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Visuomotor channels: Their integration in goal-directed prehension

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Abstract

The visuomotor transformations for producing a grasping movement imply simultaneous control of different visual mechanisms. The size, orientation and 3D characteristics of the object have to be encoded for the selection of the appropriate opposition space, within which the opposition forces will be applied on the object surface. These mechanisms also have to combine with those of the transport of the hand to the object location. Finally, biomechanical constraints impose categorical visuomotor decisions for positioning the opposition space according to object changes in size, orientation and spatial location. This paper examines possible interactions between the specialized structures for visuomotor transformation and the internal model that adapts prehension to its goals. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

The aim of this paper is to resolve a paradox concerning the organization of visually guided goal-directed actions. On the one hand, this type of action involves specialized visuomotor mechanisms for transforming each aspect of the object into motor commands: object position in space must be transformed into motor commands for orienting the eyes, its position with respect to the body into commands for reaching with the arm, its size and shape into commands for adjusting the shape of the hand, etc. On the other hand, these mechanisms must be coordinated into a global action which subserves a particular goal. Although these two aspects of the same movements are not contradictory with each other, they imply vastly different modalities of motor control. In this paper, the arguments which favor decomposition of the action into selective visuomotor mechanisms will be presented first. In the second part, a hypothesis will be submitted for explaining integration of these mechanisms into a purposeful action. The action of grasping an object localized in extrapersonal space will be used throughout as an example, as it best epitomizes the two terms of the paradox.

2. Visuomotor channels

The kinematic description of grasping suggests the co-occurrence of several submovements. Transporting the hand to the object, orienting the wrist, and preshaping the fingers into an appropriate grip each involve sets of muscles and joints characterized by different control modalities. The fast, ballistic type of movement of the arm responsible for the reach contrasts with the slower independent movements of the fingers during the grasp. These striking differences were the basis for the hypothesis of Visuomotor Channels put forward in the early 1980s (Arbib, 1981; Jeannerod, 1981). This theory held that each of the components of the act of prehension behaves as an identifiable system, characterized by its own input and output and its own intrinsic mechanisms. The theory went as far as associating each visuomotor channel with a specific mode of visuomotor transformation, such that the transport component related to the spatial (egocentric) aspects of the action – processing distance and direction – whereas the grasp processed intrinsic aspects of the object – like shape or size.

Already implicit in the work of Brinkman and Kuypers (1973), the Visuomotor Channels hypothesis received its main support from physiological and anatomical studies on monkeys. These studies took place within the general framework of identification of distinct cortico-cortical streams of connections within the visual system, which postulated that visual functions are mediated by two diverging pathways. Nearly twenty years later, this framework still raises much interest and generates new experiments. In the original version of the hypothesis, the ventral, occipito-temporal pathway was assigned a role in object identification, whereas the dorsal, occipito-parietal pathway, was considered as primarily involved in processing spatial relationships (Boussaoud, Ungerleider & Desimone, 1990; Mishkin, Ungerleider & Macko, 1983; Ungerleider & Mishkin, 1982). A more recent version, that of Goodale and Milner (1992), still preserves a similar functional separation between a ventral system for perceptual identification and a dorsal system for visuomotor transformation. As far as prehension movements are concerned, the dorsal system thus appears as the most likely place to look for a neuronal substrate. As outlined above, however, visuomotor transformation itself involves several, widely different mechanisms whether one considers transporting the hand at a desired location in space, or grasping and manipulating an object, for example. Hence the claim that the notion of parallel cortico-cortical pathways, which revealed to be operational for identifying the dorsal and the ventral streams, should also be extended to the mechanisms which operate *within* the dorsal stream itself. Arguments will be presented below supporting the existence of neural pathways for reaching and for grasping. Incidentally, the same move has been taken by researchers involved in perceptual functions, who tend to isolate pathways within the ventral stream for perception of colors, faces, etc. (for a review of the argument, see Zeki (1993)).

The visuomotor pathway for reaching can be described first. This pathway includes parietal areas where populations of reaching neurons which seem well suited for detecting the position of visual targets in head or body-centered coordinates have been recorded (Hyvarinen & Poranen, 1974; Kalaska, Caminiti & Georgopoulos, 1983; MacKay, 1992; Mountcastle, Lynch, Georgopoulos, Sakata & Acuna, 1975). More precisely, such neurons have been found in areas LIP and PO (See Fig. 1 for anatomical location and abbreviations). In area LIP (an area buried in the intraparietal sulcus at the rostral edge of area 7a), Andersen, Essik and Siegel (1985) found a population of cells, the response of which was influenced by the position of the eyes in the orbits. In area PO in the superior parietal lobule also, neurons respond to visual stimuli placed at a given spatial location, regardless of eye position (Galletti, Battaglini & Fattori, 1993). In area MIP, neuronal activity during

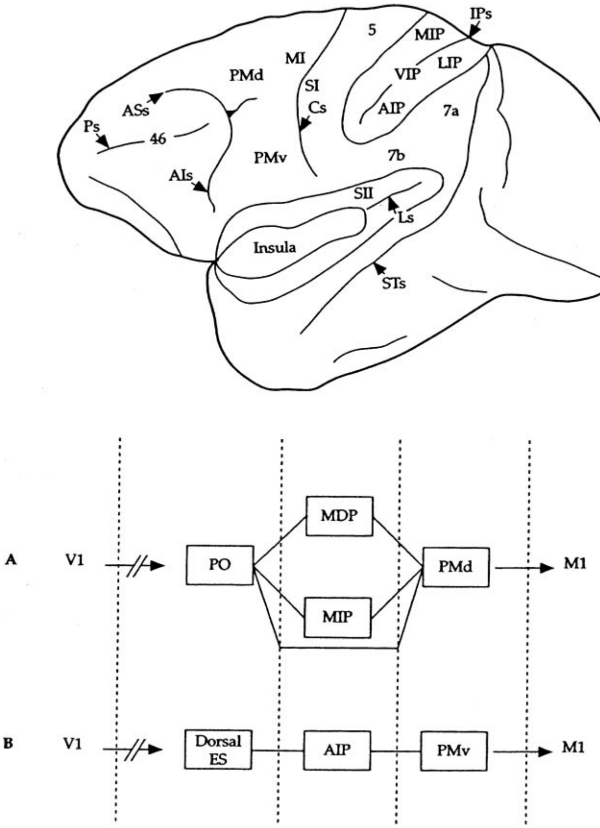

Fig. 1. Anatomy of the visuomotor channels. Upper part: Left hemisphere of a macaque brain showing the main parietal and frontal areas involved in visuomotor transformations. Cs: Central sulcus; IPs: Intraparietal sulcus; Ls: Lateral sulcus; MIP, LIP, VIP, AIP: Medial, Lateral, Ventral and Anterior intraparietal areas, respectively; PMd, PMv: Dorsal and Ventral premotor cortex, respectively. Lower part depicts two putative visuomotor channels for reaching (A) and for grasping (B). These channels connect the primary visual cortex (V1) to the primary motor cortex (M1) via occipital and parietal areas. From Jeannerod, 1997.

active arm movements is tuned in a body-centered frame of reference (Lacquaniti, Guigon, Bianchi, Ferraina & Caminiti, 1995). These parietal areas project directly on premotor cortex. Matelli, Camarda, Glickstein and Rizzolatti (1986) found that the rostral most part of area 7a does project to the dorsal area 6. Johnson, Ferraina and Caminiti (1993) also found direct connections between area MIP and the dorsal premotor area, where they recorded reaching neurons. Finally, a connection linking area PO to dorsal premotor cortex, either directly (Tanné, Boussaoud, Boyer-Zeller & Rouiller,

1995) or via the superior parietal lobule (Caminiti, Ferraina & Johnson, 1996), was disclosed. This connection, which provides a link between area PO, where the location of visual targets is coded in head-centered coordinates, and the premotor cortex, where directional output is generated (e.g., Boussaoud, 1995; Gentilucci et al., 1988), altogether reinforces the notion of an independent visuomotor subsystem for reaching movements.

The pathway for grasping has also been identified in monkey experiments (see Jeannerod, Arbib, Rizzolatti & Sakata, 1995). Neurons related to active arm movements were first recorded in the inferior parietal lobe by Mountcastle and his colleagues who identified, besides the "arm projection" neurons related to reaching, a group of "hand manipulation" neurons (Mountcastle et al., 1975). More recently, hand movement-related neurons were found to be concentrated in a small zone (the anterior intraparietal area, AIP) within the rostral part of the posterior bank of intraparietal sulcus. Using a broad variety of graspable objects, including primitive shapes such as spheres, cubes, cones, cylinders, rings and plates of different sizes, Taira, Mine, Georgopoulos, Murata and Sakata (1990), Sakata, Taira, Mine and Murata (1992), and Sakata, Taira, Murata and Mine (1995) found that AIP neurons were activated during grasping one particular type of object, also when the movement was performed in the dark. Neuron activity was not influenced by changing the position of the object in space, which shows that it was related to distal hand and finger movements rather than to proximal movements of the arm. Many of these visually responsive neurons were also activated by the sight of objects during fixation without grasping.

Area AIP is directly connected with a limited zone of premotor cortex, the subfield F5 of area 6, identified by Matelli, Luppino and Rizzolatti (1985), itself directly connected with that part of area 4 (field F1) which corresponds to the hand primary motor field (Fig. 1). Intracortical microstimulation and single neuron studies showed that F5 is specifically related to distal movements (Hepp-Reymond, Hüssler, Maier & Qi, 1994; Rizzolatti et al., 1988). Rizzolatti and his colleagues recorded single neurons from F5 in behaving monkeys during object-oriented actions. These experiments showed that most neurons located in the upper part of F5 are related to grasping. The temporal relation of their discharge with grip movements changes from neuron to neuron. Some fire during the late part of grasping, that is, during finger flexion. Others start firing with finger extension and continue during finger flexion. Others are activated in advance of finger movements and often cease discharging only when the object is grasped. An interesting property of most F5 neurons is their selectivity for different types of hand prehension.

Eighty five per cent of grasping neurons show selectivity for one of three basic types of grip: precision grip (the most represented type), finger prehension and whole hand prehension. There is specificity for different finger configurations, even within the same grip type. Thus, the prehension of a sphere, which requires the opposition of all fingers, is encoded by different neurons than the prehension of a rod, for which a palm opposition grip is used. The connections linking the parietal area AIP to the "distal" area of premotor cortex (F5) and then to F1 could thus represent another, parallel, specialized visuomotor system for encoding object primitives and generating the corresponding hand configurations (Fig. 1).

A confirmation of the parallel organization of mechanisms for reaching and grasping was provided by an experiment of Gallese, Murata, Kaseda, Niki and Sakata (1994). Transient inactivation of AIP by a GABA agonist (muscimol) produced a subtle change in the performance of visually guided movements during grasping tasks. Grasping errors were observed in tasks requiring a precision grip. These errors were due to a lack of preshaping of the hand during the approach phase of the movement. In addition, there was a clearcut dissociation of the muscimol effects on grasping and reaching. Whereas the alteration of preshaping was consistently obtained after injection in the rostral part of the posterior bank of the sulcus (where AIP is), misreaching occurred after injection within its more caudal part. This result confirms and expands those obtained by Lamotte and Acuna (1978) and Faugier-Grimaud, Frenois and Stein (1978) who had shown a combined reach and grasp deficit following surgical lesions of the posterior parietal zone. Such lesions, however, are usually too extensive to allow for a separation between such closely packed anatomical structures. This is also usually the case following pathological lesions in humans (Jeannerod, 1986; Perenin & Vighetto, 1988). In a few cases human posterior parietal lesions have been found to affect the grasp without altering the reach (Jeannerod, Decety & Michel, 1994). No case seems to exist of the opposite dissociation.

Finally, brain activation was monitored during reaching and grasping in normal human subjects, using the PET technology. Grafton, Mazziotta, Woods and Phelps (1992), using a reaching task (tracking a visual spot with the index finger) found a rCBF increase in the dorsal parietal region. The activation focus predominated in the superior parietal lobule (Brodman area 7) and in the precuneate cortex. This location is in agreement with the localization of lesions that produce misreaching (see Perenin & Vighetto, 1988). The involvement of posterior parietal areas in relation to visually-guided movements was subsequently confirmed in several studies, with the difference, however, that the main focus of activation tends to be located more ventrally and more rostrally than initially described by Grafton et al. (1992). The main focus appears to correspond to areas 39 and 40, rather than to the superior parietal lobule (Decety et al., 1994; Stephan et al., 1995). Finally, an experiment aimed at comparing activated areas in visual and visuomotor tasks was designed by Faillenot, Toni, Decety and Jeannerod (1997). The subjects were instructed either to make perceptual judgements on complex shapes made of wooden blocks (the matching task), or to grasp these shapes using a precision grip (the grasping task), or to point at the center of the blocks, irrespective to their shape (the pointing task). During grasping, the main focus was located in the anterior and ventral part of contralateral parietal cortex, including the anterior part of area 40, as well as part of area 2, part of SII and part of the insula. Because this focus persisted after subtraction of the activation observed during the pointing task, this result supports the existence of a neural pathway specialized for grasping (for a full description of the results, see Faillenot et al. (1997)).

3. The action of prehension

The notion of separate systems does not capture all the aspects of prehension. In addition to the specific visuomotor transformation effected by each channel, one has to consider the fact that all the channels concur to the same final goal of achieving a stable grasp for holding and manipulating an object. Distinct from each other as they may be, the visuomotor channels for reaching and grasping must also share a common mechanism for achieving coordination with each other.

In an experiment in which subjects grasped cylindrical objects, Paulignan, MacKenzie, Marteniuk and Jeannerod (1991a) noticed that the variability of the spatial paths of index finger and thumb tended to sharply decrease while the fingers approached the object, suggesting that the fingers were aiming at a predetermined locus on the object surface. At first sight, this observation (see also Kudoh, Hattori, Numata & Maruyama, 1997) suggests that the action of prehension is planned, not as the addition of several components with individual goals, but rather in terms of a single goal for the whole arm. Controlling the trajectory of a single effector would indeed appear optimal for reducing variability of the end-point of the limb. If this interpretation is correct, however, one should be able to find some evidence for a covariation of the spatial and/or temporal parameters of the two submovements. The search for this covariation has led to mixed results. Studies in the early 1990s stressed the fact that the two main components were far from independent from each other, because the movements at the different joints tended to covary during the action of prehension. For example, it was observed that altering the reaching movement (e.g., by varying the distance of the object) also affected the formation of the grip (a longer distance yielded a larger grip size, Chieffi & Gentilucci, 1993; Jakobson & Goodale, 1991). Conversely, altering the grip (e.g., by varying the size of the object) affected the kinematics of the reach (larger objects yielded faster transport, Bootsma, Marteniuk, MacKenzie & Zaal, 1994; Gentilucci et al., 1991; Jakobson & Goodale, 1991; Marteniuk, Leavitt, MacKenzie & Athenes, 1990; Zaal & Bootsma, 1993).

The above covariations can be interpreted in at least two different ways. First, they could reflect a cross-talk between the two components. One of the most robust findings in prehension is that maximum grip aperture is consistently achieved after the occurrence of the peak deceleration of the wrist. This also holds true when the course of the movement is perturbed (e.g., by changing object position at movement onset): in this situation, the initial sequence of peak deceleration and maximum grip aperture is followed by a second one, in the same order (Paulignan et al., 1991a; see also Haggard & Wing, 1991). By contrast, if perturbations in object position affect the grasp, perturbations in object size have little effect on the transport (Paulignan, Jeannerod, MacKenzie & Marteniuk, 1991b). Thus, the coordination between the components could rely on an information flow from transport to grip, not the reverse. The mechanism for coordination of components in prehension would therefore be twofold: the transport component would be controlled by a single feedforward controller, terminal error in transport being compensated for by a larger grip aperture when distance or velocity increases. The grasp component would also be controlled by a feedforward controller up to the time of maximum aperture, and then the closure would be feedback regulated. A full demonstration for this mechanism is still missing: so far, only the feedforward nature of the transport component has received experimental support (e.g., Jeannerod, 1984; for a discussion see Hoff & Arbib, 1993).

A second view of the coordination mechanism in prehension would be that of a top-down regulation affecting all aspects of the action. It is therefore appropriate to briefly examine the current conceptions of the modes of planning for goal-oriented actions. The question of how the motor system controls the multiple degrees of freedom of the arm, which allow for a potentially infinite number of solutions for a particular motor task (the redundancy problem), was approached by postulating that the motor system might only control a few critical variables, hence reducing its computational load. One of these variables is the limb end-point trajectory in space. In an influential paper, Morasso (1981) reported that the planar displacements of a hand-held lever toward visual targets had bell-shaped velocity profiles and followed approximately straight spatial paths. These characteristics are consistent with those one would expect for a movement planned in Cartesian coordinates and where the only parameter controlled by the central nervous system is the spatial path of the hand (see Hogan & Flash, 1987).

Other models postulate that the motor system plans movements in joint coordinates and controls the position of each of the joints contributing to the movement (Desmurget, Jordan, Prablanc & Jeannerod, 1997; Soechting & Flanders, 1992). A variant of the joint-space model is that of planning a final arm posture. The general idea is that the motor control system plans actions by using optimization principles such as minimizing the number of joints involved, avoiding biomechanical discomfort, or preserving an optimal final posture. Several results with prehension indicate that the arm tends to reach a specific final posture for each position of the target in 3D space. Desmurget et al. (1995) recorded the final arm posture when a subject reached to grasp a bar placed at different orientations. On some occasions, the orientation of the bar was changed at the onset of the reaching movement. The configuration of the arm was rapidly altered so as to match the new orientation, that is, the arm moved to the final posture that was assumed during unperturbed movements directed at a bar with the same orientation. In other words, each orientation of the bar determined a unique final posture of the whole limb.

4. Determinants of the orientation of the opposition axis

This same idea of final posture coding can also be used for explaining recent data on visuomotor control of prehension obtained by Paulignan, Frak, Toni and Jeannerod (1997). The main hypothesis of the experiment was that, because the fingers that contribute to the grasp represent the effector of the movement, their position on the object at the end of the movement should be the main parameter to be controlled in order to achieve an efficient grasp. Finger positions on the object determine the opposition axis, the axis along which the opposing grip forces are exerted on the object, such that a stable grasp will be obtained (Iberall, Bingham & Arbib, 1986;

Napier, 1955). In most daily-life situations, object properties like shape and size clearly define an opposition axis: The task of the motor system in the prehensile act is to bring the fingers into an appropriate position and to choose the optimal configuration of the arm corresponding to these positions. The experiment of Stelmach, Castiello and Jeannerod (1994) shows that a relatively small change in orientation of an object which affords only one possible opposition axis results in a major reconfiguration of the arm, including wrist pronation and shoulder abduction.

To better understand the processes involved in selecting the adequate opposition axis, however, it is more helpful to employ objects which allow for more than one opposition axis (e.g., cylinders). By analyzing prehension movements to cylindrical objects at different positions in the workspace, the limb configuration for a given object at a given position can reveal on which information the motor system predominantly relies. Will the motor system use a preferential opposition axis for all object positions, resulting in different limb postures, although other opposition axes were feasible as well? Or, alternatively, will the motor system minimize the changes in limb configuration by using different opposition axes depending on the position of the object? An experiment fulfilling these requirements was performed in four right-handed subjects. As the experiment was already published (Paulignan et al., 1997), only data relevant to the present discussion will be reported here. The objects used as targets were 9 cm high white plastic cylinders of three different diameters (3, 6 and 9 cm). Their weight was 100, 200 and 300 g, respectively. The cylinders were placed upright on a horizontal table at which the subject was comfortably seated. They were presented one at a time at six fixed locations centered on the subject's head, starting from 10 degrees on the left of subject's sagittal axis (−10°), 0 degrees (along the sagittal axis), and 10, 20, 30 and 40 degrees on the right (see Fig. 2, left). The subject's right hand rested on the table immediately to the right of the sagittal body axis, so that the thumb and index fingertips were positioned on that axis. This position approximately corresponded to a distance of 25 cm from the center of the body. The presentation of objects was randomized for both position and size. Subjects were instructed to reach, grasp and lift the objects using a precision grip. They were asked not to move their trunk and to make fast and accurate movements. The GO signal for the each movement was given by the illumination of a red LED embedded in the table in front of each object position. The recording was continued for 2 seconds after the GO signal. Ten movements were recorded for each object position and size. The movements of the right arm were recorded by means of an Optotrak 3020 system fixed 2.5 m

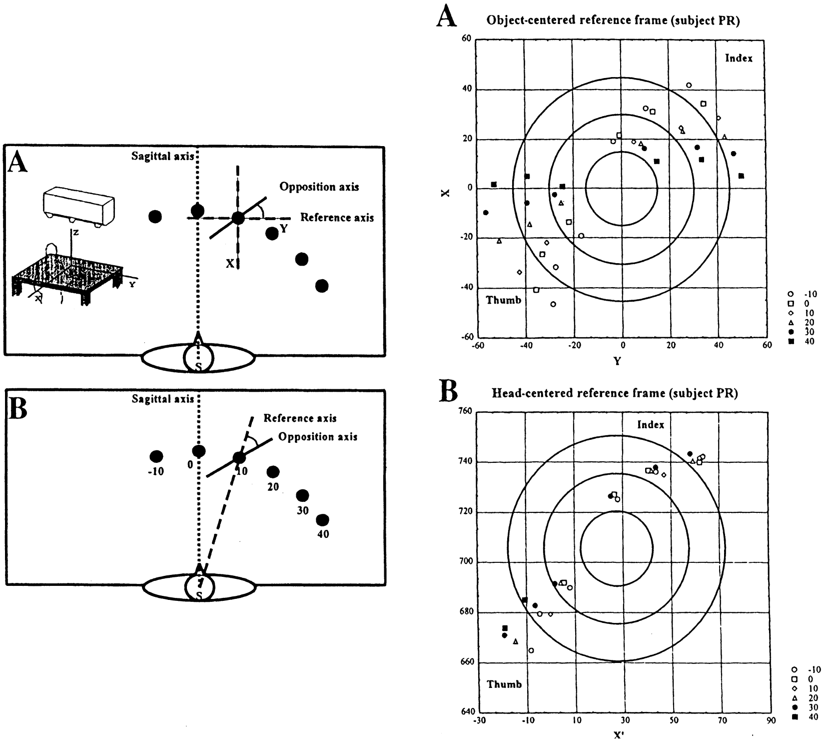

Fig. 2. A study of orientation of the opposition axis during grasping cylindrical objects. Left: Schematic representation of the experimental layout, showing the reference frames used for computing orientation of the opposition axis (A: Reference axis is the *Y* axis of the recording system; B: Reference axis is the line between subject's head and target). Right: Plot of final positions of Index and Thumb during grasping objects of different sizes and locations (locations are indicated by different symbols). The two plots are made in two different reference frames, object centered (A) and head centered (B). From Paulignan et al. (1997).

above the working space with its optical axis aligned with the vertical. Two markers were stuck on the nails of the index finger and the thumb, respectively. Another one was placed at the wrist level on the styloid process of the radius. These markers were used for measuring the two main components of prehension, namely the grasping component (the change over time of the distance between the index and the thumb markers) and the transportation of the hand (the change over time of the position of the wrist marker). Two more markers were used for measuring the wrist angle: one on the dorsal aspect of the hand immediately proximal to the metacarpophalangeal joint of the index finger, and the other on the forearm. The spatial paths of the three main markers and their variability over repeated trials were measured in three dimensions. The spatiotemporal variability of these spatial paths was quantified after time normalization of the data. The standard deviations of the mean X, Y and Z positions of each marker were calculated for each of the 100 normalized frames (Georgopoulos, Kalaska & Massey, 1981). Variability was expressed as the square root of Sd X^2 + Sd Y^2 + Sd Z^2.

In order to reconstruct the opposition axis, the position of the two fingertips was sampled at the end of the movement. The opposition axis was defined as the line connecting these two points. Its orientation was measured, for each object position and size, with respect to several different reference frames: In the *object-centered* frame, the workspace was defined by the X, Y and Z axes of the Optotrak system. The Y axis was used as the reference for calculating the angle of orientation of the opposition axis. In order to compare the values of this angle for movements directed at objects of different positions and sizes, the object center for each trial was considered as the center of the workspace. In this way, the X and Y coordinates of the finger positions on the objects (and thus the opposition axes) for all trials were referred to the same point (Fig. 2, left). In the *head-centered* frame, the orientation of the opposition axis was calculated with respect to the line connecting the center of the head and the object center. In order to compare orientations of the opposition axis for movements directed at objects of different positions and sizes, the reference axis was rotated around the subject's head, so that objects in all trials were superimposed (Fig. 2, left).

The first result was that the spatial paths of the two fingertips over repeated movements directed at the same object tended to converge on the points of contact, as indicated by the sharp decrease in variability during the final part of the trajectory. This strongly suggests that the final finger position (and therefore the orientation of the opposition axis) is the controlled variable of prehension. The second result was that this position is determined, not with respect to external (visual) coordinates, but with respect to body-centered coordinates. Although the orientation of the opposition axis apparently varied for each position of the object in the workspace, it remained invariant with respect to a reference attached to the body (e.g., the line connecting the center of the head and the center of the object). This result is shown in Fig. 2, right. The upper part of this figure represents a plot of finger positions on the object placed at different spatial locations. When finger positions are plotted in head coordinates, they appear to be aligned for all the objects (Fig. 2, lower right). In addition, this invariant angle of the opposition axis did not involve a different configuration of the forearm for each object position: the wrist angle remained identical for different object positions, which implies that the forearm and the hand were displaced as a whole, irrespective of object location. Because of this, the main changes had to occur at the level of the elbow and the shoulder joints for keeping the orientation of the opposition axis invariant.

Visual and motor factors thus compete for determining the orientation of the opposition axis. Whenever possible, the final arm posture tends to remain invariant and it is only when required by object shape that new degrees of freedom are recruited. In addition, behavioral strategies can be used for preserving an invariant forearm posture in spite of constraining object shapes: for example, a subject might rotate his body around the object until the orientation of the opposition axis afforded by the object becomes compatible with the optimal arm posture. The fact that the opposition axis is computed with respect to a body reference makes this possibility (which is excluded in most laboratory situations where a fixed position of the body with respect to the workspace is imposed) an economical one in terms of the number of degrees of freedom involved. In conclusion, the fact that, when no visual constraints are present (as it is the case with cylindrical objects), the position of the fingertips on the object reflects the selection of an invariant final posture of the arm, not an invariant visual landmark on the object, validates the idea of a global planning of prehension. This idea would be compatible with Rosenbaum et al., 1990 finding of spontaneous grasping preferences (e.g., overhand vs underhand) when grasping a bar that has to be placed on a support. In this case, the initial discomfort of the arm posture is tolerated for the sake of final comfort, because the end-state comfort is critical for the future task demands.

5. Conclusion

To what extent can the concept of visuomotor channels still account for the aspects of prehension which are described in the Paulignan et al. (1997) experiment? Indeed, the results of this experiment tend to show that the position of the fingers on the object is not independent from the proximal (transport) component of prehension. In other words, the mechanisms that determine the selection of an appropriate opposition axis would not be separate from those that determine the hand position in the workspace. A possible explanation for this fact is that, among the visual parameters that contribute to the final pattern of grasping, orientation of the object has a special status. This interpretation was used by Soechting and Flanders (1993) to explain the errors in matching the orientation of an object with a hand-held rod, in the absence of visual control of one's hand. As these errors depended both on the slant of the object and on its location in the workspace, they concluded that the neural transformation from target orientation to hand orientation is influenced by both visual spatial and arm posture parameters. In fact, a more general explanation should be looked for, as orientation is not the only object parameter to affect distal as well as proximal degrees of freedom: Increase in object size, to mention only one more, at first requires a change in grip aperture and, beyond a critical size, requires intervention of the two hands.

Although the notion of holistic programming does seem to contradict that of visuomotor channels, a hypothesis can be proposed for integrating the two. Adapting the configuration of the upper limb to the grasping situation requires taking a number of appropriate visuomotor decisions (e.g., pronation vs supination of the forearm, one or two hands, etc). This process cannot be achieved only through a direct visuomotor transformation, because it must take into account the fact that any given decision may simultaneously involve several channels. For this reason, it would be better achieved by an internal model where the consequences of the decision could be fully represented. Thus, our hypothesis suggests that an action like prehension is organized on several levels. At one level, visuomotor transformation requires the activation of specific channels characterized by their own input–output relationships. At another level, these channels are embedded into a distinct mechanism which represents the internal model of the action and exerts a top-down control on the channels. A strong argument in favor of this mode of functioning is the temporal organization of prehension movements. Several temporal landmarks can be described for prehension. First, the two components are synchronized at movement onset: the opening of the grip and the projection of the arm toward the object start within less than 50 ms as a consequence of nearly simultaneous contraction of the muscle groups involved (Jeannerod & Biguer, 1982). Second, as already mentioned, the two components are phased near the end of the deceleration of the reach. Finally, the two components simultaneously stop at the time of contact with the object. The temporal organization of prehension movements thus seems to be reducible to a few critical points on the time axis (Jeannerod, 1981). This view was taken up more recently by Hoff and Arbib (1993) in their time-based coordination model. They postulated the existence of a "coordinating schema" which receives from each of the constituent schemas (the visuomotor channels) an estimate of the time it needs to move from its current state to the desired final state. Whichever channel is going to take longer is given the full time it needs, while the others will be slowed down. The time needed by each channel is regulated by optimality criteria which are embedded in feedback controllers. This model has been found to account for the rapid corrections generated in response to sudden displacement of the target object at the onset of a reaching movement (see Paulignan et al., 1991a). It could also account for the progressive shaping of the fingers which, according to Santello and Soechting (1998), is not completed until late in the unfolding of prehension.

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