

Motor and representational framing of space

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Introduction

The intention here is to focus on some motor-oriented approaches to the spatial functions of the brain and to see how far they contribute to our understanding of the way in which the internal metric of spatial information is neurally encoded.

A motor-oriented approach assumes that the principal metric for coding spatial relationships is derived from the body's own movements in space: that is, the spatial relationship between two locations can be coded in terms of the movement required to get from one to the other. To what extent this approach can account for a plurality of sensorimotor action-spaces and also explain how a variety of spatial representations are encoded in the brain is open to question and will now be addressed.

A basic assumption of our argument is that a *sensorimotor* mode of processing spatial information coexists with a *representational* mode and that both modes are generating and storing their own mapping of space (Paillard 1987).

The *sensorimotor mode* concerns mainly that part of the physical world to which the organism is attuned by virtue of its basic sensorimotor apparatus. Local sensorimotor instruments entertain direct dialogues with that world and thus contribute to the continuous updating of a body-centred mapping of extra-corporal space where objects are located and to which actions are directed.

The *representational mode* derives from neural activities, which explore and consult internal representations of the physical environment that are embodied in memory stores. They include mental representations of local maps, spatial relationships of routes relative to landmarks, relative positions between objects, and the position of the body itself in relation to its stationary environmental frame.

The question arises as to whether the two processing modes operate in parallel, each using its own neural circuitry and generating its own mapping of space in two fundamentally different ways.

Sensorimotor dialogues and action spaces

Like a chemical molecule, the body has active sites at the cutaneous frontier that separates its internal territory from its environment. Specialized sensorimotor devices characterize these active sites: the mouth, the eyes, and the hand are prototypical examples. Each active site instantiates anatomical dispositions that are specifically tuned for a selective sensorimotor dialogue (Paillard 1971).

Each of these dialogues delimits an autonomous, regional 'sensorimotor space'. The boundaries of that space are specified by both the perimeter of its receptive field and the action radius of the motor apparatus that orients the sensory organ in its action space.

The mathematician tells us that a prerequisite for the description of a '*structure of space*' is the presence in that space of elements that are separately discernible by the observer. The discriminatory power of the sensory surface will therefore determine the basic grain of such a structure.

The mathematician also suggests that a collection of separate points is not sufficient for defining a structure of space (Arbib 1981). A rule for describing the potential relationships between the elements of the collection is mandatory. These rules, of which the choice may be arbitrary for the mathematician, define what is called the *geometry of description* of the spatial structure. Of special interest, here, are certain metric rules which define in a structure of space what is called its '*path structure*'. These rules determine, in direction and distance, the trajectory to follow in order to move from one point to another. A 'path structure', superimposed on a collection of separate points, defines the *locality* of each of these points in a vectorial map.

A plurality of sensorimotor spaces

This kind of geometry is particularly suitable for a description of a sensorimotor space. Motor commands that displace a given sensory receptive surface from one point to another of physical space are generally prescribed in terms of direction and distance. They therefore fit the requirements for the definition of a path structure (Paillard 1987).

The visual field provides the best example of this kind of organization. The grain of the retinal receptors obviously defines the grain of the visual spatial structure. Ocular saccades are programmed in direction and distance in a retinocentric co-ordinate system. A clear mapping of these programs is known to exist in the deep layers of the superior colliculus. Saccades allow the foveal zone of the retina to be transported to visual targets located anywhere in the retinal field, by computing a 'motor error' (Sparks 1989 ; and Chapter 1, this

volume), i.e. the positional error of the eye, which is coded in terms of the motor command required to move it to a new position and thus cancel the error. Such motor commands could constitute the web of a path structure defining the '*visuo-ocular motor space*' within which targets are located in a retinocentric system of space co-ordinates.

Consider now what happens when the head is allowed to move. A new spatial reality emerges, delineated by the displacement of the head as carrier of the eyes. It is the head movements and their motor instruments that now impose their own path structure on visuomotor space. In this case, it is clear that visuo-ocular motor space constitutes only a sub-space of visuo-cephalo motor space. Accordingly, the same place in extra corporal physical space can be defined by two different 'path structures': one derived from eye-movement programs and the other from the motor programs that move the head. Thus, it is imperative to establish a correspondence between these two co-ordinate systems in order to insure coherence in the visuo-ocular-cephalo mapping of the spatial surround.

This raises two problems, now well identified by experimenters in this field: the coordination of eye and head movements (Bizzi 1974; see also Chapter 3, this volume) that allows the stabilization of gaze on stable features of the environment; and the neural coding of ocular saccades in a head-centric co-ordinate system (Robinson 1975; see also Chapter 5, this volume). The analysis can, indeed, be further pursued, taking into account the orientation and displacements of the whole body as carrier of the head. A '*visuo-locomotor space structure*' then comes into play, which integrates the visuomotor sub-spaces of eye and head in order to locate objects in the stable environmental frame in which the body is moving.

Hence, the concept of a *plurality* of visuomotor space structures emerges, each having its own motor descriptions of spatial relationships in the visual field. Each description conveys its own private path structure.

Conversely, the same path structures - consequently, the same motor instruments - can be associated with different sensory inputs and then mapped onto different sensorimotor space structures which may vary according to the sensory channel involved (Paillard 1982). This is obviously the case for head-orienting movements towards visual, auditory or olfactory targets, and even toward peribuccal tactile targets to be seized by the mouth. Consequently, the light, the sound, and the smell that emanate from sources located in the same direction of physical space, which then trigger the same orienting movement of the head, would therefore have a common encoding in the head-centred path structure. This encoding, however, is restricted to the common direction of the different sensory sources and ignores their distances. Distance coding depends on mechanisms different from those of direction and is generally modality-specific.

Vision, audition, and smell, for instance, have each a very specific mode for encoding the distance of sensory sources in the head-centric system of reference.

The positioning of the hand within 'reach space' is another striking example. Motor commands that actively displace the arm (as carrier of the hand) define a path structure that relates the position of the hand within the proprioceptive field of postural body space. The hand, however, can also be looked upon as a visual target and positioned in a visuo-cephalomotor space structure. Moreover, tactile contact with physical matter in extra-corporal space, or even with the cutaneous interface of the body space, serves to calibrate autonomous tactilo-motor spaces. Here, for example, the luminous target that I touch with my fingertip has the same encoded location in the proprioceptive path structure of my motor reach space.

Likewise, the manipulation operates in a 'hand space', which has its own private hapto-motor organization. Depending on the functional goal of the action (power grip, precision grip, or palpation), a diversity of private manual-motor spaces - proprioceptive, tactile, haptic or visuo-motor (Lederman and Klatzky 1987) - is available for selection according to the demands of the task. A recent demonstration by Strick and Preston (1982) of two separate hand maps in the motor cortex - one mainly afferented by proprioceptive, and the other by cutaneous information-points in this direction; and data from single unit recordings that dissociate power and precision grip (Gotschalk *et al.* 1981) support this approach. Rizzolatti *et al.* (1987) also describe, in the inferior premotor area, units associating peri-buccal tactile space with 'hand-mouth' path structures.

By the same token, a subdivision of the retinal field into two distinct subspaces has been suggested (Frost and Pöppel 1976). They can be related respectively to the motor space of a small saccade system (cortically controlled and operating in central vision) and to the motor space linked to peripheral vision involving the system of large ocular saccades (generally co-programmed with concomitant head movements).

Likewise, a similar problem emerges in the sensorimotor fields associated with depth vision, which are related to two motor systems: binocular vergence and accommodation of the crystalline lens (Poggio and Talbot 1981).

In brief, we suggest that the properties of local sensorimotor spaces provide the conditions required for the registering of proprioceptive information (or any other signals associated with motor commands) derived from orienting movements, together with co-variant information (visual, tactile, auditory and any combination thereof) about the positional changes of targets within the sensory map of the receptive surface. Thus, the location of these targets becomes encoded within a hierarchy of specific sensorimotor path structures.

Accordingly, there must be as many sensori-motor mappings as there are associations between existing sensory channels and motor path structures (Paillard 1971, 1982).

So defined, a local sensorimotor space corresponds to a 'field of interaction' in the Lieblach and Arbid (1982) model, with the same mandatory requirement: the integration of multiple regional space structures into a super-ordinate system of space co-ordinates. Thus, the same locus of physical space - whatever the local sensorimotor space in which it is primarily registered and referred - has to be located at the same place in the spatial map of this super-ordinate system.

Although efferent copy signals appear to be a plausible component in the construction of visuo-ocular-motor path structures (without excluding the potential contribution of ocular proprioception), the generalization of their role to the somatic musculature seems unlikely (McCloskey 1978). In the latter case, the proprioceptive mapping of path structures is assumed to play a major role, and the problem of the integrative function of a 'body schema' emerges.

The body schema as a postural path structure

The basic assumption, here, is that every movement of articulated body segments is calibrated within the proprioceptive field of a postural space structure. Body space is envisaged as a proprioceptive-motor space where the distinct states of body postures are related by muscular activities that induce transition from one posture to another.

The existence of a repertoire of postural stereotypes, or motor synergies, (see Massion 1984), originally suggested by Ioffe (1973), has been clearly demonstrated by Nashner (1976). This repertoire of path structures may serve to specify the position of body segments within a space structure geocentrically oriented in the field of gravity (Paillard 1971). This *postural space structure* can be identified as the 'body schema' in the precise sense of Head and Holmes' (1911-1912) original definition: 'a combined standard against which all subsequent changes of posture are measured' and which intervenes in organizing spatially oriented activities 'before the change of posture enters consciousness'.

This postural space co-ordinate system is anchored to the invariant direction of gravity forces through the powerful mechanisms of maintaining an upright body posture. In agreement with Roberts (1973), who considered that the chief aim of postural regulation, in many species, is to stabilize the head in space, we have long emphasized (Paillard 1971) the pivotal role of the head segment in maintaining a 'geotropic statural referential', both in the stance of a static body and in its dynamic balance when moving (Berthoz and Pozzo 1989 and Berthoz in Chapter 6, this volume; Assaiante and Amblard 1990).

We consider this 'statural referential' to be the basic framework in which a super ordinate integrated sensorimotor space could operate. It would allow the organization of the body-centred, egocentric space coordinates to which every position (or change of position) of sensory targets in physical space could be referred, whatever the sensory channel used for their detection. We are, then, in the presence of very elaborate sensorimotor machinery, which can account for all the automatic posturo-kinetic adjustments that are required for the appropriate execution of spatially oriented movement.

As an illustration of these properties, we will consider two sets of experiments carried out in this laboratory: one dealing with the segregation of sensorimotor channels in the tactile modality; the other with a partition of the body-schema into a proximo-distal hierarchy of *vi suo* motor subspaces.

Encoding the same tactile form in two different motor spaces

In an earlier study (Paillard 1971), a distinction was proposed between a 'location space' ('*un espace des lieux*') and a 'shape space' ('*un espace des formes*'). This distinction was, of course, consonant with the then emerging dissociation of the 'two visual systems' (Ingle 1967; Schneider 1969; Trevarthen 1970; Held 1970) and with a functional segregation between 'identification' and 'location' in the processing of visual information. Emphasis was placed on the distinction between an 'object channel' and a 'space channel', the first dealing with the analysis of the various features of the object (including its shape) and the second with spatial problems (more specifically, the extra-personal space where objects are located). The distinction initially proposed between a shape space and a location space drew attention to the fact that visual identification and location processes both had to solve spatial problems, but within two different reference frames: one in an *object-centred* co-ordinate system, the other in a *body-centred* one. The former may use either the path structure of the ocular saccade motor system that palpates the object shape in central vision (see the scan-path hypothesis of Noton and Stark 1971), or an evaluation of the relative positions of the elements whose configuration composes the shape of the retinal image. The second uses the registration of gaze direction in a body-centred extra-personal space.

It follows that, depending on its size, a shape may be encoded either in the object-centred, retinal image system or in the body-centred, coordinate system.

An experiment carried out by Martinez (1971) addressed this type of spatial problem transposed it to tactile modality. In shape-recognition tasks, the analogy between the digital palpation of an object and its visual 'palpation' by the fovea is obvious.

Likewise, the antecedent ocular saccade (often associated with a head movement) that centers the subject's gaze on the object and allows its subsequent palpation by the fovea has an obvious analogy with the transport of the hand in reaching space to a location where the object can be seized and palpated.

Palpation is clearly object-centred: once the object is grasped, exploration can proceed whatever the change of hand position in space. In contrast, the positioning of the hand to be within reach of the object is body-centred. Thus, we are, in the presence of two different sensorimotor spaces: one *hapto-digital*, which combines cutaneous and proprioceptive information with the palpating movements of the fingers in hand space; the other *visuo-brachial*, which links visual and proprioceptive information with the proximal movements that position the hand in its grasping space.

Martinez's experiment stemmed primarily from her observations of congenitally blind children learning bimanual Braille reading. They made many more mirror-image confusions when reading than sighted children of the same age. The hypothesis was therefore that tactile information collected by the tips of left and right index fingers from Braille symbols by movements of the arm, is calibrated in a body-centred frame of reference. Because of the bilateral symmetry of the motor system with respect to the mid-sagittal plane, and the facility with which we can generate simultaneous, bilaterally symmetrical movements, it was envisaged that tactile forms encoded within two symmetrically arranged path structures could be perceived as identical, although mirror-framed in physical space. But then the question immediately arises: what would happen if the two tactile forms were encoded in the two hand spaces, which are independent of body space, postural constraints, and probably dependent on object space?

Between the ages of five and six years, sighted children also make frequent mirror-image confusions in matching shapes both visually and tactilely. In the experimental study, 40 children aged between five and a half and six, were given a task requiring the bimanual discrimination of symmetrical, tactile forms. The children were divided into two matched groups of two different conditions of tactile motor exploration. The first group relied entirely on digital manipulation; the wrist and the arm were immobilized. The second group explored the figures with the tip of the index finger by movements involving proximal limb joints, thus mobilizing the whole arm in its reaching space. The results, shown in Fig. 10.1, confirmed the initial hypothesis. Tactilo-motor exploration, referred to the sensorimotor space of palpation, did not produce significantly more errors than the analogous visual discrimination task. By contrast, the error rate increased very significantly when tactilo-motor exploration was referred to the sensorimotor space of hand positioning in 'reaching space' and thus related to the postural body frame. It is an open question whether a comparable interpretation is applicable to the domain of visual space.

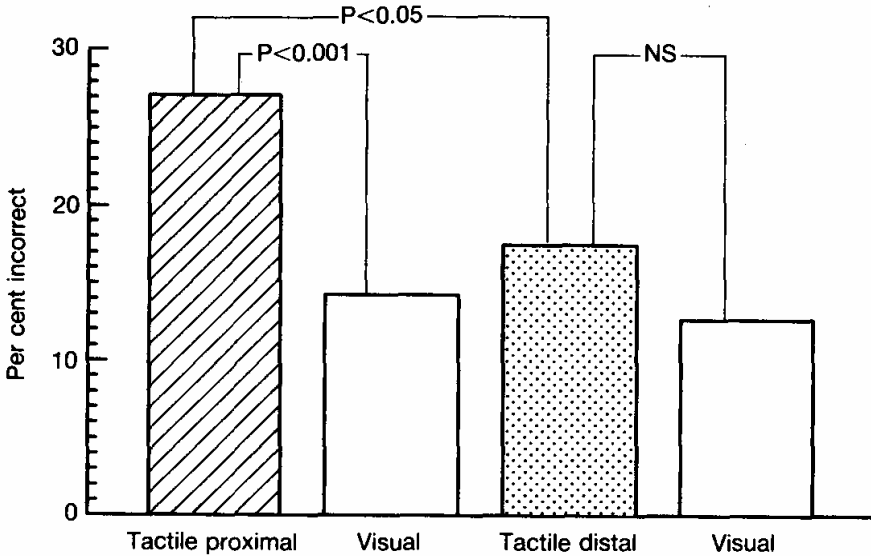


Fig. 10.1. Visual and tactile discrimination of symmetrical form (based on the data of Martinez 1971). Two matched groups of 20 children (between the ages of 5.6 and 6 years) were administered visual and tactual discrimination tests of symmetrical forms. The tests were identical for the two groups in the visual modality but differed in the tactile modality: one group used multi-digital manipulation with the arm and wrist immobilized (the tactile-distal condition: dotted column), and the other group used finger tip exploration using whole arm movements (the tactile proximal condition: hatched column). In the visual modality (white columns), both groups of children produce approximately 13 per cent mirror-image confusions when matching symmetrical visual forms. In the bimanual tactile condition, a comparable percentage of errors were found when subjects were required to identify, among three figures explored by one hand, the target form presented simultaneously for manipulation by the other hand. In this case, the exploration was multi-digital and restricted to motor hand space. In contrast, the error rate increased to 28 per cent when subjects used only the tip of their index finger and swept the figures with exploratory movements of the whole arm.

There is, however, preliminary evidence, which suggests that this might be the case.

As previously mentioned Frost and Pöppel (1976) have proposed a subdivision of the retinal field into two distinct subspaces: one corresponding to the field of central vision (up to 10 per cent of eccentricity), where the small saccade system is strongly dependent on cortical control; the other related to the peripheral retina and associated with a system of large ocular saccades that are generally co-programmed with concomitant head movement. The latter movement obviously serves the need of orienting the gaze at different places in location space whereas the former operates within the object frame of shape space, where the scan-path theory of shape perception does not accommodate much of the experimental data. Consider the analogy with the tactile modality. The palpation of an object, whose size extends beyond the manipulation space of the hand, forces the displacement of the hand along the object surface and its contours.

In like fashion, depending on the size of a visually presented object, the encoding of its form either could occur in one of the two systems or might even encompass both. The validation of such an hypothesis, however, would have to take into account the dominant strategy of the subject and the need to distinguish between 'eye movers' and 'head movers', a distinction recently introduced in a study of eye-head co-ordination in pointing (Bard *et al.* 1990). In the same vein, mirror-image confusions may be related to the observation that most young children are head-movers. They therefore appear to manipulate their visual space predominantly within a location space where the symmetrical organization of the postural schema presumably imposes its specific constraints.

A partition of the body schema into a hierarchy of local visuomotor spaces

The next set of experiments illustrates how the spatial problems involved in visuomotor reorganization after prismatic deviation of the visual field may shed light on the intrinsic organization of the body schema.

Subjects wearing prismatic goggles that displace their visual array, say 12° degrees to the right with regard to the sagittal plane of the head, misreach visual targets located in their visual field by about the same angular error: that is, they point about 12° too far to the right of the real target. In other words, they see objects that are located straight ahead of them by looking 12° to the right in head-centric space. Their normal daily experience of visuomotor spaces, however, demonstrates that motor reaching programs are more effective when oriented in the direction of gaze. This normal calibration takes into consideration the position of the eye with respect to the head and, additionally, the position of the head with respect to the trunk. If the discrepancy introduced by the prisms between eye-position calibration with respect to the trunk is not experienced in the form of an error that can be corrected with feedback, then misreaching will persist. If, however, subjects are allowed to see their moving limb through the prisms for a short exposure period, then a readjustment occurs that results in a pointing program redirected toward the correct location of the target. It is still a matter of speculation as to where this recalibration takes place and it will not be further discussed here (but see Paillard *et al.* 1981). Suffice it to say that the remarkable capacity of the 'system to reorganize the structure of its visuomotor space offers an interesting opportunity for study of the properties of our putative local sensorimotor spaces.

The possibility of segregating the visuomotor sub-spaces involved in the recalibration process has been studied by Hay (1970) in conditions where the visual recalibrating exposure was restricted to a single joint movement.

Subjects were asked to point (without seeing their arms) in the direction of three visual targets distributed in the frontal plane. The directional accuracy of

aiming was measured for single joint movements involving the wrist (W), the elbow (E), or the shoulder (S). The same measurements were made in a condition where subjects wore prismatic goggles that displaced the visual field 12° to the right.

After these pre-tests, there was a period of exposure in which subjects were instructed to look at their hand moving to and fro in the visual field, for 5 min. in three different experimental conditions, using movement either of the wrist, of the elbow, or of the shoulder.

Each period of exposure was followed by a series of post-tests. Accuracy of aiming was again measured for each of the three single joint movements, vision of the limb again being occluded as in the pre-test condition. Comparison of accuracy in pre- and post-tests evaluates the amount of recalibration that follows each condition.

Without entering the details of the experimental procedure, we may focus on the results shown in Fig. 10.2. In the condition (W), where the recalibrating experience is limited to wrist joint, there is a significant recalibration of aiming with the wrist, but accuracy of aim depending on elbow or shoulder movement does not show any significant readjustment.

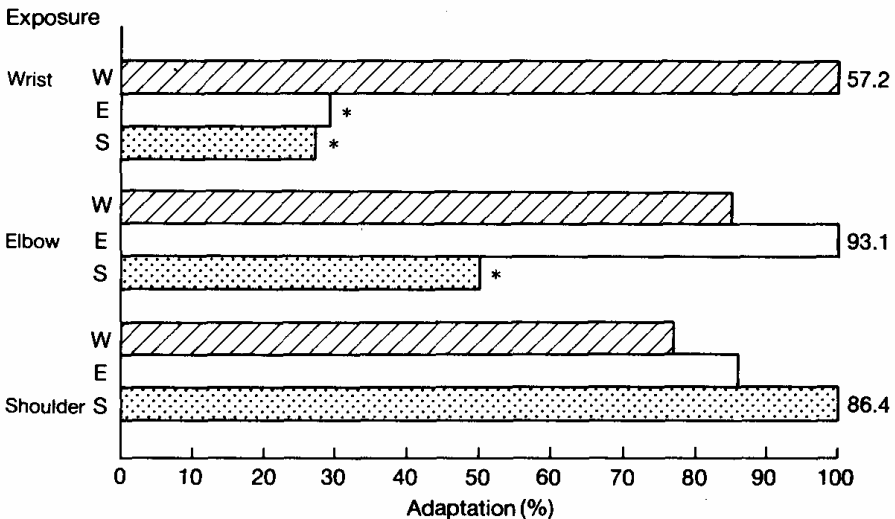


Fig. 10.2. Effects of single joint exposure on the recalibration of aiming movements after prismatic displacement of the visual field (based on the data of Hay 1970). Aiming movements were performed by movements restricted to one joint: wrist (W), elbow (E) or shoulder (S). The histograms show results obtained from 10 subjects who carried out 20 target-pointing movements for each joint. Depending on the joint whose movement was observed during the exposure period (wrist, elbow or shoulder), performance in aiming with the two other 'non exposed' joints expressed as a percentage of the amount of recalibration measured with the 'exposed' joint. The actual score (amount of readaptation) of the 'exposed' joint is given at the end of the corresponding column. The adaptation obtained from vision of shoulder movements during the exposure period generalizes significantly to elbow and wrist, whereas elbow adaptation generalizes only to the distal joint; wrist adaptation is not transferred to distal joints. Asterisks indicate significant effects.

When the period of exposure restricts vision to self-induced movements of the elbow (E), then aiming movements using the elbow joint are recalibrated, but those using the wrist joint are also significantly readjusted whereas pointing via the shoulder joint remains incorrect. Finally, the three joints are recalibrated when exposure is limited to vision only of the shoulder (S). Thus, it follows that the recalibration involves the path structure of a local sensorimotor space defined by the motor field covered by the range of movement of a given joint. Moreover, a proximo-distal hierarchical subordination links these various sub-spaces. In fact, the recalibration observed with an exposed joint always transfers to the more distal joints (see Fig. 10.2). Moreover, as was often claimed in studies of prismatic adaptation, restriction of head movements is necessary to limit adaptation in the exposed limb, otherwise the recalibrating effect generalizes to all body joints. In a recent study (Paillard and Hay 1989), we were able to confirm the generalized recalibrating effect of active movement restricted to rotation of the head on the trunk, even in conditions when the eyes were stabilized by a gaze-fixation point attached to the head.

In brief, the segmentation of the body schema into sub-spaces interleaved in a proximo-distal hierarchical structure and dominated by the head segment clearly illustrates the plurality of bodily motor spaces. Thus, the body schema can be fractionated into sensorimotor sub-systems representing the motor synergies that are involved in specifying the path structures of the visuomotor sub-spaces. One additional feature of these sub-spaces is worth mentioning: visuomotor experience limited to only one direction of movement of a multi-dimensional ball joint recalibrates movements in any direction of three-dimensional space. It is also worth mentioning that this concept of a partition of motor space into a diversity of local action spaces has been recently brought forward by Rizzolatti and Gallese (1988) in a motor-oriented theory of attention.

From sensorimotor spaces to spatial representations

As already emphasized, spatial knowledge comes from a variety of sources and uses a variety of codes for its storage. The most basic knowledge is obviously that derived from Darwinian evolutionary selection. Printed in the in-built sensorimotor circuitry, it tunes neural mechanisms to the spatial constraints of both their body architecture and their environment.

Later acquisitions will enrich the basic repertoire of the sensorimotor machinery without changing radically the direct way in which sensory input is linked to motor commands. This machinery automatically surmounts the constraints of its action spaces and does not require any elaborate 'computational mapping' in order to generate 'data-driven', goal-directed

behaviour (the 'taxon' systems of O'Keefe and Nadel 1978). In which case does knowledge, which is presumably embodied in some kind of internal map and which shapes anticipatory, memory-driven spatially oriented actions, depend on other sources of spatial information and require a specific encoding mode?

Internal representations are described by psychologists either as *images* embodied in an iconic code or as *mental representations* encoded in abstract or symbolic form. Neurobiologists, for their part, distinguish between *projectional maps*, which are relatively isomorphic with the peripheral arrangements of sensory receptors, and *computational maps*, which extract place codes from different input signals, without preserving any topographical arrangement of their constituent neurons. Sensory and motor maps of the neocortex are projectional whereas the place map of the hippocampus is assumed to be computational (see Chapter 16). The last term, borrowed from the field of artificial intelligence, may be misleading when applied to neural mapping, as Konishi (1986) has suggested. He proposed, instead, 'centrally synthesized maps' as a more neutral concept.

In fact, one important feature of biological systems (when compared with neuron-like networks) is their astonishing capacity to extract covariant signals from the flow of sensory input that impinges on their sense organs, and to stabilize in the neural circuitry selective configurations of synapses that are covariantly activated (Phillips *et al.* 1984).

The visible world and the body structure contain many redundancies and stable features. The static nature of the physical, visual background provides a stable environmental frame within which the moving body may orient itself and navigate.

Regularities of the physical environment are progressively encoded in the structure of central networks. Central space structures then emerge from the processing of a polymodal inflow of changing re-afferent information, generated by the displacements of the body within its environmental frame. Subsequently, this processing gives rise to a hierarchy of distributed and layered populations of neurons from which some kind of 'central synthesized map' could be made.

The construction of these maps, however, might differ from that of conventional neuromimetic networks, which generally do not close the external loop between motor output and re-afferent input (see, however, Kupferstein 1988; and Chapter 22, this volume). In other words, computational networks are generally not able to entertain a sensorimotor dialogue with an extended environment that is, nevertheless, a source of parametric spatial knowledge.

It is these dialogues that allow the brain and its neural network to detect and register the spatial features of its environment that remain invariant or covariant across the transformations generated in the sensory inflow by their own

motor activity. The basic concept here is that of *re-afference* - a term coined by von Holst and Mittelstaedt (1950) to denote the consequences of self-produced movement on the sensory inflow.

Representational space maps would also differ from sensorimotor path structures in that they are predominantly tied to visual information about the environmental frame, whereas the path structures are closely linked to a proprioceptively defined, postural frame of reference. This is obviously the case for the locomotor space.

All mobile species, whatever their propulsive mechanism depending upon the supporting medium - earth, air, or water - have to structure their locomotor space. In contrast with activities that move individual body segments within the postural frame of reference, locomotor programmes involve rhythmical reproduction of an ordered sequence of limb movements, resulting in a displacement of the body as a whole. In this case, and in contrast with arm movement, the corresponding proprioceptive reafferent information cannot provide the relevant information for encoding the parameters of locomotor trajectories and hence for the construction of a 'body-centred path structure'. That structure, however, may be defined by a system of inertial navigation using vestibular afference and computing the head position in an absolute physical space (see Potegal 1982; and Chapter 6). However, there are also many co-variant changes in the retinal image of the outside world when the body moves, and these signals might well serve to generate an internal representation of a stable environmental frame (Gibson 1950).

Thus, a motor-oriented interpretation of the construction of basic space structures may apply equally well to both the geotropic, body-centred frame of reference (to which most of our spatially directed actions are to be referred) and the central representation of space, which assumes an allocentric, stable environmental frame of reference (in which the ever-changing position of a moving body has permanently to be updated).

Representation of the environmental frame, however, does not exhaust the gamut of the various cognitive, mental representations of space studied by psychologists. Egocentric and allocentric descriptions of spatial relationships both refer to primitive adaptive processes in the affordance of an organism to its environment and, as such, lend some plausibility to the hypothesis of an inherited, allocentric frame of the kind envisaged by O'Keefe and Nadel (1978). Alternatively, more elaborate and abstract mappings of spatial relationships might evolve in man, especially in relation to the development of language with its propositional function, and to the extension of topographical memory within the rich resources of spatial thinking.

Focusing on the two - egocentric and allocentric - reference frames, a central issue is to understand how these two co-ordinate systems may interact and

co-operate together in the transactional processes that bind perception to action. Pointing tasks have provided a good experimental paradigm for exploring this question.

Egocentric versus allocentric reference frame in pointing

Inaccuracy in pointing at visual targets can usually be ascribed to imprecision in specifying information about the location of the target. Depending on the reference frame used by the organism, however, this location may be defined either egocentrically or allocentrically. When head and body position are fixed so that only the eyes are allowed to move, then the perceived oculocentric direction of the target is critical. In this condition, Conti and Beaubaton (1980) have shown that accuracy of pointing at a luminous target in complete darkness is significantly less than when pointing at a target illuminated in a structured visual field. The interpretation of this finding is that the perceived oculocentric direction of the target in both cases relies on two different modes of encoding. In darkness, the extraretinal signal of eye position in the orbit (presumably derived from the oculomotor command signal) is the only one that can be used to calibrate the position of the target in relation to head position. The location of the target is then defined in an egocentric reference frame. In contrast, in a structural and visual array, additional visual cues are present which allow the target to be located in the environmental frame to which the position of the body has also to be referred.

The experimental dissociation of these two encoding modes for locating visual targets has been obtained in two ways: first, in dissociating the 'perceived' and the 'registered' location of the target in a motor pointing task; second, in separating the eye-position signal from the perceived oculocentric direction of the target.

Perceived and registered location

An experiment by Bridgeman *et al.* (1979) illustrates the former line of investigation. Subjects were asked to detect if a central target, flashed on during a saccadic eye movement, was moving or not moving and, if moving, whether toward the right or the left. They were also requested to point to the actual location of the target. The striking finding was that subjects consistently pointed correctly to the right or to the left, despite their failure (due to saccadic perceptual suppression) to perceive any displacement of the target. The conclusion was that the sensorimotor system had direct access to information that was not available at the perceptual level. More specifically, we may assume that egocentric information, as measured by pointing, is available to subjects

even when exocentric information regarding displacement of the stimulus has been masked at the perceptual level.

A similar dissociation is observed in the 'blind sight' phenomenon: hemianopic patients who are not able to detect a target presented in their blind field can nevertheless point to it when forced to guess its location (see review in Weiskrantz 1989). A similar phenomenon has been observed in the tactile modality (Paillard *et al.* 1983). A patient with a de-afferented arm was able to locate correctly with her left hand punctuated stimuli on her insensitive right arm. Her astonishment was particularly interesting: 'I do not understand why I am going there because I do not feel anything. . . Where does it come from?' Asked to describe her feelings more precisely, she tried unsuccessfully to use the vocabulary of seeing and hearing, and finally said: 'It's so tenuous, so tenuous you know. . . but I know that there is a place where you were going and I went there too.' Interestingly, she was describing this very unusual experience of space without identifiable sensory content in terms of 'knowing how to get there' (see Epilogue, this volume).

Another striking example of this dissociation is displayed by the 'Roelofs effect' exploited in an experiment by Bridgeman (1989). Stable targets, presented inside a moving frame, appear perceptually to move in a direction opposite to that of the frame. Subjects invited to state the position of the target verbally gave an incorrect location, whereas they pointed at the target in its real, physical position.

In conclusion, spatially oriented movements can be accurately directed by a sensorimotor mapping of path structures, even when the perceptual system is receiving inadequate or erroneous information, or even no information at all.

Location and dependency on eye position

The above conclusion has been further strengthened by the second line of investigation, which intervenes at the level of the extra-retinal signal. These experiments (reviewed by Jeannerod 1983 and Paillard 1987) used either reversible paralysis of the ocular muscles by D-tubocurarine (Matin *et al.* 1982) or a technique of 'eye press' (Stark and Bridgeman 1983) to suppress or reversibly modify the signal of eye-head position. The following conclusions have been drawn from these experiments. When the luminous target is inaccurately located, perceived position and manual pointing coincide, in darkness because of the incorrectly biased eye-position signal which displaces the egocentric frame of reference. When, however, the target is set within a visually textured frame, its perceived position no longer depends on the extra-retinal signal that calibrates it within the egocentric co-ordinate system. Instead, it is referred to the allocentric system of space co-ordinates in the environmental frame.

Then, a correct perceptual evaluation of its real position in that frame (which coincides with the reality of the physical surrounding) is achieved. In contrast, the pointing movement continues to be driven to the wrong location corresponding to the incorrectly biased, extra-retinal signal.

Interactive contribution of egocentric and allocentric frames

Finally, we can observe the co-operative and interactive contribution of these two co-ordinate frames in experiments concerned with the recalibration of pointing programmes consequent upon prismatic displacement of the visual field. Without going into the procedural details of this experiment, (Paillard *et al.* 1981), consider here its main findings.

The two adaptation processes were dissociated, depending on the two different conditions of exposure: one condition permitted vision of hand movements against an homogeneous visual background; the other the presence of a stationary visual target or a whole structured visual field in which free hand movements were made. The former recalibration condition operates preferentially in *peripheral* vision (more than 40° eccentricity) and is suppressed by stroboscopic illumination of the visual field (at 3.5 pulses per second). Recalibration in the latter condition operates mainly in *central* vision and is not dependent upon whether the illumination is continuous or intermittent (Paillard *et al.* 1981).

The distinction made in this experiment between the recalibrational efficacy of *active* compared with *passive* movement provides an additional argument for making a clear, functional distinction between these two systems. Peripheral vision does not process visual information coming from a limb that is passively displaced during the period of exposure, whereas central vision, provided that there is a structured visual background, processes information from either the actively or the passively displaced limb to recalibrate the pointing program (see Fig. 10.3).

Our interpretation, therefore, was that adaptation provided by peripheral vision might be driven by a reshaping of path structures in the egocentric frame of reference, which needs proprioceptive, self-induced re-afferent information. In contrast, adaptation provided by central vision requires the visual localization of a moving limb within the stationary framework of a visual surround, where position and change of position of the hand are calibrated relative to the stationary cues of the visual frame. In the latter case, interestingly, the nature of the movement-active or passive-is irrelevant for the recalibration process.

We tentatively ascribed (Paillard and Amblard 1985) the central and peripheral vision system, respectively, to the X and Y visual channels described in the visual system of the cat. We now know that they may be assigned in man to the 'parvocellular' and the 'magnocellular' channels, respectively, according to

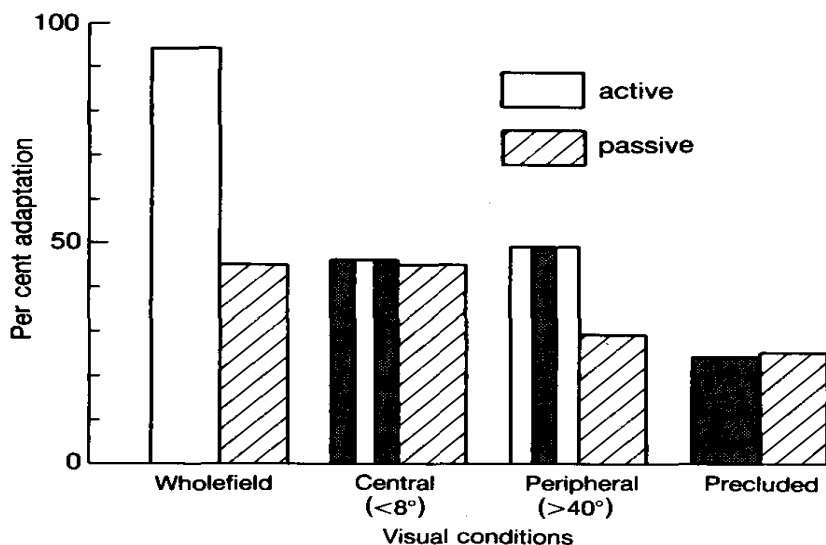


Fig. 10.3. Self-induced versus passive movements in prismatic adaptation (based on the data of Paillard *et al.* 1981). The histograms display percentage of adaptation shown after a 10 minute exposure period of the moving limb (moved actively or passively) in four different visual conditions (whole field, central, peripheral and occluded). The data were obtained from four subjects (selected as good adapters). In whole field vision, i.e. when both peripheral and central vision were involved, active movement led to near complete adaptation (94 per cent). In contrast, with vision of passive movement the amount of adaptation was significantly less, and did not exceed 48 per cent.

When restricted to central vision ($< 8^\circ$ eccentricity) the percentage of adaptation remained virtually unchanged (46 versus 45 per cent) whether the observed movement was active or passive.

When only the peripheral field was involved ($>40^\circ$ eccentricity), the percentage of adaptation, which was 49 per cent with active movement, was reduced to 29 per cent with passive movement - i.e. to the basic level of adaptation that is observed when vision of the moving limb was totally precluded, and adaptation is attributed to extra-retinal factors.

the recently proposed division of visual pathways in primates (De Yoe and van Essen 1988). If so, the parvocellular system can be considered the main instrument for the processing of relative position both within object-centred space (where information about the shape and size of the object is mainly extracted by central vision), and world-centred space (where the relative position of objects to one another is measured within the allocentric frame of the stabilized, visual world). The magnocellular pathway, for its part, conveys information about the visual changes co-variant with self-induced, proprioceptive, re-afferent information from the moving limb. Here, there is a contribution from the peripheral retina to the elaboration of visuomotor space structures, whatever the motor instrument (eyes, head, limb, body as a whole) implicated in the specification of the path structure concerned.

This notion is obviously reminiscent of the 'exproprioceptive vision' as defined by Lee (1977) and derived from the Gibson concept of 'kinesthetic vision'. An important goal for future research, therefore, is to specify how and

where proprioceptive and visual information converge in central nervous structures to align their space maps and how and where self-induced motor activities acquire their privileged role in calibrating or recalibrating our sensorimotor spaces.

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