the visually displayed distance between the cursor and the target (Fig. 5). This was emphasized by the fact that peak acceleration was scaled with initial cursor position, but not with initial hand location (Sarlegna and Sainburg 2007). These findings indicated that, for each starting cursor position, the initial movement acceleration (and therefore the initial joint torque amplitude) remained constant, regardless of variations in elbow starting angle that were as large as 158. Because of configuration dependent variations in muscle moment arm and length-tension relations, production of the same torque across different joint angles requires substantial changes in the neural commands to the muscles. In fact, Prodoehl et al. (2003) recently showed systematic and predictable changes in joint torque during maximum speed tasks across the range of elbow movements that we employed in our study. In Prodoehl et al.'s study, electromyographic (EMG) activity of elbow muscles showed compensatory changes in timing and amplitude that served to diminish the effect of configuration dependent changes in muscle moment arm and muscle length. In a similar study of ankle joint movements, Nourbakhsh and Kukulka (2004) showed that when subjects produced targeted isometric plantar flexion torques across a range of ankle positions, triceps surae EMG was modulated, so as to compensate configuration dependent variations in muscle moment arm.

We thus expect that maintaining constant acceleration amplitudes over experimentally imposed variations in starting elbow angle must have induced compensatory variations in muscle activation strategies. These findings indicate that while subjects used visual information to plan movement distance toward visual targets, proprioceptive information about hand position was used to transform that plan into variables that correspond to the joint torque required to produce the planned movement. These findings are consistent with previous research in proprioceptively deafferented patients, which indicated a major role of proprioception in transforming kinematic plans into dynamic strategies required for intersegmental coordination (Sainburg et al. 1993, 1995).

## Conclusion

In this chapter, we presented experimental evidence for the idea that vision and proprioception contribute differentially to the planning of goal-directed arm movements toward visual targets. Visual information of hand position is mainly used in a first stage to define the kinematic plan of the reaching movement within an extrinsic coordinate system. Proprioception appears to be essential in transforming this kinematic profile into the neural commands that result in the necessary forces to achieve the desired motion.

## References

The references marked with an asterisk (\*) are specifically recommended for further introduction or background to the topic.

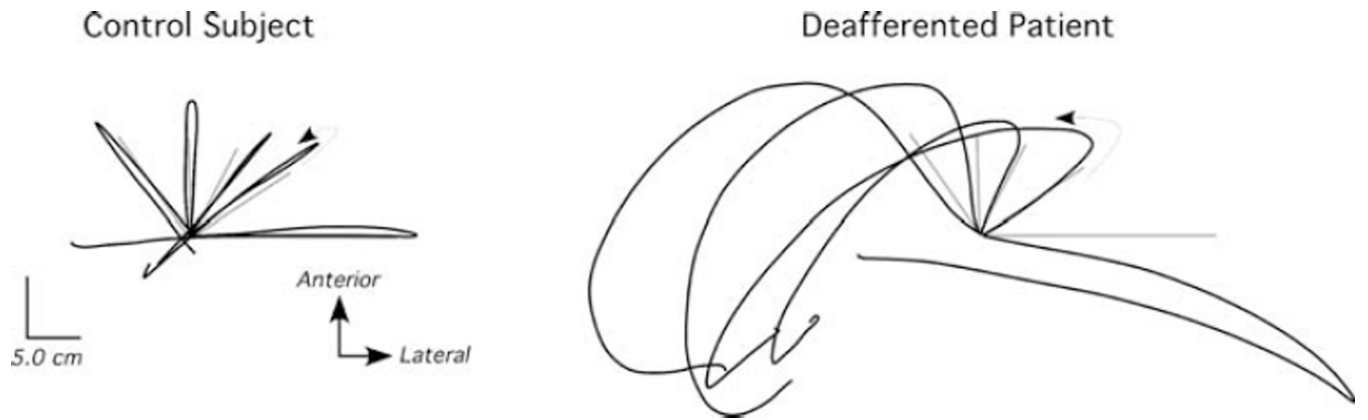
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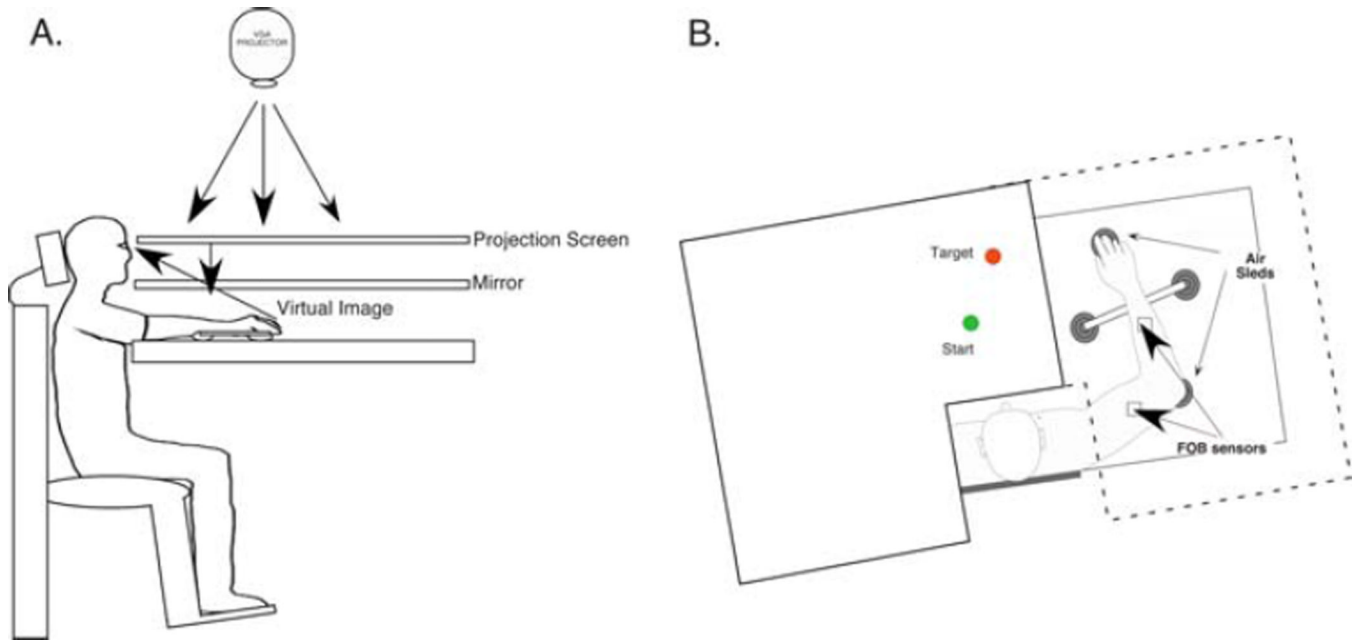
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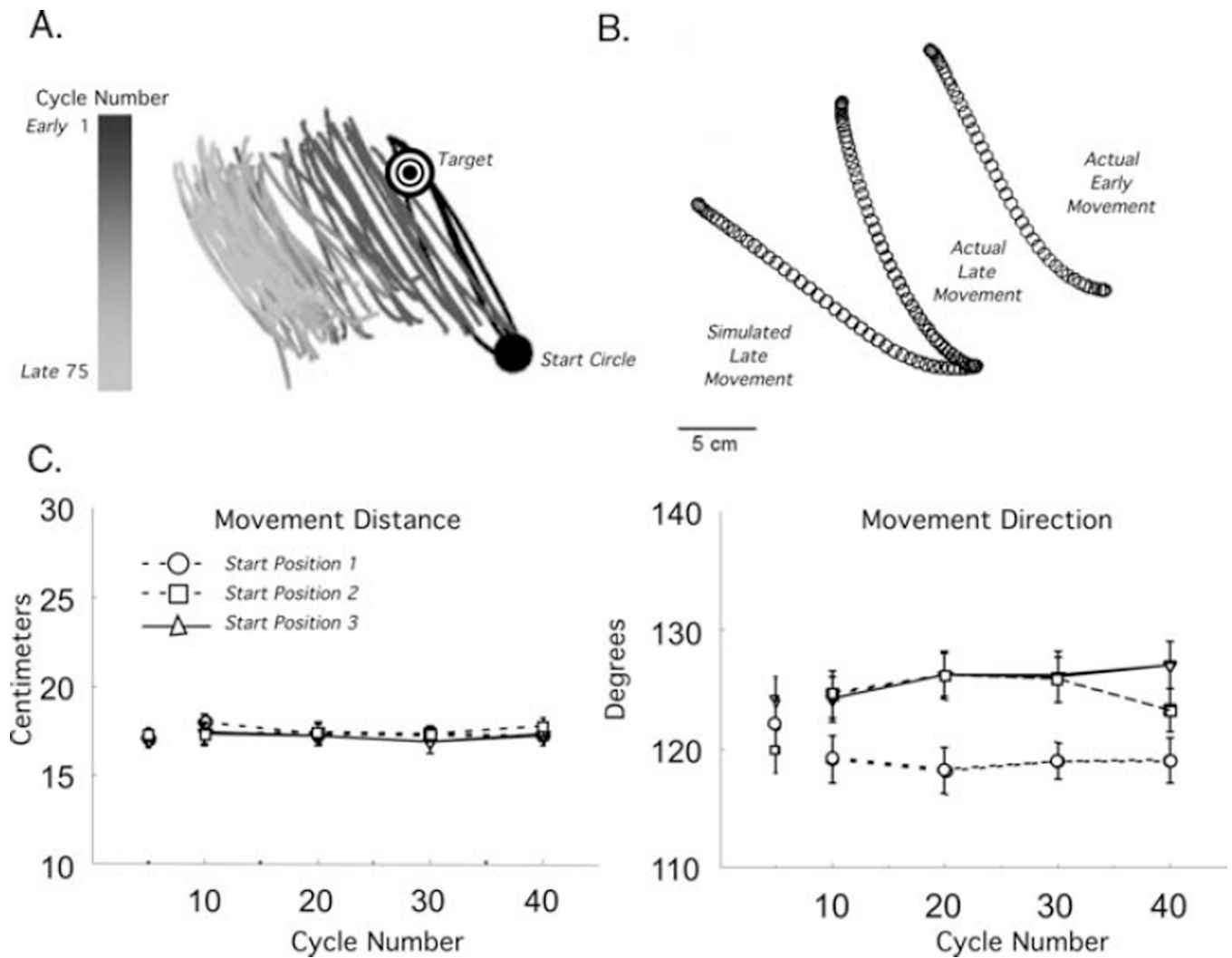


**Fig. 1.** Representative hand paths from control subjects and deafferented patients, drawn overlaying the template lines, shown for five directions

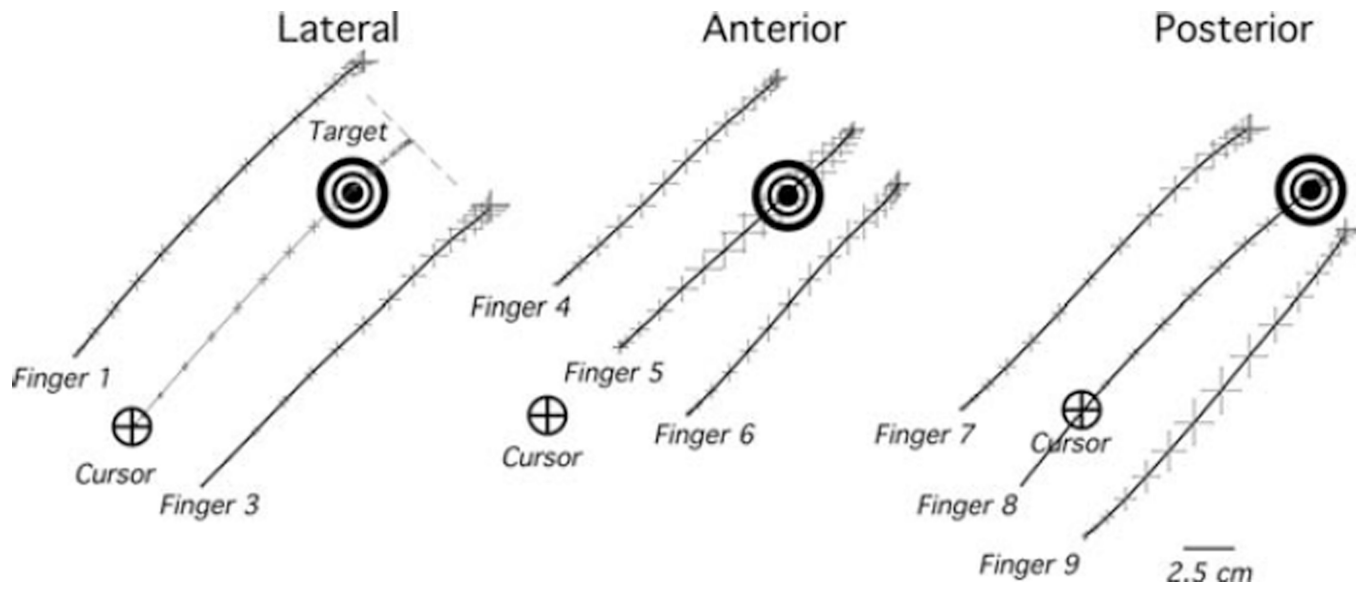


**Fig. 2.**  
Experimental set-up



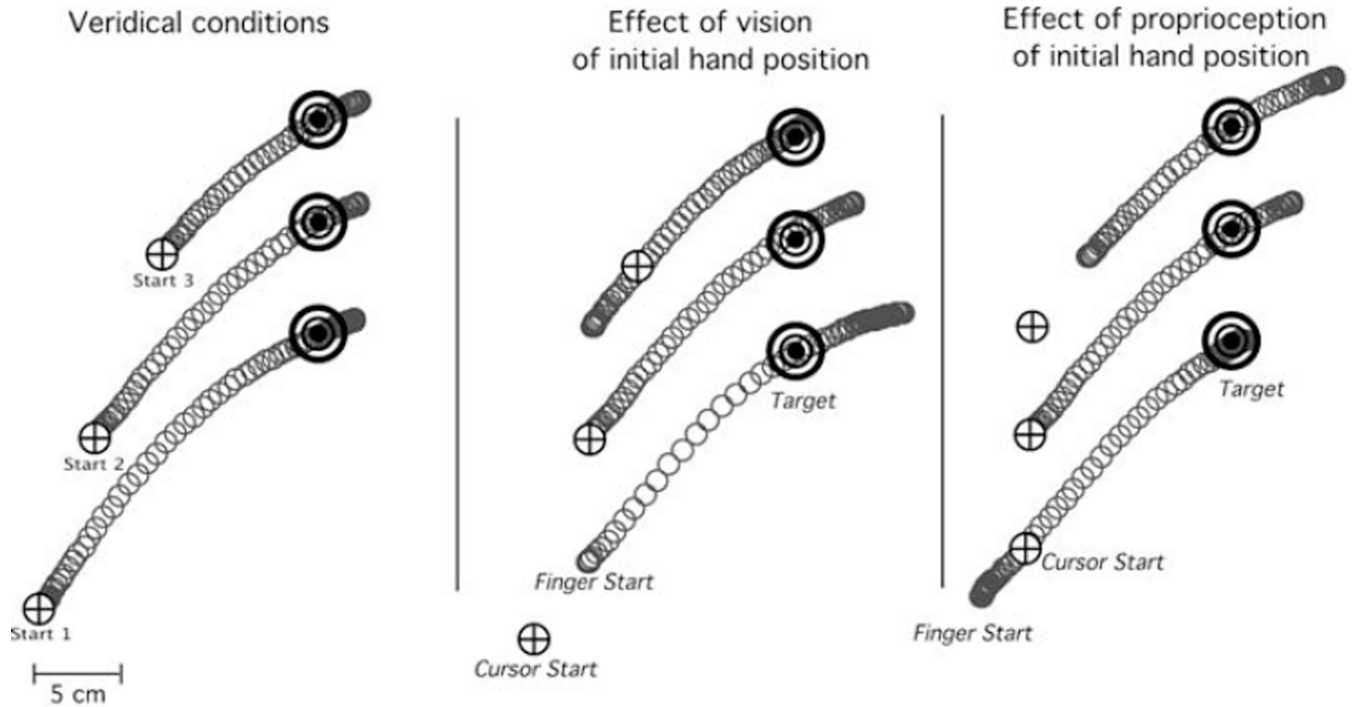


**Fig. 3.** Drift task from Brown et al. 2003a. **A.** A single 75 cycle trial. Only outward sections of movement are shown because analysis was based on this portion of movement. For the first five cycles, visual feedback of hand position was shown as a screen cursor, and then turned off prior to cycle 6. Movements progressively drifted to the left, following this. Trial number is reflected by gray scaling, as indicated by the bar at the left. **B.** Early movements and late movements in a single trial did not vary in terms of direction or distance, regardless of drift. The figure shows the outward portion of an early and a late cycle of an actual trial. The joint torques calculated from the early movement were used to drive a forward simulation from the drifted limb position, at the onset of the late movement. The simulated trial indicates the direction error expected if the altered limb configuration is not accounted for in the joint torque strategy. Thus, subjects clearly account for the drifted limb configuration in generating movement strategies. **C.** Across subjects, movement distance and direction do not change over subsequent cycles of motion, regardless of drift in limb configuration. Values for each of three start positions workspace are shown



**Fig. 4.** Ensemble averaged hand paths  $\pm$  standard errors in X and Y coordinates (*crosses*) are shown for all nine start positions of the hand. The initial position of the cursor was always on the central start, while the starting position of the finger varied between the central start location (veridical, baseline trials) and each of 8 other positions, as shown

## A. Hand paths toward a visual target



## B. Mean movement distance (cm) as a function of start location

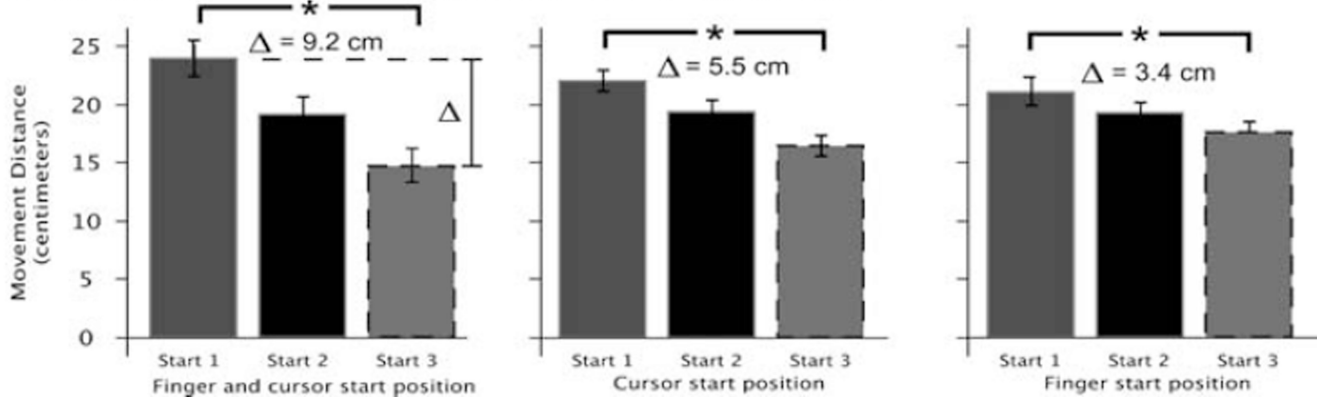


Fig. 5.

Representative hand paths **A.** from single joint movements toward a single target under three start locations when the position of the cursor and the finger were the same (*left column*), when the cursor position varied, but the finger position was constant across start positions (*center column*), and when the cursor position was constant across start positions, while the finger position varied (*right column*). Bar graphs **B.** show the corresponding distances, averaged across subjects, for the conditions shown in **A**