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# *Active and passive movements in the calibration of position sense**

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Spatially coordinated behavior is possible only because many features of the body's structure and of the structure of the world are highly predictable. From the primitive chaos of the impressions collected by our sense organs, a system of stable and permanent spatial referents progressively emerges in relation to the moving and ever-changing framework of bodily positions.

The prerequisite to the building up of motor strategies directed at the outside world lies in the establishment of a known system of spatial relationships among the different mobile parts of the body and a method of evaluating continuously their relative positions.

The initial and final positions of any moving segment must primarily be referred to the proprioceptive spatial schema upon which the various displacements related to each joint of the bony frame may be ordered.

Studies devoted to position sense have, for the most part, focused upon the problem of kinaesthesis in order to gain knowledge of our ability to estimate changes in position of our joints and to reproduce these changes with more or less precision in distance, speed, and direction. They have tended to neglect the problem of the calibration of these positions in the spatial reference system of the body, which is itself situated within, or moves itself in, invariant perceptual space. This is a problem which places the study of kinesthetic sensation at the level of the mechanisms which confer upon it its “local sign.”

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This finger which I move, or which an external force is going to displace, changes its position in relation to the other parts of my body and thereafter occupies in the physical space in which I myself am a new position referenced in relation to the objects which are found there. I am capable of directing my gaze at it, or of directing my other hand to it in order to reach and grasp it without the help of vision.

The ability we have to locate the positions of our bodies and their different parts and to reach them correctly in tactile and proprioceptive space is surprisingly good.

Recent experiments (Riesen & Aarons, 1959; Held & Freedman, 1963) have emphasized the role played by self-induced movements of the body in the construction and reorganization of the various sensorimotor fields.

We have proposed in this study to investigate to what extent active or passive conditions of displacement of a part of the body might influence the referencing of its final position by an active hand in the absence of vision or touch.

We have directed our attention particularly to the following points:

1. Are self-positioned parts more precisely calibrated than passively positioned parts?
2. Are actively maintained positions more precisely localized than passively maintained positions?
3. Is the ability to locate a body part dependent for its accuracy upon the time elapsed following displacement?

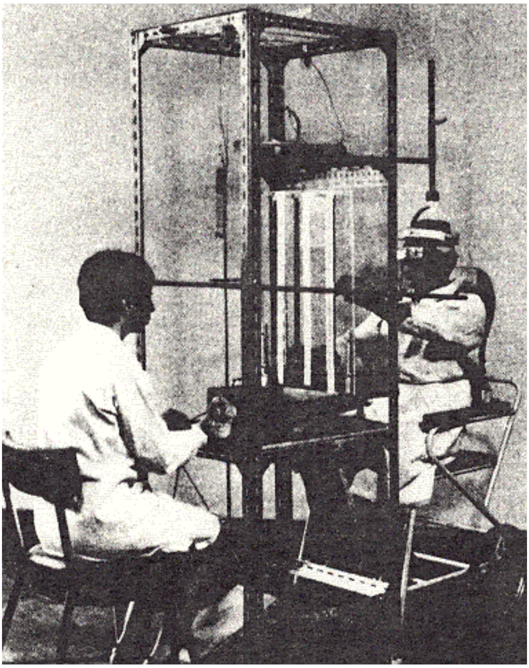
We shall describe the results obtained in two complementary series of experiments: the first was carried out under conditions of strict spatial constraint (positioning of the left hand and locating it with the right hand in a frontal plane with vertical displacement from bottom to top); the second under conditions of displacement freely selected in any direction whatever of motor space possible for the upper limbs.

## Experiment I

### *Method*

We studied the different conditions with an apparatus composed of a sheet of plexiglas set in the frontal plane about 60 cm. away from the subject and carrying two parallel tracks 60 cm. in length set vertically and symmetrically in relation to his mid-sagittal plane. Each of the subject's index fingers can operate a movable slide along one of the tracks. With head and trunk fixed, the subject's left hand is displaced actively at a speed freely adopted by him. or passively at the same speed controlled by

FIGURE 1. Apparatus for Experiment I. The subject has positioned his arm and is actively maintaining it.



the experimenter, along one of the tracks and stopped at different levels for each trial. During the condition of passive transport, the subject's arm, fixed in a cradle which restrains the wrist and elbow joints, is set into motion by a counterweight controlled by the experimenter. The final position attained by the displaced limb being maintained either actively or passively, is located by the subject with his right hand moving a similar slide along the parallel track. The size of the error committed by the subject during each trial is indicated by the difference in position of the two slides read from identical scales attached to each of the tracks.

The time intervals (0 to 12 seconds) between the positioning of the one hand and the judgment of its position by the other hand are randomly varied according to a preestablished order and signaled to the subject by a sound controlled by the experimenter.

## *Results*

Figure 2 shows the results obtained with seven normal adult subjects in each of the four conditions (140 measurements at each point) showing that precision is very significantly better ($x^2 < .001$) with active movement of the arm (the median value of the systematic error lies between ±6 mm.) than when the arm is positioned passively (the systematic error being then in the direction of an underestimation with a median value of +22 mm.). The interquartile range shows also a much greater dispersion of errors in the latter condition.

Active or passive *maintenance* of the final position of the arm does not seem to influence the results. These are identical with *active positioning* movements and not significantly different with *passive positioning* movements. In this type of task tonic information of muscular origin which is not accompanied by a movement does not seem to affect performance.

Variations in the time interval separating the positioning of the hand from its report (by the other hand) have a definite influence upon performance both in the case of active displacement and in the case of passive displacement. Figure 3 shows the means obtained with five subjects (120 measurements at each point). In the condition of active positioning, precision tends to diminish progressively in the direction of an underestimation of the position of the hand. The difference between the mean error committed with zero delay ( + 2 mm.) and the mean error committed after an interval of 8 seconds ( - 8 mm.) is significant.

In the condition of passive positioning, it is the direction of error which

FIGURE 2. Median and interquartile range of errors in locating the position of one hand with the other. Each of seven subjects made 20 trials under each condition.

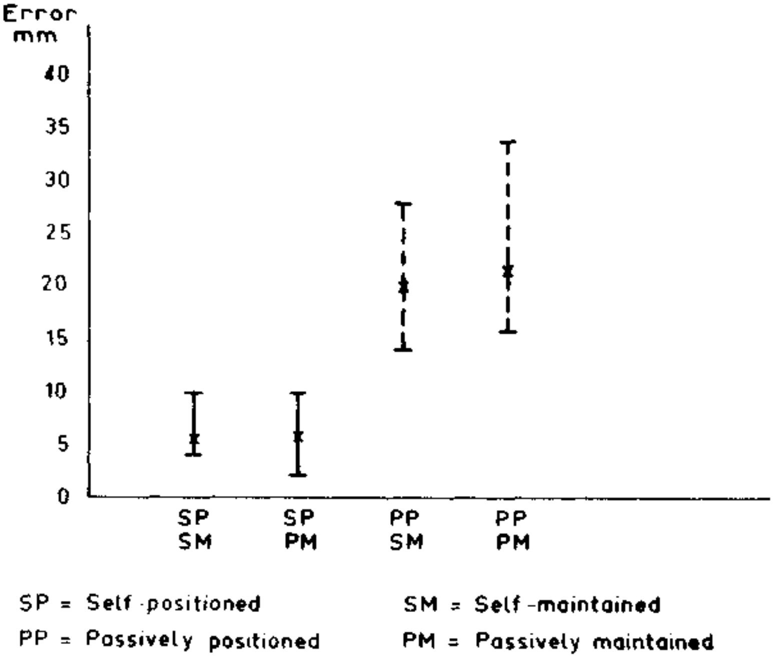
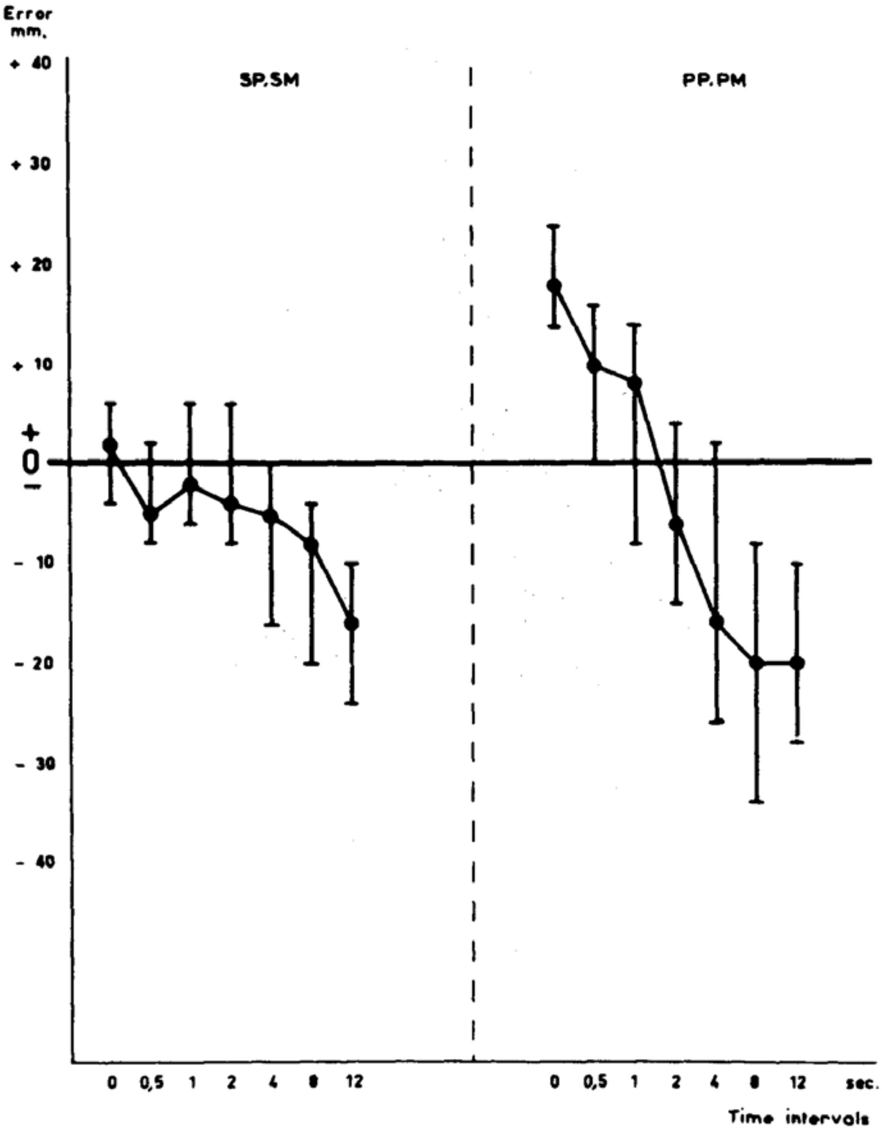


FIGURE 3. Median and interquartile range of errors in the judgment of the final position of the hand as a function of the time separating positioning and judging. Means of five subjects each of whom made 24 trials at each time interval.



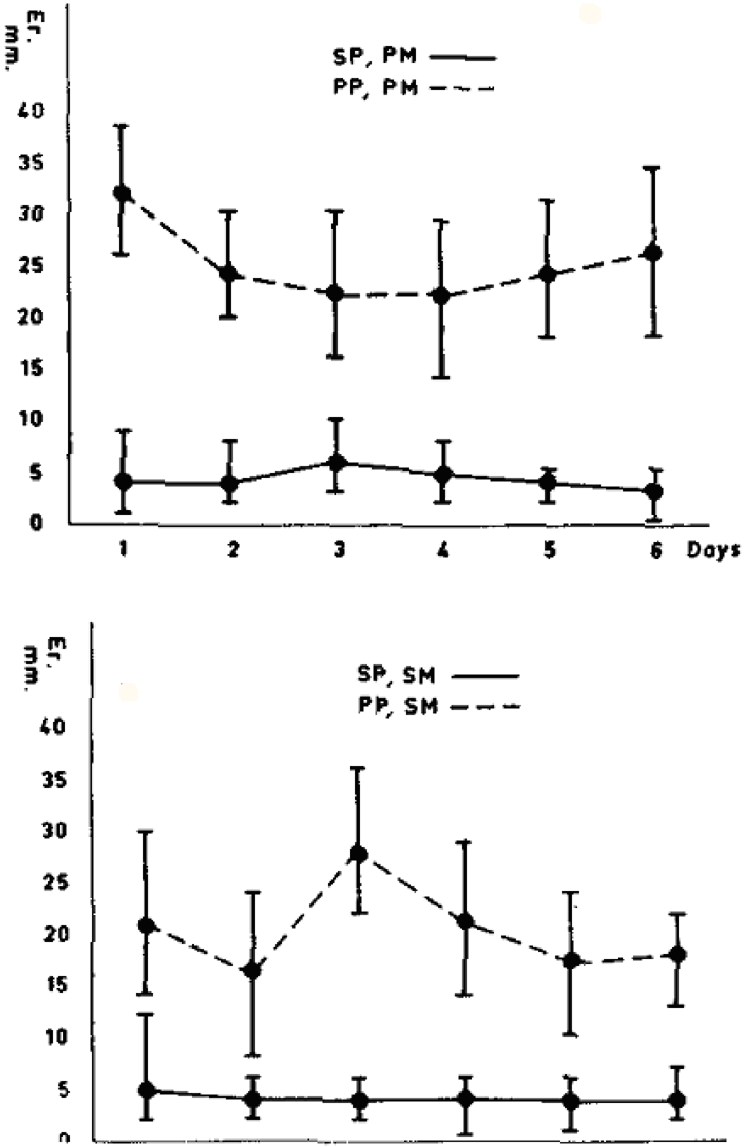
changes; it passes from an overestimation of the position of the hand (-18 mm. at zero delay) to an underestimation beginning with the 2-second interval ( 6 mm. error at that point).

In the two situations, the dispersion of errors increases as a function of the temporal interval and the systematic error becomes identical (-20 mm.) at the end of about 15 seconds for the two conditions.

The individual curves for all five subjects show the same tendencies as the combined curves with low interindividual variability in each of the two conditions.

The absence of a learning effect is shown by results with one trained subject exposed to two experimental sessions a day for six days. Figure 4

FIGURE 4. Errors and interquartile ranges in judging the final position of one hand with the other hand. Each data point = mean of 40 trials. SP = self-positioned; PP = passively positioned; SM = self-maintained; PM = passively maintained.



indicates that repeated exposure does not seem to affect the results and the differences between the two conditions of displacement remain largely significant.

## Experiment II

### *Method*

We used a lightweight target 8 cm. in diameter with a series of 15 concentric metallic conducting rings. Each ring is 1.8 mm. wide and is separated from the next by a space of 0.5 mm. The rings are connected electrically to the markers of a recording apparatus with 15 channels. Figure 5 shows this apparatus in use.

FIGURE 5. Apparatus for Experiment II. The subject is pointing with the stylus at the position of her left index finger centered under the target.

The subject holds in his right hand, aligned with his index finger, a metallic stylus connected to the marking circuit. He holds the target in his left hand with his left index finger under its center. After an active or passive displacement in some direction of space has been made with the left hand, his task is to mark the center of the target with the stylus. The error for each pointing trial is read directly from the recording apparatus. Each series is composed of 31 trials.

To these two conditions of active and passive displacement, we added a third condition in which the subject actively maintained the final position of his left hand while repeating, every 2 or 3 seconds, the operation of locating the target with the opposite index finger. After each pointing trial, he returned his right hand to any starting position he wished.

## *Results*

The results obtained with seven subjects in the active and passive conditions of displacement show a large significant difference in the accuracy of locating the index finger of one hand with that of the other hand.

The median error for active displacement was 8 mm. while for passive displacement it was 18 mm. The variability of errors was also greater in the passive condition.

Figure 6 shows the accuracy of locating the position of the index finger measured with two subjects under four different conditions. In each case, trials continued for one minute.

*a)* During training with the aid of vision, only minimal pointing errors were committed.

*b)* With active displacement of the arm, without vision, errors were relatively small with low variability, and did not change over time.

*c)* With passive displacement of the arm without vision, errors were significantly larger than with active displacement and more variable, but they did not change over time.

*d)* With active maintenance of the final position, the errors were small at first but increased progressively to reach very large values (3 cm.).

## Discussion

The results obtained in the second experiment confirm on all points those of the first. They permit us then to set forth the hypothesis of the preponderant influence of factors of spatial constraint in the interpretation of the observed phenomena. The constraints of the first experimental situation have the merit of furnishing more precise data as to the direction of error in localizing but present the disadvantage of reducing the measure to that of a simple variation

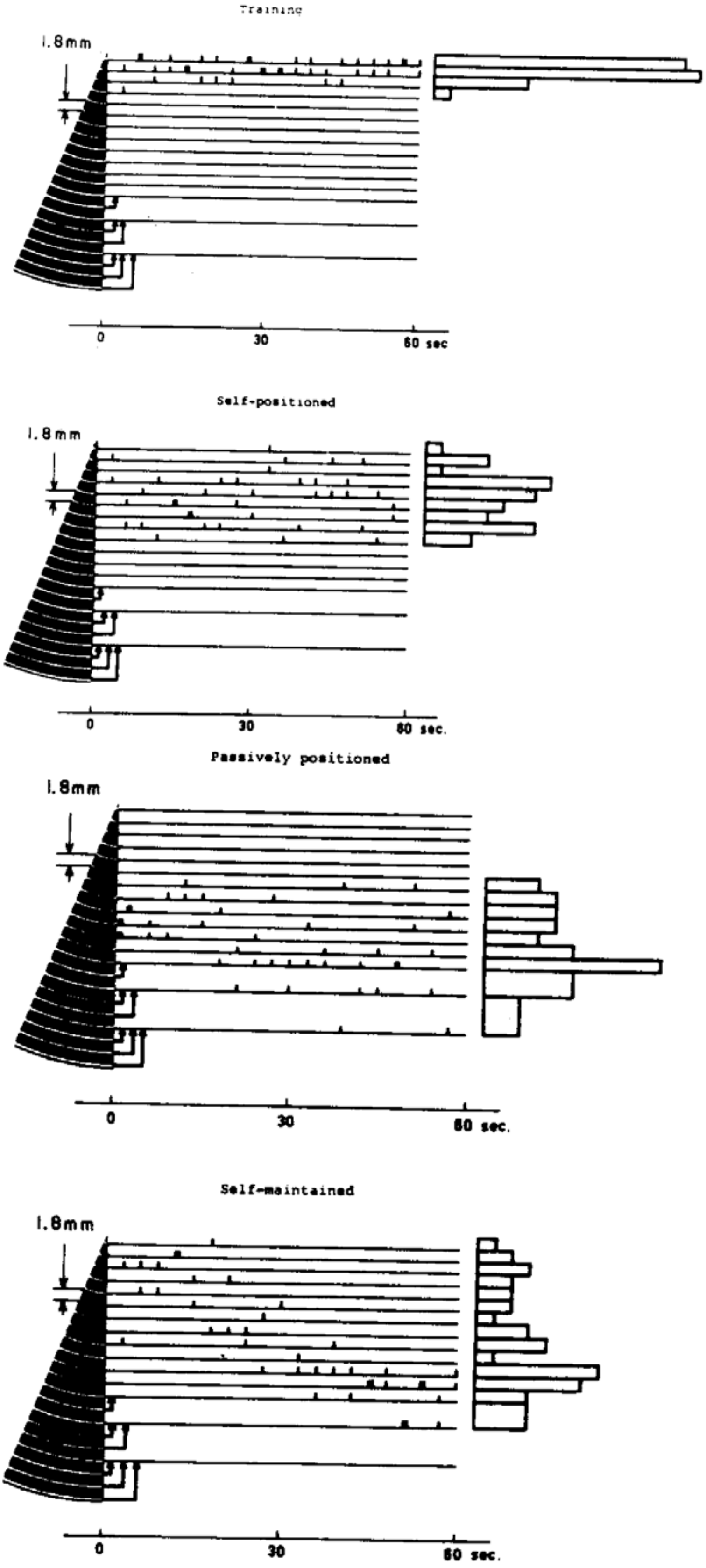


FIGURE 6. Combined records of two subjects each making 20 trials in each condition. See text.

in the amplitude of the movement, with the subject displacing symmetrically the positioned hand and the reaching hand from the same starting position and in the same vertical plane. These conditions bring us back, in short, to those used in the classic experiments on kinesthetic sensation and expose us to the same criticisms. The validation of our results obtained in a situation of pure calibration of position such as that realized in the second experiment permit us to generalize from our data and to discuss its significance.

1. Index finger approximation depending chiefly upon proprioceptive cues is significantly more accurate and less variable after self-induced displacement of the positioned hand than after passive displacement.

Goldscheider (1889) had already noted the superiority of active movement over passive movement in measures of the threshold of discrimination of the position of a finger joint. Lloyd and Caldwell (1965) found this difference also for displacement of the leg, noting however that it appeared only within the customary limits of excursion of the joint. These authors also found, as we have, an overestimation of the extent of passive movements.

In any case, it would appear that the information content of self-induced movement aids in the calibration of the final position. Conversely, this might be considered as an information deficit during passive movement of a member.

2. Our findings show no difference between the measures obtained with actively or passively maintaining a final position. We are led to conclude that the significant information derived from self-induced movement is related to the dynamic phase of the movement and is not available merely from self-maintained postures.

3. The study of the temporal decline of this information seems to be particularly interesting here.

We note that Bloch, as early as 1890, had observed the phenomenon of temporal degradation of the precision of localizing the position of an actively displaced hand with the other hand in a situation similar to ours and that he recalled this observation in a note of 1896: "The idea of position is therefore perceived with a certain exactitude at the moment when movements arc going on; it weakens during immobility and consequently is increasingly obliterated as the instant during which the movement was effected becomes more and more distant."

The same phenomenon had also already been the object of an investigation by Bowditch and Southard (1880) also under conditions of active movement. These authors reported an improvement in accuracy during the first few seconds followed by a degradation, the course of which they studied up to the 10th second.

The remarkable similarity of the curves obtained with the live subjects we have studied under active and passive conditions of executing displacements permits us to differentiate at least three sources of information contributing to the calibration of position.

*a)* Information associated with the kinematic phase of active displacement whose effect tapers off in about a 15-second period, which leads to the most precise and the most reliable localizing.

*b)* Information originating in the kinematic phase of passive displacement, which is less precise with respect to localizing since it leads to systematic overestimation of the final position; its effect also tapers off in 15 seconds.

*c)* Information derived from the active or passive static maintenance of position. This is the least precise since it gives rise to a large and lasting underestimation of the final position with a large dispersion of the results.

4. It is appropriate at this point to examine these results in the light of what we know about neurophysiology.

At least five sources of information can be called upon tentatively to explain the observed facts.

Visual and auditory as well as touch information are assumed to be absent. Afferents from muscles, tendon and joint receptors, stretch receptors, and pressure signals from the skin are available for kinesthetic judgments. The pattern of motor innervation is almost certainly also available as a source of information.

*a) Joint receptors* are unanimously recognized as necessary for the elaboration of position sense (Goldscheider, 1898; Browne, Lee, & Ring, 1954; Provins, 1958; Merton, 1964; Howard & Templeton, 1966). All sense of position and passive movement of a joint is lost when the joint capsule is anesthetized with procaine. We ought to consider this source of information as essential for the interpretation of the observed phenomena. The work of Mountcastle and Powell (1959) permits us, on the other hand, to envisage a coherent interpretation of the results obtained under conditions of passive movement of the limb. There exist in fact two principal categories of receptors. One is static (the more numerous), detecting with weak adaptation rates the position of the joint. This category can be considered responsible for the appreciation of final positions during static conditions and their maintenance. The other category is the dynamic receptors (less numerous), sensitive to the speed of displacement and detecting changes of speed by responding with a sudden emission of impulses during the kinematic phase of displacement and adapting in 15 seconds on the average. One cannot but be struck by the identity of the temporal characteristics of this adaptation with those revealed by the course of deterioration of precision of localizing final positions in our experiments. We would be inclined, therefore, to conceive that the joint detectors for speed furnish in regard to the spatial calibration of the final position of the displaced segment information which is different from that given by the position receptors. An additional argument in favor of this interpretation is supplied by the greater variability of the results observed during static conditions as compared to dynamic conditions, a difference which Werner and Mountcastle (1963) have also called attention to in their study of the regularity and frequency of discharge of joint receptors under these two conditions.

Finally, we note that the joint receptors appear to be similarly excited whether the movement be passive or the result of a muscular contraction. Although it cannot be totally excluded that active tension of the muscle can be considered responsible for a change in sensitivity of at least certain joint receptors (Skoglund, 1956), this effect may be considered of little importance and we have every reason to admit that information of articular origin is the same under both active and passive conditions of movement of the joint. Otherwise put, it is doubtful that such an effect can explain the better calibration of position in the case of active displacement.

*b) Cutaneous receptors* have been shown to fire in response to deformations of the skin, so that they could serve to indicate changing skin tensions resulting from changes in the position of a limb (Adrian, Cattell, & Hoagland, 1931 ).

There are some reports (Sherrington, 1900; Lee & Ring, 1954) that interference with skin sensation around a joint docs not affect position sense for movements at that joint. It does not seem, however, that this source of information could be a determining factor in the observed differences between active and passive movement.

*c) Tendon receptors.* The Golgi organs behave as if they are in series with the contracting muscle fibers and anatomical evidence supports this conclusion. They respond to the tension of the muscle, whether this be produced by active contraction or passive stretch. They have, however, a much higher threshold to external stretch. It is therefore most unlikely that they are in fact suited to give information from which we could make judgments of joint position in resting and in passive movement conditions.

In active contraction, however, they probably contribute to important new information. This information signals muscle tension which is determined more by the state of contraction of the muscle than by the position of the joint. On the other hand, it seems to be established that loading the moving limb (thereby increasing the Golgi contribution) has no consistent effect on the accuracy of position sense (Weber & Dallenbach, 1929).

*d) The muscle spindle* is a complex structure which lies in parallel with the surrounding, skeletal muscle. We find there are two types of specialized muscle fibers: nuclear bag fibers and nuclear chain fibers. Two types of receptors (primary and secondary ) can be distinguished associated with these fibers and two types of motor fibers controlling them (gamma fibers).

Passive stretch of the muscle increases the length of the muscle spindle and the rate of firing from the spindle afferent. Secondary afferents are recognized as static receptors and primary afferents as able to assume, depending upon their central control via the gamma systems, a function of length receptors or of velocity detectors. Interestingly enough, the time constant of adaptation of this velocity detection is about the same as that of joint velocity receptors and may also well account for the temporal decay found in our experimental results in the active conditions.

Although the joint receptors probably act in a similar way under conditions of active or of passive movement, the activity of spindle receptors is certainly different: active movement may greatly increase their activity even with small displacements, owing to their exquisite sensitivity to change of length of the muscle. Their possible role in position sense and kinaesthesis is still controversial (Howard & Templeton, 1966) and is denied by some (Merton, 1964) chiefly on the basis of the following arguments:

"Muscle spindles respond to changes in muscle length, i.e., measure relative length, but with their contractile ends they would obviously be unsatisfactory instruments for making absolute length measurements." This would be true for fixed positions of the limb, but if, as we are able to show, velocity detection with its characteristic decay in time may appear to provide potent calibrating information about the final position of the limb at the end of a movement, then the spindle becomes a not-to-be-ignored candidate for such a function.

"Muscles are insentient and non-conscious information coming from muscle may contribute to kinesthetic experience." The argument that muscle affercnts do not project to cortical structures has often been advanced in this connection. Experiments have shown unequivocally that muscle afferents from the forelimb of the cat do in fact project to the somatosensory area (Oscarsson & Rosen, 1966) and this has been confirmed for monkeys (Albe-Fessard & Liebeskind, 1966), where all four limbs project proprioceptive afferents to the motor cortex.

In the experiment with an anesthetized thumb described by Merton (1964), the subject with only motor and muscular afferent innervation intact was still able to manifest stretch reflex in response to forcible passive extension of his terminal phalanx without any change of sensation. This may by no means decisively disprove the possible role of muscle proprioceptors in calibrating conscious joint sensation in the spatial schema of our whole body when sensitized by voluntary command. What is "spatial sensation"? What are the conscious counterparts of the "local signs" of each conscious sensation? Is it not typical that when this system is at work, it is not explicitly present in the experience of the subject because it is composed of the same material without which he would have neither awareness nor sensation? The condition which is necessary to confer upon sensation its spatial dimension can not itself be sufficient for the elaboration of a consciousness without contents.

This remains, however, only a hypothesis—which seems, fortunately, to be a testable one.

*c) The pattern of motor innervation* may also help to explain the difference between active and passive conditions of execution of movements and this in two ways:

(1) Kinaesthesis and position sense may be served by the so-called "motor outflow." This concept covers the idea that some afferent control signal goes not only to the muscular organ but also has a "corollary discharge," internally derived, to some comparator or correlator structure inside the central nervous structure. First introduced by Sperry (1950) and now used by Held (1961), the term "corollary discharge" describes what von Holst (1954) designated earlier in his model of motor function as an "efferenz-kopie." The notion is in fact a very old one. Helmholtz (1925) called it "sense of innervation." This postulated, internally monitored signal may also be responsible for the "sense of effort" of the older authors, which has been newly reintroduced (Merton, 1964), and is proposed by some to account for *(a)* the stability of the visual image of the outside world despite ocular, head, and body movements, *(b)* the ability of patients deprived pathologically (Lashley, 1917) or surgically (Foerster, 1927) of most limb afferents who are yet still able to duplicate a given amplitude of movement as well as a normal person, and *(c)* the astonishing ability of surgically deafferented monkeys to perform accurate reaching even without visual control (Taub & Berman, 1964). The same mechanism is invoked by Held (1961) to explain the specific role of active movement in compensation for the rearrangement of visual-motor coordination. It is however clear that without other information (i.e., the starting position of the limb), its calibration in the body space and consequently in external space are lacking. Therefore, the motor strategy present in the engrammic repertoire of usual motor habits can only trigger a movement of desired amplitude in a given direction but without precise topological reference. It seems that vision could have acquired, in such an experienced machine as the adult organism, the capacity to affix spatial aims to this programming device even in the absence of the proprioceptive afferents which are considered necessary for position sense and kinaesthesis. This does not prove, however, the functional nonsignificance of proprioception. Proprioception is necessary not only to account for adjustments of motor commands to overcome changing conditions in the execution of movement (load compensation seems to remain the undiscussed function assumed by proprioceptors) but also to build up the spatial standards necessary in the first weeks or years of life, first to develop and then to maintain the repertoire of response patterns which are molded and conditioned by the spatial characteristics of the body and of the physical world in which they are achieved. It remains clear that, once engrammed, such standards may operate the programming of adjustment reactions which belong to the usual modes of reaction of the individual. Suprasystems of controls which emerge from this progressive organization may well be able to take charge of some reorganizations on their own, without the help of the primary

mechanisms—which remain, however, indispensable to the early construction of the edifice.

From the neurophysiological point of view, however, we are still far from having at our disposal the knowledge necessary to lay the foundation for theoretical models which are accessible to experimentation on anatomic and physiologic bases. Assumptions concerning the neural basis of the corollary discharge remain conjectural. Collaterals of the pyramidal tract have been traced at different levels of its course: the cortical level, where recurrent collaterals start from pyramidal axons, is proposed by Phillips (1966) as the origin of the feedback message which gives rise to the "sensation of innervation;" the subcortical level, where convergence of pyramidal efferents has been shown to exist (for example in the ventrolateral nucleus of the thalamus and in the rubrum), and pyramidal efferents have been shown to play a role in the control of somatosensory afferents (Towe & Jabbur, 1961; Wiesendanger & Tarneki, 1966; Kuypers, 1958).

The extrapyramidal systems may also be implicated in these theoretical schemata but the *terrae incognitae* which remain to be explored are numerous: in particular we think of the specific perturbations of visually guided behavior which accompany lesions at the midbrain level (Sprague, 1966) in relation to the frontal cortex, or again at the convergence of oculovestibular information on neurons of the pontine reticular formation (Jung, 1962). The pattern of activity of these neurons, in conformity with the schema of von Holst (1954), would differentiate active from passive movements of the head.

(2) The pattern of motor innervation is nevertheless susceptible to intervention via other more peripheral routes in the phenomena with which we are concerned. Owing to the fact that these systems are capable of furnishing the primary stock of information basic to the organization of higher standards of reference, it may be opportune to review the mechanisms.

Every motor command expressing itself upon the alpha motoneurons responsible for putting into action the contractile machinery is preceded, accompanied, and followed by a pattern of innervation of gamma motoneurons which biases the spindle receptors so as to initiate, sustain, and modulate the alpha discharge according to the state of the muscle and the peripheral demand and also according to the aim of the action to be achieved. Postural settings and postural adjustments probably constitute the main role, still rather poorly understood of this system. The central projections of the afferents which originate from the spindles are largely distributed to the cerebellum, the reticular formation, the striate structures, and in the cat (for the forelimbs) and in the monkey (for all four limbs) to the motor cortex. The identification of a double motor system controlling the intrafusal muscle fibers, the one part predisposing the primary spindle receptor to react as a speed detector (gamma dynamic), the other setting the same receptor to respond as a static position receptor (gamma static), brings a new dimension to the problem with which we are concerned. If it is true that the precise calibrating information associated with active displacements in our experiments gives us the impression of having a temporal decay very similar to that of a velocity receptor, we are led to attribute to this velocity information a preferential although ephemeral role in the precise referencing of a displaced limb in relation to the spatial schema of the body. Now, the pattern of motor innervation associated with voluntary movement has in the spindle receptors a neural pathway which is capable of magnifying this function of speed detection: the gamma dynamic system. Vedel (1966), in our laboratory, has been able to demonstrate precisely, in the cat, the selective role of the motor cortex and of the pyramidal tract in the control of the gamma dynamic system, whereas the striate functions are uniquely implicated in the control of gamma static motricity.

It is tempting to propose the hypothesis that this spindle mechanism is involved as a source of calibrating information tied to active movement and absent at the time of a purely passive movement of the limb. The testing of this hypothesis presupposes, of course, the possibility of getting into the system. It would seem to be accessible in man by selective blocking of the gamma system with procaine at the level of the motor nerve (Rushworth, 1960) or again, in a more indirect manner, by the action of cold on the muscles involved (Chase, Cullen, Sullivan, & Ommaya, 1965). We have already been able to obtain, by the action, of cold upon the musculature of the extensors of the index finger, a significant deterioration of the calibrating effects of active movement such that performance then approaches that obtained with passive displacements of the limb (Brouchon & Paillard, 1967).

The same framework of explanation can fit the interpretation of the fact that active maintenance of the final position (of the hand) does not lead to better calibration than does passive maintenance if the effective information arises in fact from information about the speed of deceleration of the limb at the end of its displacement. One should note in this case that the "sensation of innervation" is still present in the case of active maintenance just as in the case of active displacement. We are obliged then, in the framework of the theory of "outflow" to bring in also a kind of information whose calibrating or recalibrating effectiveness would depend upon a parameter of acceleration.

In addition, this hypothesis permits us to foresee that a movement which is too slow, and consequently does not effectively recruit these acceleration receptors, would be unfavorable to the processes of adaptation or readaptation which we are doing our utmost to test at the present time.

In conclusion, we do not presently have at our disposal any decisive element which permits us to choose between *(a)* the peripheral hypothesis of the intervention of spindle motor activity, and *(b)* the central hypothesis of "motor outflow" for the interpretation of the phenomena which we have observed. At the present time both appear to us to be equally conjectural and both call for experimental controls. It is probably the greater concreteness of the nervous structure implicated by the first hypothesis and its greater experimental accessibility which prompts us to engage in research on its validation; with the conviction, nevertheless, that these two theories are not mutually exclusive (nor do they even exclude several others), but probably represent two ontogenetically dependent complementary levels in the ladder of hierarchical systems responsible for the integration of sensorimotor functions which assures to organisms the adaptation of their behavior to their spatial environment.

## References

Adrian, E. D., Cattell, J. Mc., & Hoagland, H. Sensory discharges in single cutaneous fibres. *J. Physiol.,* 1931, **72**, 377-392.

Albe-Fessard, D., & Liebeskind, J. Origine des messages somato-sensitifs activant les cellules du cortex moteur chez le singe. *Exp. Brain Res.,* 1966, **1**, 127-146.

Bloch, A. M. Experiences sur les sensations musculaires. *Revue Scient.,* 1890, **45**, 294-301.

Bloch, A. M. Note à propos de la communication de Mr. Féré (expériences relatives à la notion de position). *C.R. Soc. Biol.,* 1896, **48**, 81-82.

Bowditch, H. P., & Southard, W. F. A comparison of sight and touch. *J. Physiol.,* 1880, **3**, 232-245.

Brouchon, M., & Paillard, J. Unpublished data, 1967.

Browne, K., Lee, J. & Ring, P. A. The sensation of passive movement at the metatarsophalangeal joint of the great toe in man. *J. Physiol.,* 1954, **126,** 448-458.

Chase, R., Cullen, J., Sullivan, S., & Ommaya, A. Modification of intention tremor in man. *Nature,* 1965. **206.** 485-487.

Dei.abarre, E. B. Ubcr Bewegungsempfindungen. Unpublished doctoral dissertation, Univer. of Freiburg, 1891.

Foerster, O. *Die Ieistungbahnen dies schmerzgefühl.* Berlin und Wien: Springer, 1927.

Goldscheider, A. *Gesamte Abhandlungen. Vol. 2, Physiologie des Muskelsinne.* l.eipzig: Barth, 1898.

Held, R. Exposure-history as a factor in maintaining stability of perception and coordination. *J. nerv. ment. Dis.,* 1961, **132,** 26-32.

Held, R., & Freedman, S. J. Plasticity in human sensory motor control. *Science,* 1963, **142,** 455-462.

HELMHOLTZ, H. (VON). *Treatise on physiological optics* (Transl. and Ed. By J. P. C. Southall), Vol. 3. New York: Dover, 1962.

HOLST, E. (VON). Relations between the central nervous system and the peripheral organs. *Brit. J. animal Behav.,* 1954, **2**, 89-94.

HOWARD, I. P., & TEMPLETON, W. *Human spatial orientation.* New York: Wiley, 1966.

JUNG, R. Zusammenfassung of the symposium on optic and vestibular factors in motor coordination. Proc. XXII Intern. Congress of Physiology, Leiden, 1962, Vol. l. Part 2, 518-525.

KUYPERS, H. G. J. M. An anatomical analysis of cortico-bulbar connexions to the pons and lower brain stem in the cat. *J. Anat. Land.,* 1958, **92**, 198-218.

LASHLEY, K. S. The accuracy of movement in the absence of excitation from the moving organ. *Amer. J. Physiol.,* 1917, **43**, 169-194.

LEE, J., & RING, P. A. The effect of local anaesthesia on the appreciation of passive movement of the great toe in man. *J. Physiol.,* 1954, **123**, 56-57.

LLOYD, A., & CALDWELL, L. S. Accuracy of active and passive positioning of the leg on the basis of kinesthetic cues. *J. comp. physiol. Psychol.,* 1965, **6**0, 102-106.

MERTON, P. A. Human position sense and sense of effort. *Symposium Soc. exp. Biol.,* 1964, **18**,387-400.

MOUNTCASTLE, V. B., & POWELL, T. P. Central nervous mechanisms subserving position sense and kinesthesis. *Bull. J. Hopkins Hosp.,* 1959, **105,** 173-200.

OSCARSSON, O., & ROSEN, I. Short latencies projections to the cat's cerebral cortex from skin and muscle afferents in the contralateral forelimb. *J. Physiol.,* 1966, **182,** 164-184.

PHILLIPS, C. G. Precentral motor area. In J. C. Eccles (Ed.) *Brain and conscious experience.* Berlin: Springer, 1966, 389-421.

PROVINS, K. A. The effect of peripheral nerve block on the appreciation and execution of finger movements. *J. Physiol.,* 1958. **143,** 55-67.

RIESEN, A. H.. & AARONS, L. Visual movement and intensity discrimination in cat after early deprivation of pattern vision. *J. comp.Physiol. Psychol.,* 1959,**52**, 142-149.

RUSHWORTH, G. Spasticity and rigidity. An experimental study and review. *J.* N*eurol. Neurosurg. Psychiat.,* 1960, **23**, 99-118.

SHERRINGTON, C. S. The muscle sense. In E. A. Schalfer (Ed.), *Textbook of physiology.* Edinburgh & London: Portland, 1900.

SKOGLUND, S. Anatomical and physiological studies of knee joint innervation in the cat. *Acta Physiol. Scand.,* 1956, **36**, Suppl. 124.

SPERRY, R. W. Neural basis of the spontaneous optokinetic response produced by visual neural inversion. *J. comp. Physiol. Psychol.,* 1950. **43,** 482-489.

SPRAGUE, J. M. Interaction of cortex and superior colliculus in mediation of visually guided behavior in the cat. *Science,* 1966, **153,** 1544-1547.

TAUB, E., & BERMAN, A. J. The effect of massive somatic deafferentation on behavior and wakefulness in monkeys. Paper read at Psychonomic Soc., Niagara Falls, Ont., October, 1964.

TOWE, A. L., & JABBUR, S. J. Cortical inhibition of neurons in dorsal column nuclei of cat. *J. Neurophysiol.,* 1961, **24**, 488-498.

VEDEL, J. P. Etude du contrôle supraspinal des sensibilités dynamiques et statiques des terminaisons primaires du fuseau neuromusculaire chez le chat. Unpublished these de doctorat en neurophysiologie (3e cycle), Univer. of Marseille, 1966.

WEBER, C. O., & DALLENBACH, K. M. Properties of space in kinesthetic fields of force. *Amer. J. Psychol,* 1929, **41**, 95-105.

WERNER, G., & MOUNTCASTLE, V. B. The variability of central neural activity in a sensory system and its implications for the central reflections of sensory events. *J. Neurophysiol.,* 1963, **26**, 958-977.

WIESENDANGER, M., & TARNECKI, R. Die rolle des pyramidalen systems bei den sensorimotorischen integration. *Bul. Schweiz. Akad. Med. Wiss.,* 1966, **22**,. 329-335.