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Review

Reflections on Jacques Paillard (1920–2006) — A pioneer in the field of motor cognition

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ABSTRACT

This article reviews the scientific contributions of Jacques Paillard (1920–2006), who strengthened substantially the role of physiological psychology in the field of movement neuroscience. His research began in 1947 under the direction of the French neurophysiologist, Alfred Fessard (1900–1982), with whom he then collaborated for 9 years while an undergraduate and then graduate student and junior faculty member in psychology at the University of Paris (the Sorbonne). Paillard moved to the University of Marseille in 1957 as a Professor of Psychophysiology. In parallel, he became a founding member and administrator of the Institute of Neurophysiology and Psychophysiology, which began in 1963 on the Marseille campus of the National Center of Scientific Research (CNRS). Paillard retired from his university and CNRS positions in 1991 but he continued seminal research until his demise. Paillard advanced understanding of higher brain influences on human spinal motor mechanisms and the functional role of proprioception as revealed in patients deprived of such sensibility. He remains best known, however, for his work on human motor cognition. He reasoned that brain "maps" of the external world are constructed by the body's own movements and the central effects of their resulting central and peripheral feedback. He proposed two levels of interactive brain processing for the planning and/or execution of a reaching movement: 1) a sensorimotor level, using body posture as a key reference; and 2) a "higher" cognitive level for accurate movement performance, using learned representations of the position and shape of the environmental components, including the body, itself.

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Abbreviations: C, century; CNRS, Centre National de la Recherche Scientifique [National Center of Scientific Research]; CNS, central nervous system; EMG, electromyogram; INOP, Institut National d'Orientation Professionnelle [National Institute of Vocational Guidance]; INP, Institut de Neurophysiologie et Psychophysiologie [Institute of Neurophysiology and Psychophysiology]; H reflex, Hoffmann's reflex; MS, Master of Science; PET, positron emission tomography; T reflex, Tendon reflex; UEREPS, Unité d'Enseignement et de Recherche d'Éducation Physique et Sportive [Unit of Teaching and Research in Physical Education and Sport Science]; vs., versus; WW, World War

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Contents

1. Introduction

In this article we reflect on the contributions of Jacques Paillard (1920–2006), who considerably strengthened the role of physiological psychology in the field of movement neuroscience.

When Paillard entered the field of physiological psychology in the mid-1950s it was relatively new in France, where it was then called "psychophysiology." Later, while the 1970–1986 Director of the Institute of Neurophysiology and Psychophysiology (INP), which had been founded in 1963 in Marseille, FRA by the National Center for Scientific Research (CNRS), Paillard was a key figure in the evolution of the field of motor behavior. He had begun his scientific career as both an experimental psychologist and neuroscientist working on sensorimotor control mechanisms. From the outset he emphasized behavioral aspects of motor control mechanisms, extending from their neuroscientific study, as in his first publications (Paillard, 1948a,b), to a much broader vision that eventually incorporated contributions from cybernetics, system theory, cognition, auto-organizing networks, and many other emerging life and physical science disciplines.

Paillard was above all an internationally recognized intellectual whose field was biology. He appears to have begun his scientific career with his own intuitive grasp of the overall nature of the living world. Motor control was of primary importance and interest to him because he sensed its significance for living creatures' adaptation to their environment. In reading the articles he published between 1948 and 2006, it would seem that he began with a pre-constructed biological model to which he progressively built upon throughout a lifetime of experimental and theoretical enquiry.

This article is composed of three parts. First, we summarize his academic career and the scientific concepts that were the foundation of his overall theoretical framework. We make note of his mentors, who influenced his vision.

Second, we focus on Paillard's ideas on motor control mechanisms at the spinal and cortical levels of the central nervous system (CNS). His ideas were quite original when first proposed. For the initiation of movements, he did not participate in arguments between so-called "reflexologists" and "centralists". Although influenced strongly by the reflex emphasis of Charles Sherrington (1857–1952), he was equally if not more impressed by the systems approach of Kurt Wachholder (1893–1961), who championed that the neural control of a movement was dependent primarily on its goal and that such control involved interactions between CNS command signals, peripheral feedback, and biomechanical constraints. We will emphasize Paillard's particular interest in and contributions to the understanding of skilled movements.

Third, we complete our analysis of Paillard's contributions by reviewing how he developed a model of how the CNS handles accommodation to a 3-dimensional environment by the dual interactive usage of largely unconscious sensorimotor mechanisms and conscious visually based cognitive neural mechanisms.

Paillard's emphasis on using study of the neural control of movement, hereafter termed "movement neuroscience," to advance understanding of how living organisms accommodate to their 3-dimensional environment is still considered an important contribution and it has spawned a particularly active field of research in behavioral neuroscience.

For other aspects of Paillard's life and work see Clarac and Massion (2007) and Massion and Clarac (2008).

2. A brief biography on Paillard

2.1. *Academic career and mentors*

Paillard was born on March 05 1920 in Nemours, FRA about 90 km south of Paris and he passed away quietly on July 26 2006 in Toulouse. He was influenced strongly by his father, a hero of WWI and a primary school teacher. In the 1920s most such teachers were defending a form of "humanistic

Table 1 – The academic lineage and associates of Jacques Paillard.

Scientist [a] (lifespan [b])	Origin [c]	Area of research focus [d]	Primary academic institution [e]
(A) Mentors			
Henri Piéron (1881–1964)	FRA	Experimental psychology	Univ. Paris, FRA
Alfred Fessard (1900–1982)	FRA	Neuroscience	Marey Institute, FRA
Auguste Tournay (1878–1969)	FRA	Neurology	Univ. Paris, FRA
(B) Professorial colleagues and collaborators at universities			
Monique Pinol-Douriez	FRA	Clinical psychology	Univ. Aix en Provence, FRA
Francine Orsini-Bouichou	FRA	Developmental psychology	Univ. Aix en Provence, FRA
Jean-Francois Chatillon	FRA	Experimental psychology	Univ. Montpellier, FRA
Michel Bonnet	FRA	Motor cognition	Univ. Provence/Marseille, FRA
Maurice Hugon	FRA	Neurophysiology (reflexology)	Univ. Provence/Marseille, FRA
Jean Pellet	FRA	Neurophysiology	Univ. Provence/Marseille, FRA
Daniel Beaubaton (1946–1986)	FRA	Movement neuroscience	Univ. Provence/Marseille, FRA
Jean-Marie Coquery	FRA		Univ. Lille, FRA
Jean-Pierre Roll	FRA		Univ. Provence/Marseille FRA
Jacques Crémieux	FRA	Exercise and sport sciences	Univ. Toulon, FRA
Jacques Larue	FRA		Univ. Caen, FRA
Michel Laurent	FRA		Univ. Méditerranée/Marseille, FRA
Vincent Nougier	FRA		Univ. Grenoble, FRA
Hubert Ripoll	FRA		Univ. Méditerranée/Marseille, FRA
Pierre Therme	FRA		Univ. Méditérranée/Marseille, FRA
(C) Colleagues and collaborators directing and/or active in French CNRS units			
Alice Leroy-Boussion	FRA	Developmental psychology	CNRS-Marseille, FRA
François Martinez	FRA		
Michelle Brouchon	FRA	Neuropsychology	CNRS-Marseille, FRA
Janine Blanc-Garin	FRA	Psychology	CNRS-Univ. Provence/Marseille, FRA
Monique De Bonis	FRA	Neuropsychiatry	CNRS-Paris, FRA
Jean Requin (1938–1996)	FRA	Motor cognition	CNRS-Marseille, FRA
Jean-Pierre Vedel	FRA	Neurophysiology	CNRS-Marseille, FRA
Bernard Amblard	FRA	Movement biophysics	CNRS-Marseille, FRA
Francois Clarac	FRA	Movement neuroscience	CNRS-Marseille, FRA
Laurette Hay	FRA		CNRS-Marseille, FRA
Jean Massion	BEL		CNRS-Marseille, FRA
(D) Colleagues undertaking prolonged stays (~1–3 yrs.) in Paillard's laboratory			
Robert Rigal	CAN	Neuropsychology	Univ. Quebec-Montreal, CAN
Colwyn Trevarthen	GBR		Univ. Edinburgh, GBR
Pierre Mounoud	CHE	Psychology of movement	Univ. Geneva, CHE
Marcos Turner (1925–2000)	ARG	Child neurology	Univ. Buenos Aires, ARG
Pierre Delwaide	BEL	Neurology (reflexology)	Univ. Liège, BEL
Kees (C.H.) Brunia	NLD	Cognitive neuroscience	Tilburg Univ., NLD
Richard Mark (1934–2003)	AUS	Developmental neuroscience	Australian National Univ., AUS
Robert Livingston (1919–2002)	USA	Neuroscience	Univ. California-San Diego, USA
Pierre Schenck	GER	Movement neuroscience	Univ. Freiburg, GER
George Stelmach	USA		Arizona State Univ., USA
Marjorie Woollacott	USA		Univ. Oregon, USA
(E) Prolonged stays (~3–12 mos.) by Paillard at colleagues' laboratories [f]			
Paul Bertelson	BEL	Experimental psychology	Free Univ.-Brussels, BEL
Frieda Newcombe	GBR	Neuropsychology	Univ. Oxford, GBR
Albrecht Struppler	GER	Neurology	Technical Univ.-Munich, GER
Wolfand Prinz	GER	Cognitive neuroscience	MPG-Munich, GER
Chantal Bard	CAN	Movement neuroscience	Univ. Laval, CAN
Jean Blouin	CAN		CNRS-Marseille, FRA
Jean-Louis Boucher	CAN		Univ. Ottawa, CAN
Michelle Fleury	CAN		Univ. Laval, CAN
Robert Forget	CAN		Univ. Montreal (Medicine), CAN
Yves Lajoie	CAN		Univ. Laval, CAN
Yves Lamarre	CAN		Univ. Laval, CAN
Norman Teasdale	CAN		Univ. Laval, CAN

Table 1 *(continued)*

Scientist[a] (lifespan[b])	Origin[c]	Area of research focus[d]	Primary academic institution[e]
(F) Continuous intellectual exchanges between Paillard and colleagues over many years			
Bärbel Inhelder (1913–1977)	CHE	Developmental psychology	Univ. Geneva, FRA
Maurice Reuchlin	FRA	Differential psychology	Univ. Paris, FRA
Paul Fraisse (1911–1996)	FRA	Experimental psychology	Univ. Paris, FRA
Jean Piaget (1896–1979)	CHE		Univ. Geneva, CHE
Marc Richelle	BEL		Univ. Liege, BEL
Emmanuel Pierrot-Deseilligny	FRA	Neurology	Salpêtrière Hospital-Paris, FRA
Francoise Schenk	CHE	Cognitive neuroscience	Univ Lausanne, CHE
Vincent Bloch	FRA	Neuroscience	Univ. Paris XI, FRA
Gabriel Gauthier	FRA	Motor cognition	CNRS, Univ. Méditerranée/Marseille, FRA
Alain Berthoz	FRA	Movement neuroscience	Collège de France, FRA
Marc Jeannerod	FRA		Académie des Sciences, FRA

This table is based largely on information provided by Paillard, himself, to Douglas G. Stuart, University of Arizona, Tucson, USA in January 1998[g] for a graduate student course on movement neuroscience. The authors have added some additional scientists.
Abbreviations: CNRS, Centre National de la Recherche Scientifique [National Center for Scientific Research]; MPG, Max-Planck-Gesellshaft [Max-Planck Institute].
[a] Presented alphabetically within each area of research focus in the B–F categories.
[b] Limited to complete lifespans.
[c] Country of birth. For country 3-letter codes, see http://userpage.chemie.fu-berlin.de/diverse/doc/ISO_3166.html.
[d] Paillard's own and the authors' presumed perception of the nature of the area of overlapping research focus and/or interest.
[e] Unit and institution where the association with Paillard occurred.
[f] Paillard had several shorter stays at various colleagues' laboratories, including presumably that of Wladimir Liberson (1900–1994) at the Veterans Administration Hospital, Hines, IL, USA (see Liberson and Paillard, 1963).
[g] Subsequent to January 1998, Paillard had 22 publications, many with several of the above-listed colleagues. He also published with further collaborators, including groups at the CNRS Ctr. Neurosci., Bron, FRA (Lafargue et al., 2003; Mercier et al., 2008) and the Laboratory of Music and Science of Marseille (Timsit-Berthier et al., 2004). One of his book chapters was with colleagues at the Univs. of California-Santa Cruz, USA and Geneva, CHE, and the Dresden Technical Univ. GER (Bridgeman et al., 2000).

socialism" against the long-standing Roman Catholic tradition. They promoted a secular philosophy based on high ethical standards and intellectual rigor. Paillard excelled in secondary level schoolwork at the Lakanal Grammar School in the south of Paris. By 1938, he was in his final year of secondary education at the St. Louis Lyceum in Paris, with the hope of subsequently enrolling at the prestigious Parisian high school, l'Ecole Normale Supérieure. WWII changed all his plans, however. Paillard became a soldier in 1940 and without front-line experience he soon became a prisoner-of-war and was transferred to Stalag IIID in Berlin, GER. Once there, Paillard immediately tried to escape and after several vain attempts he finally succeeded in April 1944. By then, however, he was in bad health with pleurisy and this delayed his resumption of studies until November 1945.

Paillard's tertiary education completions began with two Diplomas in 1947: one in Applied Psychology at the Institute of Psychology, University of Paris (the Sorbonne) and the other in Vocational Guidance Counseling at the National Institute of Vocational Guidance (INOP). He next completed two bachelor's level degrees at the University of Paris. The first in 1948 was in psychology, with invaluable mentoring from Henri Piéron (see Table 1). The second degree in 1950 was an "examen" with emphases in mathematics, physics, general physiology, and psychophysiology. Paillard's final degree was a doctorate at the University of Paris (Paillard, 1955).

During one of Paillard's oral examinations at the INOP in 1947 the neuroscientist Alfred Fessard (Table 1), the Director of the Marey Institute in Paris, encouraged him to finish his degrees and become a full time researcher at the institute, which had become a facility of the CNRS (National Center of Scientific Research) in 1949. Paillard began working with Fessard in 1947 and he remained with his neuroscience mentor and collaborator until 1956. Initially, there was no space for Paillard at the Marey Institute so he undertook his first research at the INOP, on Gay-Lussac Street in the Latin Quarter. (He moved to the Marey Institute in 1950).

Paillard's first task as a researcher was to decide at which level of scientific enquiry he should work. Would it be at the cellular level in surgically reduced animal preparations, using the first-class intracellular recording facilities of the Fessard group, or would he adopt a more global approach in studies on the intact human? He chose the latter because, as explained much later in his autobiography, he could not accept a "reductionist attitude": " … I evaluate the price of data obtained from anesthetized surgically reduced animal preparations in which the disruption of organic coherence seems essential for a rigorous analysis. Does not the very depth of the analysis obtainable in animal neurophysiology risk a separation of the data from the biological situations in which they have their real functional meaning?" (p. 188 in Paillard (1992a)).[1]

Like Etienne-Jules Marey (1830–1904), the renowned scientific photographer, physiologist, and instrument maker who founded the Marey Institute in 1902, Paillard was fascinated by

[1] *Je mesure le prix de ces acquisitions obtenues à partir de préparations animales anesthésiées, traumatisées, dans lesquelles la rupture de la solidarité organique semble la condition indispensable d'une analyse rigoureuse. La profondeur même des analyses à laquelle parvient ainsi la neurophysiologie animale ne risque-t-elle pas de désinsérer les faits du cadre biologique dans lequel ils trouvent leur véritable signification fonctionnelle?*

the complexity and potential richness of an exploration of human motor behavior: " … The explanatory value of these elementary data needs to be tested at the functional level of the intact organism. So I give up tentatively the seductions of experimental material that is artificially rendered more manageable and I deliberately choose for my main experimental subject the study of whom I feel I am the best prepared due to my previous psychological training: the human" (p. 188 in Paillard (1992a)).[2]

Paillard decided, with Fessard's encouragement and direction, to study neural mechanisms underlying human movements. His start was a doctoral thesis on the proprioceptive modulation of spinal reflexes (Paillard, 1955). At that time he also collaborated with, and was mentored by the neurologist, Auguste Tournay (Table 1). Interestingly, Paillard published but three refereed articles with Fessard (Fessard and Paillard, 1948; Fessard et al., 1950; Livingston et al., 1951) as compared to ten with Tournay (Fessard et al. (1950) to Lerique et al. (1962)).

Paillard was highly motivated to engage in teaching. For the period 1955–1957 he was an "assistant" (equivalent to an assistant professor in the USA) in psychophysiology at the Sorbonne under the direction of Professor André Soulairac (1913–1994). In 1957, Paillard left Paris and became a member of the Faculty of Science at the University of Marseille in the area of psychophysiology. He obtained the chair of this discipline in 1962.

The psychophysiological laboratory building in the center of Marseille was too small and quite old. Accordingly, in 1967 Paillard's laboratory migrated to St. Jérome in the north of Marseille. He stayed there for two years after which he joined a new CNRS institute at its Marseille campus (see below). In 1978, Paillard moved, while retaining his CNRS affiliation, as a Professor of Neuroscience to a new branch of the University of Marseille at Luminy in the far south of Marseille, near the famous "Calanques" between Marseille and Cassis.

Paillard had a very prominent position and active laboratory in Luminy, where for over 20 years he trained graduate students working on MS and doctoral degrees in neuroscience. While there, one of his interests was to promote the field of exercise science in the hope of it attaining the same academic level as other traditional university disciplines. Paillard encouraged some of his students to enter this field, including Michel Laurent and Hubert Ripol (Table 1; see, e.g., Laurent and Therme, 1985; Ripoll, 1989) and he, himself, regularly gave theoretical courses and participated in conferences on motor control and motor learning as applied to the exercising state (e.g., Paillard, 1986a). Paillard's efforts in this area created international interest, including that of the American, George Stelmach (Table 1), who collaborated with him in the area of cognitive movement neuroscience (Paillard et al., 1983; Paillard and Stelmach, 1999).

Soon after Paillard's arrival in Marseille, he was contacted by the CNRS, which organization had plans to develop a substantial research center outside of Paris as part of the so-called "Third National Plan." This required an expansion of the CNRS Campus J. Aiguier in the south part of Marseille. An Institute of Molecular Biochemistry had begun on this campus in 1955 and one in Physics at the same time. Within a few years, two more institutes were built, fully equipped, and the requisite researchers, technicians and engineers identified. The first was in Bacterial Chemistry (opening in 1962). The marine biologist, Pierre Drach (1906–98), championed the need for second, the INP, which opened on January 01, 1963. Georges Morin (1903–79) became the first director of the INP. He was originally from Lyon University and in 1943 he had become a professor of physiology in the medical faculty of the University of Marseille. Paillard led an INP department (see below) from 1969 to 1988. He was also the first assistant director (1963–1969) of the INP and then he became the full director for the period 1970–1986 (Fig. 1).

Paillard retired from his Luminy position in 1991 (Fig. 2) but he remained active in research until his demise in 2006. For example, in this 15-year period he published over 20 articles in refereed journals.

The INP recruited scientists from a variety of disciplines (for review, see Clarac and Massion (2007), Massion and Clarac (2008)). The overall scientific rationale was that psychophysiology should be linked with physiology such that behavior could be explored with an emphasis on its underlying physiological mechanisms. Experiments were undertaken on humans, using both healthy subjects and others with various pathophysiological diseases. Work was also undertaken on a variety of animal preparations to provide a comparative perspective.

At the beginning, the INP was composed of 80 researchers, engineers, and technicians. This number doubled by 1967 and increased to about 200 by 1977. This increase was more-or-less in parallel with the international emergence of neuroscience as an essential interdisciplinary effort. The INP contributed to this focus, particularly in the evolution of scientific ideas on sensorimotor functions. The institute was divided into seven departments. That of Paillard was termed "general psychophysiology." It was composed of psychologists, psychophysiologists,

Fig. 1 – The first administrative meeting of the INP in Marseille in 1963. From left to right: Jacques Paillard, the assistant director; Georges Morin, the director; and Maurice Dupuis, the head administrator. This photograph is available from F.C. upon request.

[2] *La valeur explicative de ces données élémentaires demande à être éprouvée sur le plan fonctionnel de l'organisme intact. Aussi je renonce provisoirement aux séductions de la matière expérimentale artificiellement rendue plus docile et je choisis délibérément pour objet d'expérimentation principale celui à l'étude duquel je me sens le mieux préparé par ma formation antérieure en psychologie: l'homme.*

Fig. 2 – Jacques Paillard after his retirement at the age of ~71 years (from first page of the Paillard website with permission of the current owner of the site, Chantal Maton, Brussels, BEL). This website includes Paillard's autobiography and a list of his publications. The latter provides access to his major papers in PDF format. See: http://jacquespaillard.apinc.org/.

physiologists, biologists, and physicists. The department's main research foci included motor programming, proprioception, visuomotor control, and the neurobiology of language. Paillard continually championed a comparative emphasis, including even the provision of support for a doctoral dissertation on the locomotor behavior of a species of crab (Clarac, 1971)!

Several prominent scientists directed the other INP departments. This distinguished group included: 1) Robert Naquet (1921–2005), a former trainee with Henri Gastaut (1915–1995), who had worked on sleep-waking mechanisms with both Giuseppe Moruzzi (1910–1986) and Horace Magoun (1907–1991), and became best known for his work on photosensitive epilepsy (see, e.g., Naquet et al., 1987); 2) Michel Dussardier who, with Noel Mei, advanced understanding of visceral afferent and efferent systems (Dussardier and Roman 1965; Mei, 1978); 3) Angélique Arvanitaki (1901–1983) who, with Nicolas Chalazonitis (1918–2004), pioneered analysis of the neural networks of the local marine mollusc, *Aplysia depilans* or *Aplysia punctata*; and 4) Valentine Bonnet (1902–1988), a former trainee of Frederic Bremer (1892–1982), who worked on the cerebellum, the reticular formation, and audition. She was later replaced by Jean Massion (Table 1) who focused this department's research on the red nucleus (e.g., Massion, 1967) and the physiology of motor pathways within the CNS. Massion was also the INP's sub-director for the period 1973–1977. In 1986 he succeeded Paillard as Director of the Functional Neuroscience Laboratory [Laboratoire de Neuroscience Fonctionelles] that was composed of the majority of the INP units. The remaining two original INP departments focused on the neurobiology of invertebrate behaviors, as directed by Georges Le Masne and Edouard Deleurance (1918–1990), respectively.

As the INP evolved, some new disciplines were developed. These areas and their leaders included: motor cognition with Jean Requin (Table 1) and his work on attention and the preparation for action (e.g., Requin, 1978); the mathematical analysis of animal behavior with Henri Durup (1930–2002) and his work on the golden hamster (Lavergne and Durup, 1969); invertebrate cellular neurophysiology with Maurice Moulins (1936–1995) and his work on the stomatogastric ganglion (Selverston and Moulins, 1987); molecular and neurochemical approaches with André Calas (Landry et al., 2003) and André Nieoullon (Nieoullon, 2002); modeling of motor systems with Gabriel Gauthier (Table 1; Vercher et al., 2003); and robotics with Nicolas Franceschini and his work on artificial flying insects (Franceschini et al., 2007).

From its outset the INP was comprised of one of the most renowned and active concentrations of movement neuroscientists in France and abroad.[3] It had a special relationship with the Brain Research Institute in Zurich, CHE, which was directed for many years by Konrad Akert. The success of the INP was also symbolized by a widely attended and recognized international symposium that was organized by Paillard and Massion and held in Aix-en-Provence in 1973. It was entitled "Comportement moteur et activités nerveuses programmées" ["Motor aspects of behaviour and programmed nervous activities"] (Paillard and Massion, 1974).

Another initial and subsequent feature of the INP was the emphasis on international exchanges. These included not only those with the majority of European countries (e.g., BEL, CHE, GBR, GER, and ITA) but also with more distant neuroscience centers in CAN, JPN, and the USA. Usually, ~15% of the researchers working at the institute were foreigners. Exchange programs were also undertaken with Eastern countries, in particular with the Warsaw, POL group of Jerzy Konorski (1903–1973) and the main USSR centers in Kiev, Leningrad, and Moscow. INP researchers also participated in Black Sea meetings organized by Professors Alexander Gydikov (1929–89) and Gantcho Gantchev, Bulgarian Academy of Sciences, Sofia. The original goal of these latter meetings was to be a vehicle for interactions between western and eastern scientists that were impeded substantially up to 1989 by "Iron Curtain" policies.

In Europe, Paillard was one of the leaders in the creation of the European Brain and Behavior Society, which held its first meeting in Marseilles in 1969, with Paillard as the primary organizer. His connections were also particularly close with

[3] A comparison of the INP to other international centers of neuroscience in general, and movement neuroscience in particular, is beyond the scope of this review. For such information the reader is referred to reviews like those of Magoun (1992), Swazey (1992), and Gurfinkel and Cordo (1998). What can be said briefly, however, is that the INP had a near-unique combination of life and physical scientists working in areas of movement neuroscience in a fashion somewhat similar to what was occurring in the 1960s–1970s in the Institute of Problems of Information Transmission in Moscow, USSR (see, e.g., Gelfand et al., 1966).

researchers in Quebec, CAN. These interactions were initially encouraged by Jean-Pierre Cordeau and Yves Lamarre (Table 1), two of the founding members of a neurological research center at the University of Montreal. When Paillard retired from his CNRS and university positions in 1991, he undertook most of his subsequent research in Montreal and more frequently at Laval University in Quebec City. For over 15 years he studied the famous patient G.L., in collaboration with Chantal Bard, Jean Blouin, Michelle Fleury, Yves Lajoie, Yves Lamarre, and Norman Teasdale (Table 1). One of Paillard's research missions throughout his career was to determine the specific role(s) of proprioception in various human motor behaviors. G.L., a patient of Lamarre, was an ideal subject! After two episodes of sensory neuropathy, she suffered a permanent loss of the large sensory myelinated fibres in all four limbs. This resulted in a total absence of the senses of touch, vibration, pressure, and kinesthesia (Fourneret et al., 2002). Tendon reflexes were also absent. This patient was very cooperative thereby providing Paillard with the unique opportunity to test hypotheses that he had proposed at a much earlier time. After 1991, Paillard also continued to pursue his interest in physiological mechanisms underlying the motor command signals of humans. For these studies he collaborated in Marseille with the research group of Jean-Pierre Vedel (Table 1) and Annie Schmied. His final publication in this area was in 1996 (Schmied et al., 1996).

2.2. Origins and main features of Paillard's scientific vision

In discussions with Paillard, his broad knowledge and eclectic culture were ever evident. He also had a very open mind, particularly about new theoretical concepts concerning motor behavior. For example, he was strongly attracted to and influenced by cybernetics, which discipline he related to various control loops within the CNS that provide the possibility of animals adapting optimally to their environment: " … It is an incontrovertible fact of contemporary neurophysiology that a consolidated repertoire of motor capacities, either inherited (and developed during growth) or acquired (and secondarily engrammed in the nervous circuitry), exists in all animals. Likewise, it is clear that the processes of coordination and control involved in the working out of this inbuilt machinery, remarkably mimic cybernetic modes of regulation. The developing and functioning brain must instantiate the dynamic processes that are required to select, assemble and coordinate the interacting elements of a systemic circuit, thus reflecting some kind of self-organizing process" (pp. 415–416 in Paillard (1986c)).

The initial background of Paillard's scientific originality was based on a combination of his own intuition and his enthusiasm for the ideas of three of the professors who mentored him during his predoctoral training in Paris. First there was Piéron, who was Paillard's primary model for an academic combination of teaching and research (Fraisse, 1970). Piéron had first become internationally renowned for his chemical theory of sleep (Piéron, 1913). Throughout his long career he promulgated the need for psychophysiology to be an independent discipline that was taught and studied at all French universities (Noizet, 1965). Piéron also founded the INOP in 1928 to facilitate the career possibilities of students interested in vocational guidance.

In contrast to most behaviorists, Piéron argued that it was necessary to penetrate the "black box." In parallel, he emphasized that behavioral sciences should address global processes in contrast to physiology that focuses on more restricted mechanisms. Piéron believed that psychophysiology provides an essential bridge between behavioral science and physiology with studies undertaken from infants to adults and from intact subjects to those with pathophysiological problems. He also promulgated the need for a comparative, zoological emphasis in both behavioral science and physiology with issues addressed in a variety of animals, from coelenterates to humans. In his promotion of comparative psychophysiology he sought both unifying principles and specialized animal adaptations. This comparative approach was often evident in the publications of his pupil, Paillard: e.g., " … The evolution of vertebrates and especially that of mammals is marked by a simultaneous synergic and competitive interpenetration of the motor apparatus of prehension and that of locomotion" (p. 1680 in Paillard (1960)).

Paillard's second and primary mentor was Fessard, the visionary leader of French neurophysiology after WWII (Buser and Naquet, 1983). Fessard read widely in the field of neuroscience. He knew of and visited many of the leading neuroscience centers of his time. He had a particular interest in German neuroscience, particularly the work of Wachholder, the key features of which he focused on in a French publication (Fessard, 1926–1927). Fessard was equally interested in analytical cellular physiological research, including the studies of Arvanitaki and those of Ladislav Tauc (1926–1999), whom he asked to work at the Marey Institute. Fessard also contributed to behavioral research. For example his group was the first to demonstrate that the EEG "Berger rhythm" could be learned and adapted (Durup and Fessard, 1935).

The third influence on Paillard was Tournay, a trainee and collaborator of the Polish-born neurologist, Joseph Babinski (1857–1932), who is best known for his studies on the cutaneous plantar reflex ("signe de l'éventail"; Babinski, 1896; Jay, 2000). Tournay helped develop the idea that asynergy is one of the main deficits of cerebellar damage, which he studied in the patient, H. Mounoulou, who had several cerebellar lesions (Tournay 1967; see also Van Bogaert, 1970). Tournay introduced Paillard to pathological studies on motor behavior, particularly those undertaken during the 19th C. by an array of great neurologists. In particular, Babinski emphasized the work of the renowned French neurologist, Guillaume Benjamin Armand Duchenne de Boulogne (1806–1875), and his concept of motor synergy.

With this impressive background, Paillard progressively developed his overall concept of how all animals live in a biological world that is primarily biochemical: " … It is recognized today that, properly speaking, there is no living matter but only living systems, organized beings whose recognizable unity is the organization of the physical elements of which they are composed" (p. 1379 in Paillard (1986b)).[4]

[4] *Il est aujourd'hui reconnu qu'il n'y a pas à proprement parler de matière vivante mais seulement des systèmes vivants, des êtres organisés dont la seule unité reconnue est du domaine de l'organisation des éléments matériels qui les composent.*

Paillard was also influenced strongly by ideas developed separately by the biophysicist, Henri Atlan, the Nobel Laureate chemist, Ilya Prigogine (1917–2003), and the mathematician, René Thom (1922–2002). These ideas were based on new perspectives made possible by the emergence of information theory (see Atlan, 1972; Prigogine, 1972; Thom, 1972). Paillard argued that the living being is controlled by an array of appropriate functional elements. His idea here was supported by attendant discoveries in genetics, which were demonstrating the presence of an "order generator" ("générateur d'ordre"), the genome. Paillard was attracted to the concepts of the 1965 Nobel Laureate, François Jacob, who opined that: " … We cannot now dissociate the structure from its significance, not only in the organism but in the course of the events that have led the organism to be what it is" (from Jacob (1970); cited on p. 1378 in Paillard (1986b)).[5]

For Paillard, this order generator also exists in the nervous system: " … About identifying a significance and functional purpose of organization in the nervous system … We can say that a function of such organization is expressed by a transformation of the system on which it exerts its action within a new structural or functional order that defines a new organization" (p. 1381 in Paillard (1986b)).[6]

Paillard's gestalt included the idea that the nervous system is partly a machine for data processing and as such, needs appropriate specificity in its informational relationships with the environment. He thought that the genetically-based order generator evokes processes that build animals as an ensemble of structures and functions that are able to ensure the survival of the organism and its success in coping within the environment in which it must thrive. The genetic program also accommodates non-rigid (plastic) potentialities, which enable later auto-organizing properties of the nervous system: " … The coherence of the spatial environment where we localize our perceptions and where we conduct our actions is the result of the coordination and integration of information collected by our sense organs on the state and events of the external world, and on the position and displacements of our mobile body in an organized and oriented universe" (p. 7 in Paillard, 1974).[7]

It followed to Paillard that the nervous system is the key element in animals' participation in the manifold world in which they live (Paillard, 1980). The different sensations of animals function to supply particular and specific descriptions of reality, depending upon the sensory channel(s) active at any one time. Following the explanation of the French philosopher, Étienne Bonnot de Condillac (1715–1780), who was the first to propose a distinction between information received passively vs. actively (Bonnot de Condillac, 1755), Paillard reflected on the exploratory component of human perception. He supported the conceptions of the Swiss biologist, Jean Piaget (1896–1980), about human development, including the idea that infants possess some elementary motor control programs, which are linked with each sensory modality (Piaget, 1937). The individual needs sufficient coordination between these sensory and motor functions to construct internally a coherent and stable physical "space" in which actions can be planned and elaborated (Piaget, 1967). Paillard extended on this concept when he wrote about a "calibration" of sensory-motor "spaces" within the CNS, with an emphasis on the active part of these operations. Paillard opined that the functioning of the nervous system included two essential neuronal assemblies, with one stable albeit partially flexible and the other far more plastic. The first is dominated by auto regulating "loops," e.g., sensory loops. The second assembly has the capacity to be modified by experience and practice thereby progressively enriching the reactional repertoire of the organism in relation to its external environment (Paillard, 1985).

Paillard was an enthusiastic promulgator of the role of CNS comparators that match the efferent copy of a central command and the reafferences of the ongoing movement thereby enabling an update of the trajectory of an ongoing movement, or of a perceived limb position, movement, or force, or of the environment surrounding the moving body or body part. This idea was first proposed by Nicolai Bernstein (1896–1966) for the execution of motor programs by the human (see 1930s'–1950s' articles in Bernstein (1967)). The same idea was championed by Eric von Holst (1908–1962) for several species, including insects (e.g., von Holst and Mittelstaedt, 1950), and by the Nobel Laureate, Roger Sperry (1913–1994), for fish (see Sperry, 1950). The latter study addressed stabilization of the visual world during eye movement.

Paillard had an all-encompassing view of the motor system. For example, he appreciated and profited from the contributions of Bernstein well before this Russian's work became well known in western countries, which did not really occur until the late 1960s and early 1970s (Gelfand et al., 1966; Bernstein, 1967). Paillard supported Bernstein's views on the degrees-of-freedom in multijoint movements. The muscle synergies studied by Paillard (see below) were like those studied by Bernstein. They emphasized optimal joint combinations that resulted from learning. The holistic experimental approaches Paillard used in this research seemed to him to be a natural extension of the methodologies used by Marey when he combined kinematic analysis with chronophotography thereby enabling the recording of several phases of a movement on one photographic surface (Marey, 1873; Braun, 1992). This "outside-in" behavioral approach was in sharp contrast to the reductionism approach favored by Claude Bernard (1813–1878) and his students (see, e.g., Bernard, 1865).

The "lambda" model of Anatole Feldman, an extension of Bernsteinian thought (Feldman, 1966, 1986), also intrigued Paillard. This model is a version of the so-called "equilibrium-point hypothesis," which proposes that the CNS controls movement by regulating equilibrium states of muscle effectors.

[5] *On ne peut plus dissocier la structure de sa signification, non seulement dans l'organisme mais dans la suite des évènements qui ont conduit l'organisme à être ce qu'il est.*

[6] *Parler de la fonction d'organisation du système nerveux suppose l'identification d'une signification, d'une finalité fonctionnelle… On peut dire qu'une fonction d'organisation a pour expression une transformation du système sur lequel elle exerce son action en un nouvel ordre structurel ou fonctionnel qui définit une nouvelle organisation.*

[7] *La cohérence de l'environnement spatial où nous localisons nos perceptions et où nous dirigeons nos actes est le résultat de la coordination et de l'intégration des informations collectées par nos organes des sens sur l'état et les évènements du monde extérieur, sur la position et les déplacements de notre corps mobile dans cet univers ordonné et orienté.*

This model is similar in some but not all ways to the "alpha" model of Polit and Bizzi (1978), which was based on analysis of processes controlling arm movements in intact and deafferented monkeys. At the same time, Kelso et al. (1979) presented yet another such model, which was based on attractors for the control of bimanual coordination. They proposed a mass-spring form of control wherein the resultant stiffness of antagonist muscle groups determines both the kinematic trajectory of movements and the frequency and amplitude of their terminal oscillations.

When Paillard's biological vision became prominent in the late 1950s and 1960s it was considered to be very innovative by giving the motor system a far more prominent position in psychology than had hitherto been present. For those who then thought that perception was the main object of psychological studies, motor activity was considered to be a more-or-less automatic process without any great psychological value (Bonnet et al., 1994). Paillard had the exact opposite opinion by bringing the motor system to the forefront of psychological reasoning! His main thinking on this issue can be summarized quite briefly: " … One of the most impressive features of our brain is its ability to process information from a wide variety of sensory signals thus producing an integrated and coherent representation of the outside world and that of our own body … Motor action is assumed to play a crucial role in accounting for the astonishing capacity of the nervous system to extract regularity and covariant features from changing surroundings … Basic sensorimotor mechanisms are automatically orienting sense organs and anchor them to a coherent, stable and unified perceived world" (p. 95 in Paillard (1999)).

Paillard's biological vision had a strong and everlasting influence on all of his trainees and on the broad psychology and neuroscience communities, particularly in France but extending quickly to other countries (see, e.g., Jeannerod, 1989, Berthoz, 1997).

3. Contributions on the overall control and coordination of movements

In this section it will be shown that Paillard's contributions extended from spinal pattern generation and reflexology to the highest CNS processes involved in the elaboration of skillful movements.

Paillard's initial research was in the field of movement neuroscience. During those first years while being mentored by Fessard, he worked with Tournay and a relatively young American neuroscientist, Robert Livingston (Table 1). The four of them were very influenced by the far earlier work of Duchenne de Boulogne; particularly his analysis of different types of movements. In particular, their goal was to identify activation patterns of various muscles when they operated in synergy, which can be defined as two or more muscles' activation in concert across one or more joints to elaborate a movement and/or sustain a posture. Duchenne de Boulogne (1867) had written about synchrony under the rubric of the propositions of the Danish-born anatomist, Jacob Winslow (1669–1760), who, again at a far earlier time, had classified muscles depending upon their contribution to movement. He defined "prime movers" as those whose activation primarily produced a movement, the "moderators" that oppose the same movement (the antagonists), and "the directors" that assist the movements (Winslow, 1732). Today, we call the latter muscles the synergists of the movement.

Paillard's initial concepts about motor control were a mixture of classical Sherringtonian neurophysiology on reflexes and their pathways (Sherrington, 1906) and the ideas of several German workers. Being fluent in German, he was quite familiar with the monosynaptic (*Eigenreflex*) reflex described by Paul Hoffmann (1884–1962) for the human leg (Hoffmann, 1910, 1922, 1934). Paillard also absorbed the electromyographic (EMG) techniques and ideas of Wachholder, who advanced understanding of the programming of muscle activity. Wachholder's major contribution was to extend on and add rigor to the idea that the CNS focuses on the goal of voluntary movements, and not the details of the muscles brought into play and the specific trajectories of moving body parts. This goal emphasis had already been proposed (Foerster, 1902; Kohnstamm, 1901) but Wachholder considerably advanced it by his addition of quantitative rigor (Wachholder, 1928; see also Sternad, 2001; Wiesendanger, 1997).

Fessard gave the introductory lecture at the above-mentioned 1973 Aix-en-Provence meeting. He included notions on CNS programming circuits, which he had long discussed with Paillard, including some that had presumably been stimulated by their attendance at a 1951 workshop in Paris entitled "Calculating machines and the human mind" ["Les machines à calculer et la pensée humaine"] (Fessard, 1953; see also de Broglie, 1951). For example, Fessard opined that: " … The term programme … that in the computer age seems to be spreading out everywhere … (is) … a notion that has been difficult to comprehend clearly and be well defined in physiological terms. I myself came to understand its significance when I started to practice electromyography and when I read articles published in Pflüger's Archiv in 1925 by two German pioneers, Wachholder and Altenburger, at the beginning of the use of electromyography… It was found then that a selected pair of muscle groups became active before the onset of a movement" (p. VI in Fessard (1974)).[8]

Paillard refined and updated Fessard's above statement about 25 years later with the comments that " … The nervous system has long been considered as a machine built to react to external stimulation in an adaptive way in the pure tradition of James' teleological functionalism (James, 1890). This dominant view provided undeniable success for reflexological theories of brain functions. However, recent approaches put more emphasis on the conception of the brain functioning as an *anticipating machine* (see Paillard, 1990; Berthoz, 1997), that is, a machine able to build an internal model of its most predictable

[8] *Le mot programme … qui à l'ère de l'ordinateur court les rues semble … une notion qui ait eu du mal à se dégager clairement et à se matérialiser en termes physiologiques. J'avais eu moi-même la révélation de son importance en lisant les articles de deux précurseurs allemands, Wachholder et Altenburger parus dans les Pflüger's Archiv dans l'année 1925 au temps où je commençais à pratiquer l'électromyographie…On s'aperçut alors que le couple musculaire interrogé prend ses relations de phase avant que le mouvement ait commencé.*

environment and to use it for driving action" (p. 96 in Paillard (1999)).

Paillard was impressed when the term "pattern generator" was first introduced for invertebrate locomotor circuitry (Wilson and Wyman, 1965) following some classical findings in the early 1960s (see Stuart, 2007). For Paillard, however, the idea of central pattern generating networks was evident in the concepts of Duchenne de Boulogne!

Paillard was similarly interested when Pierre Buser and his trainees Denise Viala and Claude Perret described spinally controlled locomotor rhythms for the rabbit (Viala and Buser, 1971) and cat (Perret, 1976). In particular, Paillard considered that such spinal control was not a rigid process but rather, one requiring integration with peripheral sensory based adjustments and the actions of descending supraspinal pathways. In his review, "Tonus, posture and movement" (Paillard, 1976a), he emphasized the significance of the spinal pattern generating rhythms described by Grillner and Zangger (1975). This review included much about the evolution of motor behavior because this area had always reinforced Paillard's notions on hierarchical motor control involving interactions between commands descending from supraspinal structures, brainstem/spinal cord motor programs, and sensory feedback (viz. Wetzel and Stuart, 1976; Stuart and McDonagh, 1998).

3.1. *Peripheral control of movement*

When Paillard started his human research in 1947 he made use of the recording needles of the American, Detlev Bronk (1897–1975), and he was able to record EMG activity with a new oscilloscope obtained by Tournay. As mentioned above, one of his first projects was to characterize muscle synergies. Duchenne de Boulogne had defined them as being very automatic and rigid. Paillard studied the hand catching an object, which involves a coactivation of finger flexors and wrist extensors. His colleagues and he compared flexor movements under very different conditions of external constraint (speed, under water, supporting weight). They found that contrary to Duchenne de Boulogne's results, responses were very variable depending upon their external constraints thereby emphasizing the fundamental plasticity and adaptation of such movements (e.g., Livingston et al., 1951).

In his initial research, Paillard demonstrated the astonishing capability and precision that subjects displayed when they synchronized different movements. He studied in detail the extension of two fingers in response to an external timekeeper. In addition, he used a more complex task by asking the subject to move two muscles of different limbs, e.g., to extend simultaneously the fingers and to raise a heel. The response was different depending upon the motor command schedule: i.e., if the movement was triggered by an external signal (reactive condition) or if it was self induced (self-paced condition; Paillard, 1948a,b). In the reactive condition, finger extension preceded heel rising by 30 ms. He suggested that this delay corresponded to the difference observed in the reaction time of the two muscle systems when measured independently. He proposed that the two motor commands were simultaneously released through a common triggering signal in the motor cortex. The longer distance to the foot as compared to the hand explained the longer conduction time to the foot. When the subject generated spontaneously the simultaneous activation of hand and foot, the heel raised in advance of finger extension by 20 ms. Paillard suggested that this result was attributable to the temporal target used for scheduling the onset of the two commands being the synchronous return of reafference information to the cerebral cortex as generated by the two movement commands. It was proposed that such "sensory simultaneity" was required when the aim was to execute simultaneously two voluntary movements that shared a common temporal goal (Fessard and Paillard, 1948).

The above late 1940s' hypothesis was confirmed more than forty years later when Paillard was in Canada working with the deafferented patient, G.L. A major finding was that she adopted the same reactive pattern in both conditions (Bard et al., 1992). G.L. was unable to produce the responses of normal subjects in the self-paced mode when heel action preceded finger extension. This result reinforced Paillard's notions on the role of proprioception in the sensory induction of simultaneity. More recently, Paillard used positron emission tomography (PET) to explore the neural substrate underlying self-initiated vs. externally triggered synchronized movements. In addition to responses in cortical areas already described in the literature, he found a prominent activation of the left postero-caudal hemi-cerebellum during self-initiated synchronized movements when compared to externally triggered movements. It was suggested that such cerebellar activity was related to motor timing processes (Blouin et al., 2004).

Following the above and allied research that culminated in several 1950–53 published articles (see http://jacquespaillard.apinc.org/) Paillard next focused on his doctoral research (Paillard, 1955). He considered the reflex paradigm to be quite useful as an experimental model because it afforded the opportunity for a careful and rigorous analysis of spinal cord function during selected movements (viz. Stuart, 2002). It seemed to Paillard at that time to be a much more precise approach than studying a spontaneous movement, which occurred in what he called "projective conditions" (i.e., self-initiated conditions). Accordingly, he studied spinal reflexes in humans, with the hope that the data accumulated previously in the cat by the Sherrington School would be very informative for his human studies, as would be the above-mentioned results of Hoffmann, of course.

In reality, Paillard was not interested by reflexes in and of themselves but by the fact that such responses were a clear-cut tool for examining the activity of the spinal cord and some of its supraspinal input. Fig. 3 shows how he compared two reflexes in great detail, the H reflex of Hoffmann, as induced by electrical stimulation of the external popliteal (posterior tibial) nerve in the poplitea fossa, and the tendon (T) reflex evoked by mechanical stimulation of the Achilles tendon. An important feature of his doctoral dissertation was the detailed review of the H and T reflex literature such that Paillard (1955) remains a classic article, indeed a review that emphasized all of the notable precedents to his own seminal findings, including, e.g., the remarkable human H reflex measurements of the American neurologist, John Magladery (1911–1977) (see, e.g., Magladery, 1955).

The Fig. 3 EMG responses in Paillard (1955) were recorded in soleus muscle. These responses to electrical and mechanical

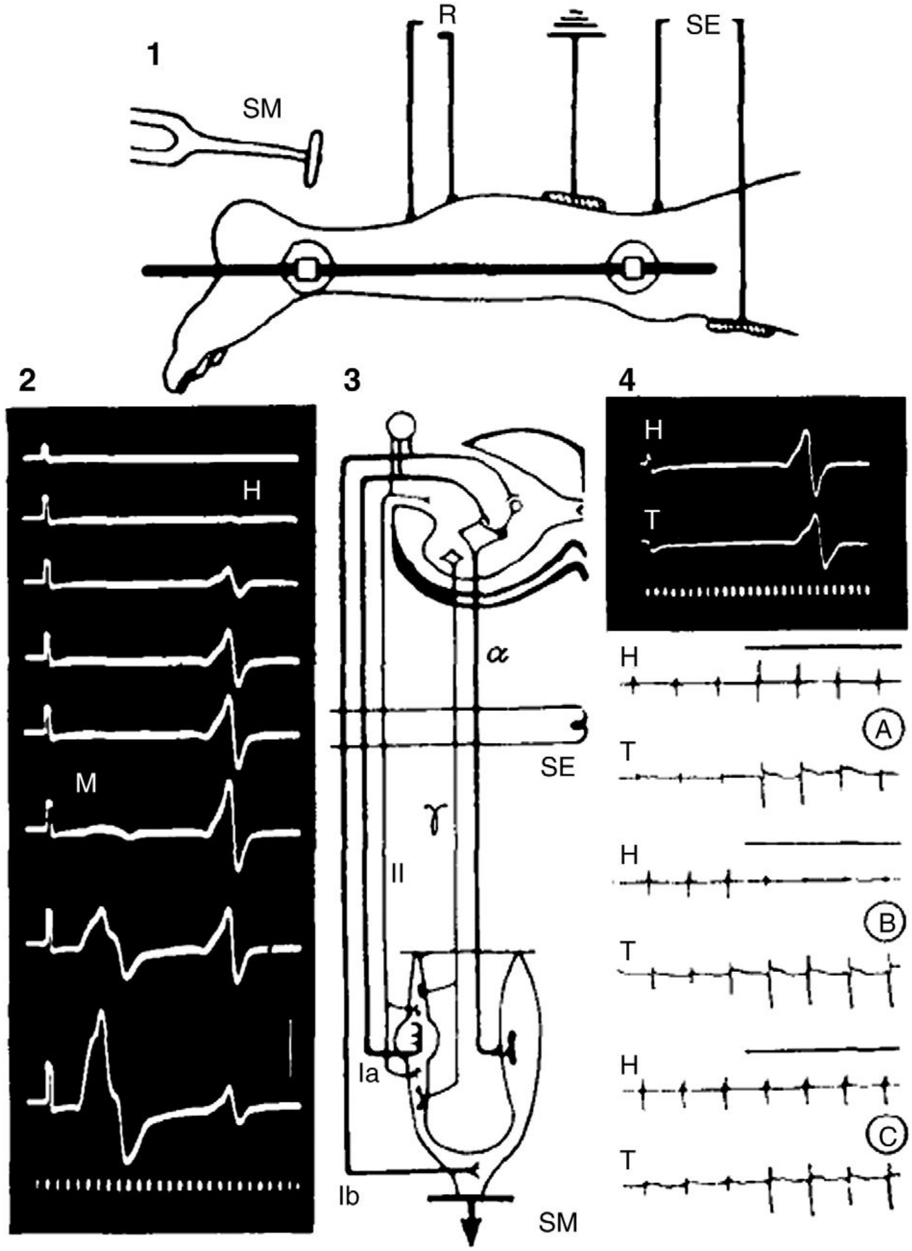

Fig. 3 – Experimental arrangement and some results from Paillard's doctoral research in which he compared tendon (T) reflexes to Hoffmann (H) reflexes in the human. (1) shows the experimental arrangement. R, EMG recording from the soleus muscle; SE, single shock electrical stimulation of the external popliteal (posterior tibial) nerve; SM, mechanical single tap of the Achilles tendon. (2) shows EMG H reflex responses to a progressively increasing strength of SE stimulation. These responses are preceded by a stimulus artifact (far left) and a growing direct muscle response (M), which progressively occludes the H reflex response by antidromic action. Calibrations: amplitude, 1 mV; time, 2-s intervals. (3) shows a schematic diagram of the relevant neuronal pathways. Ia, primary muscle spindle axons, II, secondary muscle spindle axons; Ib, Golgi tendon organ axons; α, alpha motoneuron axons; γ, gamma motoneuron axons. (4) Compares H reflex responses to SE (right-side soleus) and SM (left-side soleus) during voluntary pushing down of the foot (A), voluntary pushing up of the foot (B), and a voluntary Jendrassik manoeuvre (C) for durations indicated by solid lines. Same time scale as in (2). From Fig. VI-I in Paillard (1976a) (using figure components from Paillard (1955)) with permission of the publisher.

stimulation are attributable to sensory reflex input to the spinal cord emanating largely from muscle spindles: i.e., like reflexes demonstrated in the cat with the sensory input conducted by the largest afferent fibres; the so-called group Ia afferents of David Lloyd (1911–1985). A systematic comparison of the responses obtained with the two modes of stimulation allows inferences about the reflex action of afferent input from muscle spindles when spinal motoneurons are at various levels of excitability. Using alternatively electrical and mechanical stimulation, Paillard demonstrated that some stimuli could modify the T reflex without changing the H reflex. In the former case, the response is attributable in part to muscle spindle activation by both the mechanical stimulus and the spindles' efferent innervation by gamma motoneurons. In contrast, electrical stimulation bypasses spindle responsiveness and its gamma influence thereby indicating the state of motoneuron excitability. This comparative method demonstrated clearly the importance of the regulation of spindle muscular tension. For example, Paillard showed that the Jendrassik maneuver, mental calculation, and other cognitive activities had a strong effect on the T reflex and not the H reflex. These results intrigued and further motivated Paillard because the method provided a means to assess the presence and excitability of the gamma state, which the Swedish neurosurgeon, Lars Leksell (1907–1986) had studied so effectively (Leksell, 1945) in the Stockholm laboratory of the Finnish-born Nobel Laureate, Ragnar Granit (1900–1991). Later, Paillard used the same T vs. H reflex approach to study motoneuron excitability in patients with a spinal cord injury (Liberson and Paillard, 1963; see also Footnote f in Table 1), as did several subsequent groups who immediately recognized the significance of Paillard's doctoral research (see, e.g., Ishikawa et al., 1966).

Paillard continued to write and speculate on the functional significance of bias imposed on muscle spindles by gamma motoneuron discharge. He reasoned early on that the command delivered to muscle spindles by dynamic gamma axons prepared the primary spindle afferents to function as a speed detector of changes in muscle length whereas the command from static gamma axons increased the response of the secondary spindle afferents to changes in static muscle length. Concerning the role of the so-called "gamma loop" (i.e. gamma motoneuron-to-muscle spindle-to-spinal cord/motoneuron-to muscle), Paillard always acknowledged two early-developed theories, the "follow-up length servo" of Merton (1953) and the increasingly more accepted "servo-assistance" theory of Matthews (1964, 1972). Paillard tended to adopt an intermediate position about the two theories (see Paillard, 1976a,b). He remained convinced that the gamma loop presets the muscular state and prepares it for its main activation. He was very excited about the results of Ribot et al. (1986) when they pioneered the provisional recording of gamma motoneuron discharge in humans: " … The work of Ribot et al. (1986) deserves special attention in this connection. Cautious neurographic investigation led Ribot et al. to identify the activity of 12 efferent fibers from the lateral peroneal nerve in man. Their classification as alpha or gamma fibers was based on different criteria such as the presence or absence of associated EMG activity and spontaneous discharges, as well as their discharge frequency range. The most striking dissociation between the two groups of fibers, however, concerns the exquisite reactivity of the gamma fibers during "reinforcement manoeuvres" (like clenching the fist, twisting the pinna, or performing mental calculation) compared to the rather complete imperviousness of other fibers to these manoeuvres … These data fit remarkably well with former studies of mine on the human spinal reflex (Paillard, 1955, 1959) in which I introduced the concept of fusorial tone to designate the tension of intrafusal fibers that was not directly detectable in the EMG and contributed to tuning the sensitivity of the spindle receptor to stretch … The original idea, however, is that a change in the stiffness of intrafusal fibers could result from the gamma dynamic drive without having an immediate effect on the output of spindles unless the muscle was stretched by external forces (see Emonet-Denand et al., 1985)" (p. 786 in Paillard, 1992b).

Paillard's concepts of fusimotor tone and a presetting control of the gamma loop have not been accepted universally by the movement neuroscience community. He was upset about this and even at the end of his life, he was thinking about new experiments to confirm his hypothesis. The problem was probably that theories on muscle spindle function are dominated by work on conscious cats performing an array of movements whereas Paillard focused on what could be accomplished when studying humans. Presumably, Paillard was much encouraged when Ribot-Ciscar et al. (2000) refined the 1986 work of Ribot et al. by ensuring that their human subjects were fully relaxed subjects, both mentally and physically. Under these more stringent behavioral conditions, unitary muscle spindle recordings clearly supported Paillard's view that during arousal and expectancy the gamma motoneuron-fusimotor system can operate independent of the alpha motoneuron-skeletomotor system (for further advances on this and allied issues, see Ribot-Ciscar et al., 2009).

Paillard considered the muscle spindle and its gamma loop to be a biologically ideal auto-regulated system that operated as a complex cybernetic module with its double motor innervation composed of static and dynamic gamma motoneurons (Matthews, 1964, 1972). This interest in muscle spindle function was shared with his first doctoral trainee, the physiologist Jean-Pierre Vedel (Table 1), who studied the control exerted by supraspinal pathways on dynamic and static gamma motoneurons in the acute cat (Vedel, 1970). One of the findings was that the pyramidal tract excited dynamic gamma motoneurons whereas the basal ganglia excited the static cells (Vedel and Mouillac-Baudevin, 1970).

3.2. *Active vs. passive movements*

Paillard had a life-long interest in the role of proprioception in the neural control of active vs. passive movements and its psychophysiological relevance. For example, in his lectures he often emphasized the pioneering work of Held and Hein (1963) on the development of visuomotor systems in the neonatal kitten. They showed that when kittens were prevented from actively locomoting while still receiving the same visual stimulation as their normally locomoting counterparts, they failed to execute many visually guided tasks in a normal fashion. Paillard thought that such data were of primary importance in demonstrating that active movements are essential in calibrating the external world. He fostered study of the specific role of active movement in kinesthesis (particularly position sense) as exemplified in the interesting findings of his collaborators, Michèle Brouchon and Laurette Hay (Table 1; see, e.g., Brouchon and Paillard, 1966; Hay, 1970; Paillard and Brouchon, 1974). In an open loop (no visual feedback) pointing task, the above articles showed that error in the final position was much reduced when the new position was obtained by an active arm displacement as compared to a passive displacement. This observation suggested that the perception of the final position required sensory input from proprioceptive arm afferents that had been generated by the active movement.

" … It is tempting to propose the hypothesis that this spindle mechanism is involved as a source of calibrating information tied to active movements 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) … We have been able to obtain by the action of cold upon the musculature … a significant deterioration of the calibrating effects of active movements such that performance then approaches that obtained with passive displacements" (p. 52 in Paillard and Brouchon, 1968). Again, Paillard was able to confirm his intuition in his later study of G.L. For example, he often explained that when she slept, she was obliged to have a light in her bedroom. Without this reference, she was totally lost, and ignored the close surroundings (Cole and Paillard, 1995).

3.3. *Cerebrocortical-spinal interactions*

When Paillard considered descending pathways for motor activity, he first considered their very close association with ascending sensory pathways, the two processes, and their interactions that occur in several intricate loops (Fig. 4).

In his own research on the overall control of movement, Paillard tended to focus on reflex behavior as affected by descending cerebral cortical control and sensory input at the spinal level. He compared their various roles in the elaboration of different types of movement (Paillard, 1960). Paillard was influenced strongly by the classical views of the English neurologist, John Hughlings Jackson (1835–1911). Paillard emphasized a double CNS control "keyboard," with different programmed activities corresponding to different musical melodies: " … The specificity with which the spinal keyboard responds to cortical commands depends upon the refinement of the organization of the upper-motoneurone keyboard and the relative strength of connectivity between the two structures" (p. 157 in Paillard (1978)).

Paillard emphasized that there were substantial differences between the upper and lower levels in their operation during learning processes: " … The central command is bound to operate upon the spinal keyboard through the pre-existing arrangements of its inherited or habitual repertoire of action. To execute purposefully a new act, of which the aim is beyond the limit of flexibility of the existing repertoire, a complex selective operation is involved that characterizes the initial phase of every learning process … Once the difficulties encountered by the central command in shaping the newly planned act have been resolved, a second important phase of the learning process begins. It concerns the cleaning and polishing of the new action in order that performance becomes progressively faster, smoother, more economical and more accurate. It then becomes what we call a skill" (pp. 426–427 in Paillard (1986c)).

Paillard had a particular interest in skilled movements, including those requiring postural training: " … The ability of certain mammals to learn astonishing postural skills (the juggling seal, the acrobatic elephant, the dancing horse or the cycling bear) seems to justify their high rank in terms of pyramidal tract equipment despite a low rank on the elaborate control of basic inbuilt programs of posture and movement. We have then to explain how the pyramidal tract contributes to both the skillful use of the delicate motor instrument of the five-fingered hand and the enrichment of the primitive repertoire of posturo-kinetic skills" (p. 428 in Paillard (1986c)).

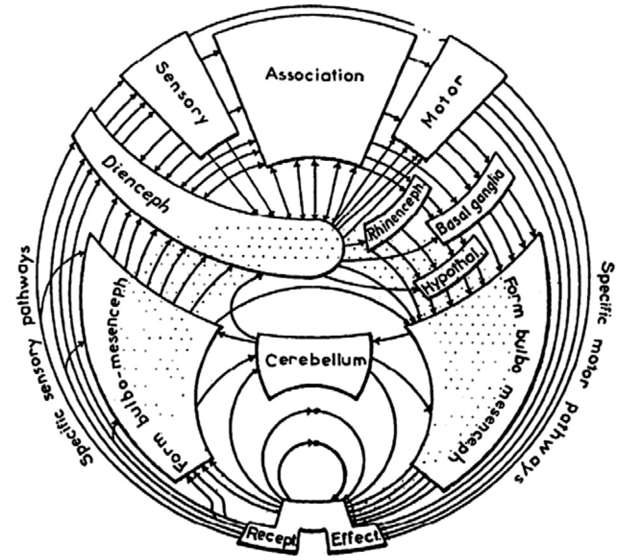

Fig. 4 – Schematic Paillard diagram of selected major sensory, associative, and motor paths throughout the brain. His purpose was to emphasize the essentially circular organization of sensorimotor interactions at all levels of the CNS. Paillard stated (p. 1702) that "… Only the 'output-informed' circuits are represented. Some direct sensory connections to various higher structures have been intentionally omitted." Abbreviations from above downwards: Dienceph, diencephalon; Rhinenceph, rhinencephalon; Hypothal, hypothalamus; Form bulbo-mesenceph, bulbo-mesencephalic portion of the reticular formation; Effect, motor effectors; Recept, sensory receptors. From Fig. 10 in Paillard (1960) with permission of the publisher.

In his various writings and presentations on the neural control of different types of movement, Paillard considered that the pyramidal tract was a structure of primary importance due to its role in coordinating cerebrocortical and spinal actions. He analyzed in detail the complexity and the diversity of the pyramidal tract (Wiesendanger, 1969, 1984). In Paillard (1978), which was a provocative paper entitled "The pyramidal tract: two millions fibres in search of a function," he proposed that this tract's descending activity could modify the behavior of basic genetic patterns elaborated within spinal cord networks. Paillard dissociated clearly the programming actions of central CNS modules from peripheral sensorimotor loops that added flexibility to motor output. He further emphasized that the pyramidal system played two roles during the acquisition of a new motor skill: " … Either pyramidal commands bypass the established repertoire of inbuilt motor programmes and then play their own original kinetic melody on the spinal keyboard; or pyramidal commands are able to rearrange the existing programmes, thus generating new sets of coordinated activity by tuning older ones. We suggest that both systems can operate and that they are complementary" (p. 430 in Paillard (1986c)).

Paillard also emphasized the importance of the role of the neocerebellum in the elaboration and adaptation of skilled movements: " … The neocerebellum thus becomes the chief modulator mode of the cortical keyboard in the programming and execution of the transport movements of the arm in grasping space. The 20 million fibres composing the cortico-ponto-cerebello-cortical loop in man … reflect the functional importance of this control system which shunts the main cortico-spinal routes for movement control. The segregation of the output of the lateral cerebellum in two specific nuclei-the interpositus and the dentate-may correspond to a functional dissociation (Evarts and Thach, 1969): the proactive role of the dentate nucleus in the initiation of preprogrammed movement and the retroactive control of ongoing movement through the interpositus" (p. 38 in Paillard (1993)).

3.4. *Human motor skills and their evolutionary development*

In his vision of the biological world, Paillard paid particular attention to evolutionary aspects that occurred in prehistoric times as living beings interacted with their environment (Paillard, 1986d). He reasoned that each individual in each species lived in an environment (ecosystem) that provided the necessities for individual and species survival. Three needs were critical: a source of usable energy, a space for useful actions, and a source of useful information.

In an anatomical sense, the need to exploit the environment as a source of usable energy led to a specialization between rostral oral structures for the absorption of food and caudal motor structures for various forms of rejection: i.e., an oro-caudal organization in most species, including mammals.

A space for useful actions was exemplified to Paillard by the form of locomotion used for the transportation of the mouth toward the source of energy. The milieu was then used as a physical support for the propulsive organs whatever their mode of propulsion – terrestrial, aquatic, or aerial – and it was directly dependent on the oral function. The moving articulated body supported the "capturing buccal organ" and thereby ensured the stability of the cephalic segment and "the postural anchoring function" of this segment.

Paillard further reasoned that the environment was also a source of useful information for performing the operations of choice and selective capture of materials. The sensory organs and their motor apparatus act as an "information mouth" around the "capturing mouth" for guiding the effectors' activities within the environment. The mobile eye was another example.

Paillard focused on the evolutionary processes that resulted in the capability to lead the hand to the mouth as required for effective utilization of the environmental "milieu" (Paillard, 1986d). One such aspect was the relation between legged locomotion and manipulation by the hands. He compared primitive monkeys' use of their forelimbs for walking to primitive humans as they started to elaborate manual manipulations by their hands: " … The evolution of manual skill is a major zoological trend which appears to result in a transformation of cerebral architecture that is characteristic of all primate brains … The liberation of the hand from the requirement of locomotion and its promotion to the rank of a privileged interface between the organism and its material environment have profoundly remodeled the architectural landscape of the primate brain compared with that of other mammals" (pp. 36–37 in Paillard (1993)). He further opined that " … The hand is no longer just the organ for grasp, displacement, attack and defense and eventually for using an external object as an extension of the body. It now becomes a tool-maker and an instrument for symbolic communication" (p. 43 in Paillard (1993)).

A second hand-to-mouth example Paillard considered in several articles was the profound evolutionary modification that occurred with mouth development from its primitive essentially spatial reference for food convergence before ingestion to that in advanced non-human primates and the human where the mouth is a particularly complex structure that has the additional responsibilities of facial expression and the control of phonation: " … The regression of the technical functions of the mouth does not involve a complementary restriction of cortical areas devoted to the control of facial motricity. In fact, oral technicity in man progressively generates a motricity that is finely co-ordinated to emit a wide range of structured sounds. This new skill is the result of a long training whereby the sounds produced by the vocal organ mainly contribute to tune and organize its motor command" (p. 43 in Paillard (1993)).

4. Paillard's two levels of "space" processing: sensorimotor and cognitive

In his autobiography, Paillard emphasized that his "space" theme was the research area in which he had the most invested and in which he made his most original contributions: " … Among the diversity of research topics that were developed in the INP department, I remember in particular the two great themes to which I personally contributed during this second period of my career: visuo-motor co-ordination and spatial reference frames" (p. 193 in Paillard (1992a)).[9]

By "space," Paillard meant the 3-dimensional world in which humans and other animals live. His main interest was to understand " … how the spatial constraints that are specific to our terrestrial environment have moulded our physical architecture and its sensory and motor instruments, and in what they have shaped our nervous system to cope with the quasi-Euclidian space in which we live" (p. 461 in Paillard (1991c)).

A basic postulate of Paillard was that two levels of processing of space coexist: " … A functional distinction between two levels of information processing by the nervous system has been suggested (Paillard, 1985). One concerns the direct dialogue that the organism entertains with the part of the physical world to which it is attuned by virtue of its sensori-motor apparatus. The other is related to cognitive activities that operate on mental representations of physical

[9] *Parmi la diversité des sujets de recherche qui ont été développés dans ce département de l'INP, je retiendrai plus spécialement ceux qui relèvent des deux grandes thématiques que j'ai personnellement contribué à développer au cours de cette seconde période de ma carrière: celle des coordinations visuo-motrices et celle des référentiels d'espace.*

reality embodied in memory stores. The general idea is that the progressive evolution of the cognitive apparatus has created new control systems of action that enlarge the adaptative capacity of the organism but without, at the same time, undermining the more primitive and far more economic control that characterizes the sensori-motor level" (p. 432 in Paillard (1986c)). The subdivisions of this section of the article illustrate various aspects of Paillard's ideas about space.

4.1. *"Espace des lieux [target space]" vs. "espace des formes [shape space]"*

Paillard's concept of a dual CNS control of space was proposed in his early investigations at his Marseilles' INP laboratory and the overall idea was refined progressively over the years (Paillard, 1971, 1987, 2005). The concept was based on his own findings, those of his co-workers, and the findings of other neuroscientists in the international community who were addressing the same issue. Many of the above attended the symposium organized at his retirement (Paillard, 1991a) at which he presented two papers that summarized his own views as compared to those of other contributors to the field (Paillard, 1991b,c).

Paillard's ideas on space were based on two fundamental features of animal (including human) motor behaviour: moving body parts or the body as a whole from one place to a new target in what he termed their "action space", and tactually or visually palpating objects for their identification in what he termed "exploring unvisited local spaces." The former transport process involved his "espace de lieux," i.e., an action space where targets are located vectorially in a body-centric coordinate system. In contrast, he proposed that the latter exploratory process uncovered his "espace des formes," wherein local spaces are shaped by their boundaries and stored in the CNS in a stable configuration, with their component parts and relative positions incorporated into word- or object-centric space coordinate systems (see p.90 in Paillard, 2005).

To facilitate understanding of his space concept, Paillard provided the Fig. 5 diagram, which shows the key components and interactions required between sensorimotor (essentially neurophysiogical) and cognitive (essentially psychological) processing for effective space control to be achieved (see, in particular, Paillard (1985, 2005)).

The ideas of Piaget (1967) clearly influenced Paillard's Fig. 5 model. Piaget argued that higher cognitive functions have their foundation first in basic sensorimotor mechanisms needed primarily to ensure survival of the organism. Such sensorimotor processing is largely an inherited mechanism, interacting directly with the physical environment, and serving to supply vital functions. This process was at the "knowing how" level of Paillard's space concept and the earlier "savoir faire" of Piaget. The second level of Paillard's concept concerned the cognitive processing apparatus with its stored abstract memorized representations of the internal and external world, including the ability to process the variety of mental states that characterize higher brain functions. This was Paillard's "knowing what" level, analogous to the "savoir faire" of Piaget. Paillard considered the question of the degree of interaction between the above two processing levels and the possibility of their parallel functioning. His reference to the predominant involvement of the cerebral neocortex in the cognitive level suggested, however, that he favored a hierarchy between the two levels.

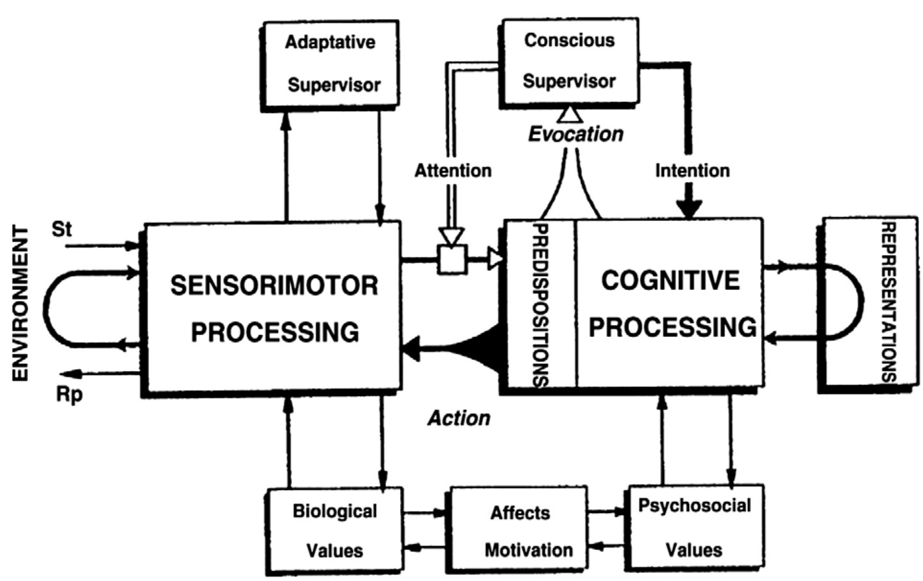

Fig. 5 – Paillard's schematic representation of the two keys of information processing in the CNS. Sensorimotor processing is accomplished subconsciously by the sensorimotor machinery, which interacts directly with its external physical environment using mainly its genetically pre-wired circuitry (St, stimulus; Rp, response). Cognitive processing requires conscious actions, which exploit the full resources of neocortical structures, and is thereby able to process the full variety of mental states that characterize higher brain functions. From Fig. 1 in Paillard (2005) with permission of the publisher.

Paillard's concept of a dual organization of space was supported by demonstration of two distinct visual systems, which were proposed initially by Ingle (1967), Schneider (1969), Trevarthen (1968), and Held (1970). The key paper was that of Schneider (1969). He showed for the hamster that two visual systems could be identified during evolution: a retino-tectal system for orienting head and body toward the source of the stimulus, to answer the question "where is it?" and a cortical visual area for perceptual discrimination and recognition of visual form to answer the question "what is it?" It was later realized that both systems were "corticalized" in human and non-human primates (Mishkin et al., 1983). The basic assumption of the above research was that visual information is distributed from the primary visual areas to the associative cortex along two main axonal streams: one dorsal, projecting through the posterior parietal association cortex (see Stein, 1991) and sub-serving the function of knowing "where;" and the other ventral, projecting mainly into the temporal association areas and providing the neural substrate for the function of knowing "what." Two parallel visual pathways from the retina to the primary visual cortex have indeed been shown in mammals (especially in primates) to provide appropriate visual information to the dorsal and ventral streams. The magnocellular system originates from "parasol" retinal ganglia cells, which project to large cells in layers 5 and 6 of the lateral geniculate body. These, in turn, project to area V1 in the visual cortex. The cells of the magnocellular pathway are achromatic, have large receptive fields, and their activity is "dynamic," being characterized by low spatial frequency and high temporal frequency, such as to make the system highly sensitive to movement. In contrast, the parvocellular pathway originates from retinal "midget" ganglia cells, which project to parvocellular cells of layers 1–4 of the lateral geniculate body. These, in turn, project also to area V1. The cells of the parvocellular pathway have small, color-opponent receptive fields, exhibit tonic activity, and have high spatial frequency and low temporal frequency, which facilitate object shape detection (Callaway, 2005; Dacey and Petersen, 1992).

Interestingly, the retinal distribution of the receptive cells related to ganglia cells at the origin of each pathway is quite different. The receptive cells (cones) in relation to the "midget" ganglia cells at the origin of the parvocellular pathway are concentrated mainly in the fovea, whereas those (predominantly rods) in relation to the "parasol" ganglia cells at the origin of the magnocellular pathway are activated primarily from the periphery of the retina (peripheral vision) (Dacey and Petersen, 1992). This foveal vs. peripheral visual stimulation prompted Paillard (1991c, 1996) to plan reaching experiments using either source of peripheral feedback and theorizing on the preferential activation of the magnocellular vs. parvocellular system for fast "on-line" adjustment of movement during reaching (see Footnote 11 below). This exercise lead to Paillard's idea of two main components in space organization: "espace des lieux" ["target space"], using the dorsal visuospatial system and being responsible for sensorimotor processing in a body-centric space coordinated system; and "espace des formes" ["shape space"], using the shape recognition ventral system and being responsible for object recognition in a object-centric space coordinate system (Paillard, 1991b,c).[10]

4.2. Concept of "local sensorimotor spaces"

Paillard's sensorimotor space is composed of a plurality of "local" sensorimotor spaces (Paillard, 1991b). " … The body has active sites at the cutaneous frontier that separates its internal territory from its environment. Specialized sensori-motor devices characterize these active sites: the mouth, the eyes, and the hand are prototypical examples … The boundaries of each regional sensori-motor 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" (p. 164 in Paillard (1991b)). He defined "structure of space" as a collection of elements separately discernible by the observer and by rules describing the potential relationship between the elements: i.e., the "geometry of description" of the spatial structure. Certain metric rules defined what he called the "path structure", i.e., the trajectory followed when moving from one point to another. The path structure superimposed on a collection of separate points defined for Paillard the "locality" of each point in a vectorial map.

Examples of the plurality of sensorimotor spaces include the (1) visuo-oculomotor space based on a retino-centric coordinate system, (2) visuocephalic motor space coordinated with the visuo-oculomotor space for coding gaze direction, (3) visuo-locomotor space for integrating the visuomotor subspaces of the eyes and head in order to locate objects in the stable environmental space in which the body is moving, (4) tactual-motor space, involving hand space for manipulation and object exploration, and so on (including mouth space, etc., etc.).

Paillard proposed that " … the properties of local sensorimotor spaces provide the conditions required for registering of proprioceptive information … derived from orienting movements, together with covariant information (visual, tactile, auditory …) about the positional changes of the target within the sensory map of the receptive surface. Thus the locations of these targets within a sensory map becomes encoded within a hierarchy of sensorimotor path structures (p. 166) … The same

[10] Goodale and Milner (1992) proposed an alternative perspective on the functions of the dorsal and ventral stream. They argued that the main difference between the two streams is their specific function in perception and active movement. The ventral stream's inferotemporal cortex plays a major role in the perceptual identification of objects (i.e., knowing "what") whereas a function of the dorsal stream's posterior parietal cortex is to achieve the sensorimotor transformations required for the visually-guided reaching to and grasping of these objects (i.e., knowing "how"). The appropriate hand aperture for such grasping would then be calculated in viewer-centered egocentric coordinates of the surface of the object or its contour. Paulignan et al. (1990) showed that a fast on-line adaptation of wrist and finger orientation did occur when the orientation of the object to be grasped was changed at the onset of movement. In optic ataxia associated with a lesion of the posterior parietal cortex in man, Gréa et al. (2002) reported that such on-line adjustment of wrist and finger orientation was abolished, thereby suggesting a posterior parietal cortex function for on-line adjustment of hand and finger orientation to the object.

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 of the spatial map of this superordinate system" (p. 167 in Paillard (1991b)).

In movement neuroscience, the body schema of Henry Head (1861–1940) can be considered as a postural path structure in which each movement of the multijoint body is calibrated within the proprioceptive field of that structure (Head et al., 1920; see also Gurfinkel and Levick, 1991). This coordinate space system (egocentric reference frame) is anchored to the invariant direction of gravity forces (geocentric reference frame). Paillard emphasized for many years that the role of the head segment was essential for maintaining a "geotropic statural referential" (p.167 in Paillard (1991b)) in both the stance of a static body and its dynamic balance when moving. He argued that prehension and manipulation required target position and displacement in space to be referenced to the external world through the target's retinal projection, the coding of eye position with respect to the head and trunk, and the head's detection of the gravity axis.

In Paillard's space model, a hierarchical proximo-distal organization of local visuomotor subspaces was illustrated by the visuomotor adaptation that occurred in a pointing task when subjects wore prismatic goggles that deviated from the perceived target position (Hay, 1970; Paillard, 1991b). Subjects pointed to a target with a wrist, elbow, or shoulder movement. After donning prismatic goggles, an error in pointing movement was observed immediately during the first trial. The error was minimized, however, after performing the movement to and fro with goggles on for 5 min. This showed that adaptation did indeed occur. Interestingly, when aiming movements were performed with the wrist, such adaptation was restricted to the wrist, itself. In contrast, with elbow aiming movements, adaptation extended to elbow and wrist movements, and it extended to all three joints with shoulder aiming movements. Later, a generalized recalibration effect was shown with rotatory aiming movements of the head. This suggested a " … segmentation of the body schema into sub-spaces interleaved in a proximo-distal hierarchical structure, and dominated by the head segment …" (p. 173 in Paillard (1991b)).

4.3. *Spatial representation in visuomotor reaching tasks*

Internal representations within the CNS are described by psychologists as " … images embodied in an iconic code or as mental representations encoded in an abstract or symbolic form" (p. 174 in Paillard (1991b)). Neurobiologists distinguish between "projection maps," which are relatively isomorphic with their arrangement of sensory receptors (e.g., neocortical sensory maps), and "computational maps," which extract place codes from different input signals, without preserving any topographical arrangement of their constituent neurons (e.g., place cells in the hippocampus; Rolls, 1991). Spatial representation maps are somewhat like the computational maps of conventional neuromimetic networks but they differ from them in that " … the computational networks do not close the external loop between motor output and reafferent input" (p.174 in Paillard (1991b)). This was the key point in

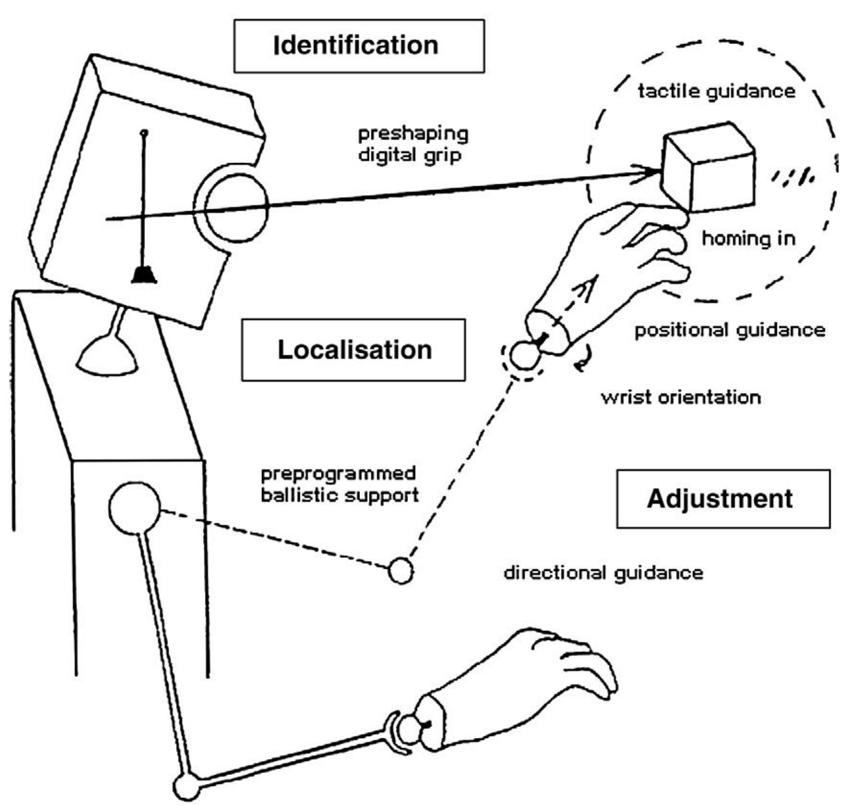

Fig. 6 – Schematic representation of the three fundamental visuomotor operations – identification, localization, adjustment – as a subject reaches to grasp an object. From Fig. 1 in Paillard (2000) with permission of the publisher.

Paillard's concept of spatial representation maps. He believed that " … 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. … 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 co-variant 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 movements on the sensory inflow" (pp. 174–175 in Paillard (1991b)).

Paillard's spatial representation maps assume an allocentric (space centered), environmentally stable frame of reference. Representational maps differ from sensorimotor path structures in that they are predominantly tied to visual information about the environmental frame, whereas path structures are closely linked to a proprioceptively defined postural frame of reference. How these two reference frames may interact and co-operate in a given movement is an important question that is still not fully resolved (see Arbib, 1991).

4.4. *Interactions between egocentric and allocentric reference frames during pointing*

Paillard and his co-workers used various pointing tasks to show that two visual feedback systems, foveal and peripheral, were involved in the guidance of a movement, as dependent on the phase of the task (Paillard, 1991c, 1996). Usually, the sight of the target initiated a task. The reaching movement included two key components: the ballistic transportation of the hand toward the target (transportation phase), and the terminal adjustment of the hand on the target. Concerning the visual retroactions in this task, Paillard's main interest was to identify their role in the guidance of the hand toward the target during the transportation phase and during the final adjustment (Fig. 6).

The Fig. 6 investigation was undertaken by Paillard and Daniel Beaubaton (1946–1986), who was his main co-worker for many years. Colin Trevarthen (Table 1) introduced them to the use of the split (including the optic chiasm)-brain monkey model, which he had studied previously in Sperry's laboratory. This preparation provides the means to test independently the role of the eye seeing the target vs. the moving hand vs. the side of the movement (Beaubaton et al., 1979). The work showed that the foveal visual system (shape recognizing system) was used not only for triggering the action but also for guiding the hand toward the target during the final phase of the movement. Peripheral (magnocellular) vision was involved in the transporting phase of hand movement. In the absence of vision of the target, it was possible to improve the precision of the movement by restricting vision to that of the hand movement during its trajectory (Conti and Beaubaton, 1976; Paillard, 1982). The improvement was attributable to the use of both visual systems: the dynamic magnocellular one, which was active during limb displacement; and, the more static parvocellular one, which came into play during the final adjustment of the hand to the target. This work, and its broad theoretical significance, have been further developed by the Jeannerod laboratory (e.g., Jeannerod and Prablanc, 1983).[11]

Both egocentric and allocentric reference frames were shown to be involved in a pointing task according to the visual conditions. For example, pointing was performed in one experiment under two conditions: to a luminous target in complete darkness vs. in a rich visual environment. The precision of the task was more accurate in the latter case. The interpretation of the result was that the oculocentric position of the target was calculated in two different reference frames. In the dark, using an egocentric reference frame, the direction of the target with respect to the body was calculated through the position of the eye in the orbit (proprioceptive or efference copy cues) and of the head with respect to the trunk. In contrast, in a rich visual environment, additional visual cues were present which allowed the target to be located in the allocentric environmental frame to which the body has also to be referred, thereby providing more precision in the perception of the target's position (Conti and Beaubaton, 1980).

Interactions between egocentric and allocentric reference frames were also shown to exist in a prismatic adaptation task (Paillard et al., 1981). Pointing movements were performed

[11] Somewhat different views on the central organization of reaching were proposed by Jacques Paillard and Marc Jeannerod. Paillard (1996) argued that errors in reaching movements were adjusted by (1) the foveal parvocellular visual pathway, which coded target position during the terminal phase of a movement, and (2) visual afferent "proprioceptive" input from the peripheral retina, when such afferents were activated by hand movement during the movement's trajectory. The delay of the movement's visual feedback varied according the type of experimental set-up and conditions, but it could be as short as 100 ms, which was compatible with an on-line correction. In contrast, Jeannerod (1991) considered that feedback visual delay was too long for fast on-line adjustments of human arm trajectories, particularly when they occurred during the double-step presentation of a target. In his interesting protocol, the subject had to track briefly presented visual targets by eye and by hand with no vision allowed of the moving hand, itself. Occasionally, the targets were presented as double steps. In such case, the first step (e.g., from 0° to 40°) was followed by a second step of smaller amplitude (e.g., from 40° to 44°), which was triggered at the time of maximum eye velocity. The distribution of pointing positions for double step trials was significantly shifted with respect to that of the corresponding single step trial, thereby indicating that subjects did correct their hand's trajectory in order to reach the final target positions. The increased duration in double step trials reflected only the additional distance that the hand had to move, thereby indicating that there was no reprogramming of movements to accommodate the secondary target's displacement. Jeannerod proposed the existence of a predictive internal model of the movement's final position that could be used as a reference to which the ongoing movement could be compared for the on-line calculation of errors in the execution of ongoing movement. In this model of fast on-line adjustments of a movement's trajectory, peripheral sensory signals are not used directly in a feedback mode, but rather for feedforward corrections of memorized information. Interestingly, a PET study (Desmurget et al., 2001) provided evidence for the contribution to Jeannerod's model of a restricted neural network, which included the posterior parietal cortex on one side, the contralateral intermediate cerebellum, and the ipsilateral motor cortex.

during the adaptation process using various visual conditions and active vs. passive movements. During active movements and exposure with prismatic goggles to the whole visual field resulted in an adaptation of 94%. Using foveal vision alone, however, the adaptation was reduced to not exceed 48% during both active and passive movements. Using peripheral vision alone, active movements adapted to 49%. In contrast, using peripheral vision alone, no significant adaptation of passive movements was observed. " … Our interpretation … was that adaptation provided by the peripheral vision might be driven by a reshaping of path structures in the egocentric frame of reference, which needs proprioceptive self induced reafferent 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 (*allocentric*) visual frame. In the latter case, interestingly, the nature of the movement – active or passive – is irrelevant to the recalibration process" (p. 178 in Paillard (1991b): see also Paillard and Amblard, 1985).

4.5. *Significance of body schema vs. body image, as illustrated by deafferented subjects*

Human pathology has provided interesting observations showing that an unconscious sensorimotor vectorial mapping of space in an egocentric reference frame can be identified in the absence of a representational conscious mapping of space in an allocentric reference frame. This dissociation has been described for the visual system as "blind sight" (Weiskrantz, 1989).

Paillard extended on the above observation in a study that included his above-mentioned subject, G.L., who is deafferented in all body segments except for the head. When her vision was prevented, she was unable to point with the right hand to a stimulated point on the left arm. She was well aware of the stimulated site, however, which she proved by accurately localizing the stimulated site both verbally and on a body picture. Thus, while G.L. was unable in the blindfolded condition to point with her finger in vectorial sensorimotor space, she could nonetheless localize the stimulus on her visual configural body image. A second patient in this study had a partial deafferentation of her right arm below the elbow with complete preservation of her motor control. When blindfolded, she was unable to detect and perceive any stimulation on her right hand. Much to her own surprise, however, she could point with her left hand to the stimulated places on her right hand. This phenomenon was considered equivalent to "blind sight" (Paillard et al., 1983). This latter subject was obviously unable to perceive her stimulated insentient hand by using her visually configured body image but she retained the ability to automatically move her left hand toward the correct stimulated place on her right hand using her proprioceptively framed body schema.

The above observations are in keeping with the classical description of a body schema, as provided by Head and Gordon Holmes (1876–1966). They argued that such a schema operated as a combined standard against which all changes of posture were measured (egocentric reference frame) before postural changes enter consciousness. They contrasted this to body image, which property they considered was necessary to provide an internal representation of the conscious experience of visual, tactile, and motor information of corporeal origin (allocentric reference frame) (Head and Holmes, 1912; see also p. 103–104 in Paillard (2005)).

4.6. *Summary on the framing of visually guided behavior*

In one of his 1991 review papers, Paillard emphasized that the distinction between egocentric and allocentric reference frames is generally accepted: " … My personal view has always been that both are basically derived from the geocentric framework (within which all terrestrial living have been moulded (Paillard, 1971) and that they cannot be studied independently. In fact, we have to consider that the framing of our visually guided behaviour in the 'locus space' depends on four fundamental referents organized around the invariant vertical organization of gravity forces" (p. 471 in Paillard (1991c); see also Berthoz, 1991). In this article, Paillard used Fig. 7 to comment further on his four fundamental referents and to emphasize the dominant role of the force of gravity.

For his Fig. 7 model Paillard argued that " … The *body frame* provides reference for posture and movements in all spatially oriented actions. The standing posture, which is actively maintained and species-specific, remains the main framework within which our environmental space is tailored for actions, and also the vertically oriented container for our perceptions (Paillard, 1971) … The *object frame* refers here to the object-centred view of the observer. We know that the recognition of an object depends on its orientation with respect to the direction of gravity forces or on its relationship to the orientation of the body axis. The perceived orientation of both body and object may also be dependent on environmental landmarks … The *world frame* includes both the object frame and the body frame as local spaces. Gravity forces also constrain the arrangement of physical matter around us. From our own limited living space,

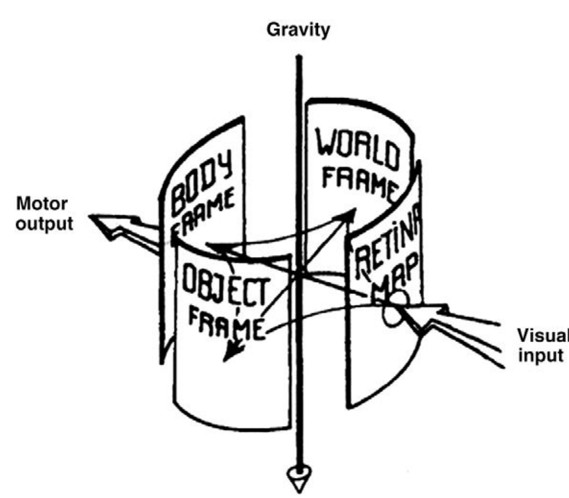

Fig. 7 – Paillard's conception of the four fundamental reference frames organized around the invariant vertical orientation of gravity forces, which together subserve visually guided behavior. From Fig. 24.1 in Paillard (1991c) with permission of the publisher.

the surface of water is perceived as a horizontal plane, and the trees as growing vertically. Accordingly, the basic natural spatial constraints of our terrestrial environment, which have moulded our body architecture during the course of evolution, compel our organism to accommodate a quasi-Euclidean space … Finally, the object and environmental frames are both derived from visual information that is first processed within the *retinal frame*. In most species with mobile eyes, this frame is automatically stabilized with respect to the horizon" (p. 471 in Paillard (1991c)).

In a schematic diagram (Fig. 24.2 in Paillard (1991c)), Paillard went on to show the parietal and temporal areas in which he thought processing of each frame takes place (area 5 for the body frame, infero-temporal cortex for the object frame, areas 7a and 7b for the world space and their connections; see also Stein, 1991). An interesting aspect of his gestalt is that his world frame included both body frame, which is egocentric, and object space, which is allocentric. The fast, unconscious trajectory corrections related to dynamic vision of movement in the egocentric frame coexist with slower corrections of the trajectory close to the target in an allocentric reference frame.

Note finally in Fig. 7 how Paillard illustrated his view that the ubiquitous geotropic (force of gravity) constraint dominates the four reference frames used in the visuomotor control of actions and perceptions and thereby becomes a crucial factor in linking them together.

5. Some summary thoughts on Paillard

As mentioned above, Paillard began his research career with a very elaborate and sophisticated view of the biological world. Throughout his subsequent scientific life, he tried to confirm his initial intuitive hypotheses, albeit learning much and modifying them along the way. He envisioned an evolutionistic world with some relatively rigid neural networks within the CNS of each species that could adapt substantially under selected circumstances. He thought the human species to be the major phylogenetic achievement to this point because of its progressively developing autonomy from the surrounding environmental medium.

Paillard emphasized that the motor system was controlled hierarchically with the spinal cord being at the base, the cerebrocortical areas at the summit, and the cerebellum with linkages to both and a crucial structure in motor learning. He considered the more basal structures to operate relatively rigidly and automatically in contrast to the higher structures' more elaborate and adaptable processing. This latter belief is reminiscent of the classical views of the British neurologist, Hughlings Jackson. Unique to Paillard, however, were his ideas on animals, including the human, attempting to master their environment by exploiting the self-organizing properties of their nervous systems.

Paillard analyzed many different types of behavior and even wrote a very long article in French on "consciousness" (Paillard, 1994), which included his attempt to define the term. He found it strange that most behaviorists rejected the functional significance of cerebrocortical activity and were seemingly content to view the CNS as a "black box". In this review he referred to a Fessard article written fifty years before when the midbrain reticular formation was considered as the "deus ex-machina" to explain all central activation (Fessard, 1953). Paillard's overall gestalt clearly emphasized the idea of "enduring" central CNS mechanisms, some relatively rigid and some very plastic. He was attracted to the concept that the CNS operated via modular structures as proposed by Fodor (1983).

After a long-sustained contact and innumerable conversations with him, the authors (particularly F.C. and J.M.) can say that Paillard was optimistic about science. He was not a "naive scientist" in the sense of those of the 19th C. and he recognized all the tragedies of the 20th C. He was Darwinian in his thinking, however, and he always believed that in the face of the different troubles and tragedies of life, the strong would survive. During the French students' revolution of May 1968, Paillard maintained a very open mind. In no way was he a demagogue but he argued forcefully for his students to face up to their responsibilities. Politically, he was to the left and often expressed the view that this had disadvantaged his administrative career.

Moreover, Paillard was always expectant of new trails being blazed in science, imagining that new experiments would explain many current unsolved problems. He, himself, was always dreaming up new experiments that would link different levels of analysis. For example, when considering the pyramidal tract, he opined that " … A neuro-ethological approach that combines micro-electrophysiological investigation ... with all the resources of a behavioural analysis, based on the ethology and including comparative studies, could provide the new tools we need to attack these problems with fresh thought. It may lead the way to a better understanding of the function of the pyramidal tract as well as the solution of many unanswered questions in classical neurophysiology" (p. 162 in Paillard (1978)).

Paillard often referred to synapses as being the fundamental elements of plasticity. Like most of the psychologists of his generation, he was influenced strongly by Donald Hebb (1904–1985) and his model of synaptic learning. In sharp contrast, he never considered neurotransmitter neuroscience, which developed remarkably throughout his scientific career. This was not in his "culture": his conception of the nervous apparatus was much more focused on complex wiring systems than the "soup" of neurochemical substances (Valenstein, 2005).

Paillard was an extraordinary teacher and, in most instances, a very good speaker. His lectures and seminars were always received with much enthusiasm. Fortunately, his conceptualizations on the motor system are available in excellent articles that demonstrate the brilliant and far reaching value of his intellectual contributions. In the field of movement neuroscience, Paillard was on the forefront among his peers in the transition from Sherrington thought in the early 20th C to the elaborate cognitive thought that is so evident at the beginning of 21st C.

6. Note added in proof

Two recent in-press articles by the same authors deserve mention in our present article. The first of these is: Will B., et al. The concept of brain plasticity-Paillard's systemic analysis and emphasis on structure and function (followed by the translation of a seminal paper by Paillard on plasticity). Behav Brain Res (2008) doi:10.1016/j.bbr.2007.11.008.

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