

Motor learning through the combination of primitives

F.A. Mussa Ivaldi and E. Bizzi

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Motor learning through the combination **of through the complete**
of primitives

F. A. Mussa-Ivaldi¹ and **E. Bizzi**^{2*}

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¹Department of Physiology, Northwestern University Medical School, Chicago, IL, USA

² Massachusetts Institute of Technology, Cambridge, MA, USA ²*Massachusetts Institute of Technology, Cambridge, MA, USA*

²*Massachusetts Institute of Technology, Cambridge, MA, USA*
In this paper we discuss a new perspective on how the central nervous system (CNS) represents and
solves some of the most fundamental computational problems o In this paper we discuss a new perspective on how the central nervous system (CNS) represents and solves some of the most fundamental computational problems of motor control. In particular, we consider the task of transfor In this paper we discuss a new perspective on how the central nervous system (CNS) represents and solves some of the most fundamental computational problems of motor control. In particular, we consider the task of transfor solves some of the most fundamental computational problems of motor control. In particular, we consider the task of transforming a planned limb movement into an adequate set of motor commands. To carry out this task the CN the task of transforming a planned limb movement into an adequate set of motor commands. To carry out is a hard computational challenge because of the need to coordinate multiple limb segments and because tion from a desired motion to the forces that are needed to drive the limb. The inverse dynamic problem
is a hard computational challenge because of the need to coordinate multiple limb segments and because
of the continuo is a hard computational challenge because of the need to coordinate multiple limb segments and because
of the continuous changes in the mechanical properties of the limbs and of the environment with which
they come in cont of the continuous changes in the mechanical properties of the limbs and of the environment with which
they come in contact. A number of studies of motor learning have provided support for the idea that the
CNS creates, upd they come in contact. A number of studies of motor learning have provided support for the idea that the CNS creates, updates and exploits internal representations of limb dynamics in order to deal with the complexity of in CNS creates, updates and exploits internal representations of limb dynamics in order to deal with the complexity of inverse dynamics. Here we discuss how such internal representations are likely to be built by combining th complexity of inverse dynamics. Here we discuss how such internal representations are likely to be built
by combining the modular primitives in the spinal cord as well as other building blocks found in higher
brain structu by combining the modular primitives in the spinal cord as well as other building blocks found in higher brain structures. Experimental studies on spinalized frogs and rats have led to the conclusion that the premotor circu brain structures. Experimental studies on spinalized frogs and rats have led to the conclusion that the premotor circuits within the spinal cord are organized into a set of discrete modules. Each module, when vectorial combination of the corresponding fields. We regard these force fields as computational primitives that are used by the CNS for generating a rich grammar of motor behaviours. activated, induces a specific force field and the simultaneous activation of multiple modules leads to the

Keywords: force field; dynamics; module; spinal cord; cortex; internal model

1. INTRODUCTION

1. INTRODUCTION
When we learn to move our limbs and to act upon the
environment our brain becomes to all effects an expert in ENTRODUCTION
When we learn to move our limbs and to act upon the
environment, our brain becomes to all effects an expert in
physics. While we are still very far away from under-When we learn to move our limbs and to act upon the
environment, our brain becomes to all effects an expert in
physics. While we are still very far away from under-
standing how this feat is accomplished great strides have environment, our brain becomes to all effects an expert in
physics. While we are still very far away from under-
standing how this feat is accomplished, great strides have
been made in the last few decades through the comb physics. While we are still very far away from understanding how this feat is accomplished, great strides have
been made in the last few decades through the combined
efforts of biologists computer scientists physicians phy standing how this feat is accomplished, great strides have
been made in the last few decades through the combined
efforts of biologists, computer scientists, physicians, physibeen made in the last few decades through the combined
efforts of biologists, computer scientists, physicians, physi-
cists, psychologists and engineers. In this paper we review
some of this progress. In particular we focu efforts of biologists, computer scientists, physicians, physicists, psychologists and engineers. In this paper we review
some of this progress. In particular we focus on one issue:
What are the building blocks or to borrow cists, psychologists and engineers. In this paper we review
some of this progress. In particular we focus on one issue:
What are the building blocks or, to borrow from linguis-
ties, the 'modules' that the brain may use fo some of this progress. In particular we focus on one issue:
What are the building blocks or, to borrow from linguistics, the 'modules' that the brain may use for generating What are the building blocks or, to borrow from linguistics, the 'modules' that the brain may use for generating the competence in physics that is necessary to act and move? And what do we know of how and where these tics, the 'modules' that the brain may use for generating
the competence in physics that is necessary to act and
move? And what do we know of how and where these
modules are engraved into the circuits of the central the competence in physics that is necessary to act and
move? And what do we know of how and where these
modules are engraved into the circuits of the central
nervous system (CNS)? In move? And what do we know of how and where these modules are engraved into the circuits of the central \bigcup nervous system (CNS)? − modules are engraved into the circuits of the central

● nervous system (CNS)?

● To illustrate the complexities of ordinary motor beha-

→ viours, let us consider the task that the CNS must solve

To illustrate the complexities of ordinary motor beha-To illustrate the complexities of ordinary motor behaviours, let us consider the task that the CNS must solve every time a planned gesture is transformed into an action. If the goal is to move the band from an initial viours, let us consider the task that the CNS must solve
every time a planned gesture is transformed into an
action. If the goal is to move the hand from an initial
position to another point in space, then clearly there ar every time a planned gesture is transformed into an action. If the goal is to move the hand from an initial position to another point in space, then clearly there are a number of possible hand trajectories that could achie action. If the goal is to move the hand from an initial
position to another point in space, then clearly there are
a number of possible hand trajectories that could achieve
this goal: the solution of this elementary motor position to another point in space, then clearly there are
a number of possible hand trajectories that could achieve
this goal: the solution of this elementary motor problem a number of possible hand trajectories that could achieve
this goal: the solution of this elementary motor problem
is not unique. Even after the CNS has chosen a particular
path for the band, its implementation can be achi this goal: the solution of this elementary motor problem
is not unique. Even after the CNS has chosen a particular
path for the hand, its implementation can be achieved
through multiple combinations of joint motions at the is not unique. Even after the CNS has chosen a particular
path for the hand, its implementation can be achieved
through multiple combinations of joint motions at the
shoulder, elbow and wrist—again the solution is not path for the hand, its implementation can be achieved
through multiple combinations of joint motions at the
shoulder, elbow and wrist—again the solution is not

unique. Finally, because there are many muscles around unique. Finally, because there are many muscles around
each joint, the net force generated by their activation can
be produced by a variety of combinations of muscles be produced by a variety of combinations of muscles.
Perhaps what makes the issue of sensorimotor transducch joint, the net force generated by their activation can
produced by a variety of combinations of muscles.
Perhaps what makes the issue of sensorimotor transduc-
pn such a complex problem is the fact that we have not

the produced by a variety of combinations of muscles.
Perhaps what makes the issue of sensorimotor transduction such a complex problem is the fact that we have not
found a satisfactory way to incorporate motor learning Perhaps what makes the issue of sensorimotor transduction such a complex problem is the fact that we have not found a satisfactory way to incorporate motor learning into our thinking about motor planning While everybody tion such a complex problem is the fact that we have not
found a satisfactory way to incorporate motor learning
into our thinking about motor planning. While everybody
agrees that throughout our life we learn a great varie found a satisfactory way to incorporate motor learning
into our thinking about motor planning. While everybody
agrees that throughout our life we learn a great variety of into our thinking about motor planning. While everybody
agrees that throughout our life we learn a great variety of
movements and that the memory of these movements is
stored more or less nermanently in the cortical areas agrees that throughout our life we learn a great variety of
movements and that the memory of these movements is
stored more or less permanently in the cortical areas of
the frontal and parietal lobes and the cerebellum, we movements and that the memory of these movements is
stored more or less permanently in the cortical areas of
the frontal and parietal lobes and the cerebellum, we do
not know whether we use framents of what has been stored more or less permanently in the cortical areas of the frontal and parietal lobes and the cerebellum, we do not know whether we use fragments of what has been learned when we produce a motor response to a new the frontal and parietal lobes and the cerebellum, we do not know whether we use fragments of what has been
learned when we produce a motor response to a new
contingency (Toni *et al.* 1998; Shadmehr & Holcomb
1997) In this paper we adopt the point of view that motor 1997) In this paper we adopt the point of view that motor
1997) In this paper we adopt the point of view that motor
1997) In this paper we adopt the point of view that motor
1997) In this paper we adopt the point of view t contingency (Toni *et al.* 1998; Shadmehr & Holcomb 1997) In this paper we adopt the point of view that motor learning consists of tuning the activity of a relatively small group of peurons and that these peurons constitu 1997) In this paper we adopt the point of view that motor
learning consists of tuning the activity of a relatively
small group of neurons and that these neurons constitute
a 'module' Combining modules may be a mechanism f learning consists of tuning the activity of a relatively
small group of neurons and that these neurons constitute
a 'module'. Combining modules may be a mechanism for
producing a vast repertoire of motor behaviours in a small group of neurons and that these neurons constitute a 'module'. Combining modules may be a mechanism for producing a vast repertoire of motor behaviours in a simple manner. producing a vast repertoire of motor behaviours in a

2. THE PROBLEM OF INVERSE DYNAMICS

According to the laws of Newtonian physics, if we want to impress a motion upon a stone with mass *^m*, we must According to the laws of Newtonian physics, if we want
to impress a motion upon a stone with mass m , we must
apply a force, F , that is directly proportional to the
desired acceleration a . This is the essence of Newt to impress a motion upon a stone with mass m , we must
apply a force, F , that is directly proportional to the
desired acceleration, a . This is the essence of Newton's
equation $F - ma$. A desired motion may be expressed apply a force, F , that is directly proportional to the desired acceleration, a . This is the essence of Newton's equation $F = ma$. A desired motion may be expressed as a sequence of positions x that we wish the stone t desired acceleration, *a*. This is the essence of Newton's equation $F = ma$. A desired motion may be expressed as a sequence of positions, *x*, that we wish the stone to assume

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at subsequent instants of time, *^t*. This sequence is called a `trajectory' and is mathematically represented as a funcat subsequent instants of time, *t*. This sequence is called a 'trajectory' and is mathematically represented as a function, $x = x(t)$. To use Newton's equation for deriving the needed time sequence of forces we must calcul 'trajectory' and is mathematically represented as a function, $x = x(t)$. To use Newton's equation for deriving the needed time sequence of forces, we must calculate the first temporal derivative of the trajectory the veloci tion, $x = x(t)$. To use Newton's equation for deriving the needed time sequence of forces, we must calculate the first temporal derivative of the trajectory, the velocity and then the second temporal derivative the accelera needed time sequence of forces, we must calculate the first temporal derivative of the trajectory, the velocity and then the second temporal derivative, the acceleration. temporal derivative of the trajectory, the velocity and
then the second temporal derivative, the acceleration.
Finally, we obtain the desired force from this acceleration.
The above calculation is an example of what in rob then the second temporal derivative, the acceleration.
Finally, we obtain the desired force from this acceleration.
The above calculation is an example of what in robotics
is called an 'inverse dynamic problem'. The 'direc Finally, we obtain the desired force from this acceleration.
The above calculation is an example of what in robotics
is called an 'inverse dynamic problem'. The 'direct'
dynamic problem is that of computing the trajectory The above calculation is an example of what in robotics
is called an 'inverse dynamic problem'. The 'direct'
dynamic problem is that of computing the trajectory
resulting from the application of a force $F(t)$. The solutio is called an 'inverse dynamic problem'. The 'direct' dynamic problem is that of computing the trajectory resulting from the application of a force, $F(t)$. The solution of this problem requires a complex computational dynamic problem is that of computing the trajectory
resulting from the application of a force, $F(t)$. The solution
of this problem requires a complex computational
process called integration through which the motion of resulting from the application of a force, $F(t)$. The solution of this problem requires a complex computational process, called integration, through which the motion of the stone that is the function $x(t)$ is derived from of this problem requires a complex computational
process, called integration, through which the motion of
the stone, that is the function $x(t)$, is derived from the
known acceleration $a(t) = F(t)/m$ process, called integration, through which the motion of
the stone, that is the function $x(t)$, is derived from the
known acceleration, $a(t) = F(t)/m$.
Direct problems are the bread and butter of physicists,
who may be concer

known acceleration, $a(t) = F(t)/m$.
Direct problems are the bread and butter of physicists,
who may be concerned, for example, with predicting the
motion of a comet from the known pattern of gravita-Direct problems are the bread and butter of physicists,
who may be concerned, for example, with predicting the
motion of a comet from the known pattern of gravita-
tional forces. Unlike physicists, the brain deals most oft Omotion of a comet from the known pattern of gravita-

ional forces. Unlike physicists, the brain deals most often

with inverse problems: we routinely recognize objects and

differences between the multijoint vertebrate s motion of a comet from the known pattern of gravitational forces. Unlike physicists, the brain deals most often with inverse problems: we routinely recognize objects and people from their visual images—an 'inverse optical tional forces. Unlike physicists, the brain deals most often
with inverse problems: we routinely recognize objects and
people from their visual images—an 'inverse optical
problem'—and we find out effortlessly how to distri with inverse problems: we routinely recognize objects and
people from their visual images—an 'inverse optical
problem'—and we find out effortlessly how to distribute
the forces exerted by several muscles to move our limb i people from their visual images—an 'inverse optical
problem'—and we find out effortlessly how to distribute
the forces exerted by several muscles to move our limb in
the desired way—an inverse dynamic problem problem²—and we find out effortlessly how to distribute
the forces exerted by several muscles to move our limb in
 $\bigcap_{n=0}^{\infty}$ the desired way—an inverse dynamic problem.

Exercise exerted by several muscles to move our limb in

Exercise dynamic problem.

In the biological context, the inverse dynamic problem

In the biological context, the inverse dynamic problem

sumes a somewhat different the desired way—an inverse dynamic problem.
In the biological context, the inverse dynamic problem
assumes a somewhat different form from the case of the
moving stone. One of the central questions in motor In the biological context, the inverse dynamic problem
assumes a somewhat different form from the case of the
moving stone. One of the central questions in motor
control is how the CNS may form the motor commands assumes a somewhat different form from the case of the
moving stone. One of the central questions in motor
control is how the CNS may form the motor commands
that guide our limbs. One proposal is that the CNS solves moving stone. One of the central questions in motor control is how the CNS may form the motor commands that guide our limbs. One proposal is that the CNS solves an inverse dynamic problem (Hollerbach $\&$ Elash 1982) control is how the CNS may form the motor commands
that guide our limbs. One proposal is that the CNS solves
an inverse dynamic problem (Hollerbach & Flash 1982).
A system of second-order nonlinear differential equations that guide our limbs. One proposal is that the CNS solves
an inverse dynamic problem (Hollerbach & Flash 1982).
A system of second-order nonlinear differential equations an inverse dynamic problem (Hollerbach & Flash 1982).
A system of second-order nonlinear differential equations
is generally considered to be an adequate description of
the passive limb dynamics. A compact representation f A system of second-order nonlinear differential equations
is generally considered to be an adequate description of
the passive limb dynamics. A compact representation for
such a system is is generally consider
the passive limb d
such a system is

$$
D(q, \dot{q}, \ddot{q}) = \tau(t), \qquad (1a)
$$

 $D(q, \dot{q}, \ddot{q}) = \tau(t)$, (1*a*)
where *q*, *q* and *q* represent the limb configuration
wetter—for example the vector of joint angles—and its where q, \dot{q} and \ddot{q} represent the limb configuration
vector—for example, the vector of joint angles—and its
first and second time derivatives. The term $\tau(t)$ is a vector where q , \dot{q} and \ddot{q} represent the limb configuration vector—for example, the vector of joint angles—and its first and second time derivatives. The term $\tau(t)$ is a vector of generalized forces for example join vector—for example, the vector of joint angles—and its
first and second time derivatives. The term $\tau(t)$ is a vector
of generalized forces, for example, joint torques, at time *t*.
Conceptually, this expression is nothin of generalized forces, for example, joint torques, at time *t*.
Conceptually, this expression is nothing else than
Newton's $F = ma$ applied to a multi-articular rigid body. Conceptually, this expression is nothing else than
Newton's $F = ma$ applied to a multi-articular rigid body.
In practice, the expression for *D* may have a few terms
for a two-ioint planar arm (see figure 4b) or it may take Newton's $F = ma$ applied to a multi-articular rigid body.
In practice, the expression for D may have a few terms
for a two-joint planar arm (see figure 4*b*) or it may take
several pages for more realistic models of the arm In practice, the expression for D may have a few terms
for a two-joint planar arm (see figure $4b$) or it may take
several pages for more realistic models of the arm's multi-
ioint geometry. The inverse dynamic approach for a two-joint planar arm (see figure $4b$) or it may take
several pages for more realistic models of the arm's multi-
joint geometry. The inverse dynamic approach to the
control of multiioint limbs consists in solving e several pages for more realistic models of the arm's multi-
joint geometry. The inverse dynamic approach to the
control of multijoint limbs consists in solving explicitly for
a torque trajectory $\tau(t)$ given a desired tra control of multijoint limbs consists in solving explicitly for a torque trajectory, $\tau(t)$, given a desired trajectory of the control of multijoint limbs consists in solving explicitly for
a torque trajectory, $\tau(t)$, given a desired trajectory of the
limb, $q_D(t)$. This is done by plugging $q_D(t)$ on the left side
of equation (1): a torque trajecto:

limb, $q_D(t)$. This

of equation (1):

$$
\mathbf{t}(t) = D(q_D(t), \dot{q}_D(t), \ddot{q}_D(t)). \tag{1b}
$$

Another significant computational challenge comes FROM HOW HOW
Another significant computational challenge comes
from the need to perform changes of representation, or,
more technically coordinate transformations, between Another significant computational challenge comes
from the need to perform changes of representation, or,
more technically, coordinate transformations, between
the description of a task and the specification of the body from the need to perform changes of representation, or,
more technically, coordinate transformations, between
the description of a task and the specification of the body
motions. Tasks, such as 'bring the band to the glass more technically, coordinate transformations, between
the description of a task and the specification of the body
motions. Tasks, such as 'bring the hand to the glass of
water on the table' are often described most efficie the description of a task and the specification of the body
motions. Tasks, such as 'bring the hand to the glass of
water on the table', are often described most efficiently
and parsimoniously with repect to fixed referenc motions. Tasks, such as 'bring the hand to the glass of water on the table', are often described most efficiently and parsimoniously with respect to fixed reference points in the environment. For example, the glass may be water on the table', are often described most efficiently
and parsimoniously with respect to fixed reference points
in the environment. For example, the glass may be 10 cm
to the left of a corner of the table. The hand may and parsimoniously with respect to fixed reference points
in the environment. For example, the glass may be 10 cm
to the left of a corner of the table. The hand may be
20 cm to the right of the same corner. So, the hand wi in the environment. For example, the glass may be 10 cm
to the left of a corner of the table. The hand may be
20 cm to the right of the same corner. So, the hand will

need to be displaced 30 cm along a straight line in the left
direction. This is a very simple description of the needed need to be displaced 30 cm along a straight line in the left
direction. This is a very simple description of the needed
movement. However, this description cannot be used to meed to be displaced 30 cm along a straight line in the left
direction. This is a very simple description of the needed
movement. However, this description cannot be used to
derive the joint torques as specified by equati direction. This is a very simple description of the needed
movement. However, this description cannot be used to
derive the joint torques, as specified by equation (1*b*). To
this end, one must represent the trajectory of movement. However, this description cannot be used to derive the joint torques, as specified by equation (lb) . To this end, one must represent the trajectory of the hand in terms of the corresponding angular motions at e derive the joint torques, as specified by equation $(1b)$. To this end, one must represent the trajectory of the hand in terms of the corresponding angular motions at each joint. This is a complex transformation known in this end, one must represent the trajectory of the hand in
terms of the corresponding angular motions at each joint.
This is a complex transformation known in robotics as
'inverse kinematics' (Brady et al. 1982) terms of the corresponding angular motions at each joint.
This is a complex transformation known in robotics as

'inverse kinematics' (Brady *et al.* 1982).

Does the brain carry out similar inverse dynamic is is a complex transformation known in robotics as
werse kinematics' (Brady *et al.* 1982).
Does the brain carry out similar inverse dynamic
leulations for moving the arm on a desired trajectory?

The intersect increases in the brain carry out similar inverse dynamic calculations for moving the arm on a desired trajectory?
A clear-cut answer is still to come but several alternatives Does the brain carry out similar inverse dynamic
calculations for moving the arm on a desired trajectory?
A clear-cut answer is still to come but several alternatives
have emerged from studies in robotics and computational calculations for moving the arm on a desired trajectory?
A clear-cut answer is still to come but several alternatives
have emerged from studies in robotics and computational
neuroscience neuroscience.

3. SOLUTIONS BASED ON FEEDBACK

Many of the problems that the brain must face to S. SOLUTIONS BASED ON FEEDBACK

Many of the problems that the brain must face to

control movements are indeed similar to those that engi-

neers must solve to control robots. In spite of the great Many of the problems that the brain must face to control movements are indeed similar to those that engineers must solve to control robots. In spite of the great differences between the multiioint vertebrate system and differences between the multijoint vertebrate system and neers must solve to control robots. In spite of the great
differences between the multijoint vertebrate system and
current robotic arms, the field of neuroscience, unques-
tionably has derived benefits from the theories an differences between the multijoint vertebrate system and
current robotic arms, the field of neuroscience, unques-
tionably, has derived benefits from the theories and proce-
dures that have guided the construction of man-m current robotic arms, the field of neuroscience, unquestionably, has derived benefits from the theories and procedures that have guided the construction of man-made limbs. For instance, from early on neuroscientists have tionably, has derived benefits from the theories and procedures that have guided the construction of man-made limbs. For instance, from early on, neuroscientists have dures that have guided the construction of man-made
limbs. For instance, from early on, neuroscientists have
been influenced by the notion of feedback. Feedback
control is a way to circumvent the computation of inverse limbs. For instance, from early on, neuroscientists have
been influenced by the notion of feedback. Feedback
control is a way to circumvent the computation of inverse
dynamics. At each point in time, some sensory signal control is a way to circumvent the computation of inverse dynamics. At each point in time, some sensory signal control is a way to circumvent the computation of inverse
dynamics. At each point in time, some sensory signal
provides the information about the actual position of the
limb. This position is compared with a desired positi dynamics. At each point in time, some sensory signal
provides the information about the actual position of the
limb. This position is compared with a desired position
and the difference between the two is a measure of the provides the information about the actual position of the
limb. This position is compared with a desired position
and the difference between the two is a measure of the
error at any given time. Then a force may be produced limb. This position is compared with a desired position and the difference between the two is a measure of the error at any given time. Then, a force may be produced and the difference between the two is a measure of the error at any given time. Then, a force may be produced with amplitude approximately proportional to the amplitude of the error in the direction of the desired position error at any given time. Then, a force may be produced
with amplitude approximately proportional to the ampli-
tude of the error in the direction of the desired position.
This method of control is appealing because of its with amplitude approximately proportional to the amplitude of the error in the direction of the desired position.
This method of control is appealing because of its great simplicity simplicity. This method of control is appealing because of its great
simplicity.
Multiple feedback mechanisms have been found in

simplicity.

Multiple feedback mechanisms have been found in

both vertebrates and invertebrates. These mechanisms

were discovered by Sherrington at the beginning of the Multiple feedback mechanisms have been found in
both vertebrates and invertebrates. These mechanisms
were discovered by Sherrington at the beginning of the
last century (Sherrington 1910) They have been shown to both vertebrates and invertebrates. These mechanisms
were discovered by Sherrington at the beginning of the
last century (Sherrington 1910). They have been shown to
control the muscles' level of contraction, the production were discovered by Sherrington at the beginning of the
last century (Sherrington 1910). They have been shown to
control the muscles' level of contraction, the production
of force and the position of joints. Sherrington obs last century (Sherrington 1910). They have been shown to control the muscles' level of contraction, the production of force and the position of joints. Sherrington observed that when a muscle is stretched the stretch is co control the muscles' level of contraction, the production
of force and the position of joints. Sherrington observed
that when a muscle is stretched the stretch is countered of force and the position of joints. Sherrington observed
that when a muscle is stretched the stretch is countered
by an increase in muscle activation. This 'stretch reflex' is
caused by sensory activity that originates in that when a muscle is stretched the stretch is countered
by an increase in muscle activation. This 'stretch reflex' is
caused by sensory activity that originates in the muscle
spindles—receptors embedded within the muscle by an increase in muscle activation. This 'stretch reflex' is
caused by sensory activity that originates in the muscle
spindles—receptors embedded within the muscle fibres.
Sherrington put forward the daring hypothesis tha caused by sensory activity that originates in the muscle spindles—receptors embedded within the muscle fibres. spindles—receptors embedded within the muscle fibres.
Sherrington put forward the daring hypothesis that
complex movements may be obtained by combining
stretch reflexes as well as other reflexes in a continuous Sherrington put forward the daring hypothesis that
complex movements may be obtained by combining
stretch reflexes as well as other reflexes in a continuous
sequence or 'chain'. In this way movement patterns as complex movements may be obtained by combining
stretch reflexes as well as other reflexes in a continuous
sequence or 'chain'. In this way, movement patterns as complex as the locomotion cycle could be generated by sequence or 'chain'. In this way, movement patterns as
complex as the locomotion cycle could be generated by
local reflexes, without central supervision. A similar idea
was later proposed by Merton (1972) who suggested tha complex as the locomotion cycle could be generated by
local reflexes, without central supervision. A similar idea
was later proposed by Merton (1972), who suggested that
central commands via the gamma system might initiate local reflexes, without central supervision. A similar idea
was later proposed by Merton (1972), who suggested that
central commands via the gamma system might initiate
the execution of movement, not by directly activating was later proposed by Merton (1972), who suggested that
central commands via the gamma system might initiate
the execution of movement, not by directly activating the
muscles, but by triggering a stretch reflex through the central commands via the gamma system might initiate
the execution of movement, not by directly activating the
muscles, but by triggering a stretch reflex through the
modulation of muscle mindle activities. Both Sherringto the execution of movement, not by directly activating the
muscles, but by triggering a stretch reflex through the
modulation of muscle spindle activities. Both Sherrington
and Merton's hypotheses are attempts at explaining muscles, but by triggering a stretch reflex through the
modulation of muscle spindle activities. Both Sherrington
and Merton's hypotheses are attempts at explaining
movements as automatic responses to sensory feedback modulation of muscle spindle activities. Both Sherrington
and Merton's hypotheses are attempts at explaining
movements as automatic responses to sensory feedback,
thus limiting the role and the arbitrariness of voluntary and Merton's hypotheses are attempts at explaining
movements as automatic responses to sensory feedback,
thus limiting the role and the arbitrariness of voluntary
commands commands. thus limiting the role and the arbitrariness of voluntary
commands.
However, both Sherrington's ideas on compounding of

reflexes and Merrington's ideas on compounding of
reflexes and Merton's hypothesis have taken a new
form following subsequent experiments which clearly However, both Sherrington's ideas on compounding of
reflexes and Merton's hypothesis have taken a new
form following subsequent experiments which clearly

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demonstrated the generation of movements in the absence
of sensory activities. For example Taub & Berman (1968) demonstrated the generation of movements in the absence
of sensory activities. For example, Taub & Berman (1968)
found that monkeys can execute various limb movements demonstrated the generation of movements in the absence
of sensory activities. For example, Taub & Berman (1968)
found that monkeys can execute various limb movements
after the surgical section of the pathways that convey of sensory activities. For example, Taub & Berman (1968)
found that monkeys can execute various limb movements
after the surgical section of the pathways that convey all
sensory information from the limb to the nervous sys found that monkeys can execute various limb movements
after the surgical section of the pathways that convey all
sensory information from the limb to the nervous system.
Shortly thereafter Vallbo (1970) was able to record after the surgical section of the pathways that convey all
sensory information from the limb to the nervous system.
Shortly thereafter, Vallbo (1970) was able to record sensory information from the limb to the nervous system.
Shortly thereafter, Vallbo (1970) was able to record
muscle spindle discharges in human subjects and to
compare these discharges with the activation of the Shortly thereafter, Vallbo (1970) was able to record muscle spindle discharges in human subjects and to compare these discharges with the activation of the muscles as revealed by electromy ography (EMG) Vallbo's muscle spindle discharges in human subjects and to
compare these discharges with the activation of the
muscles, as revealed by electromyography (EMG). Vallbo's
study showed that in a voluntary movement muscle acticompare these discharges with the activation of the muscles, as revealed by electromyography (EMG). Vallbo's study showed that, in a voluntary movement, muscle activation does not lag but leads the spindle discharges, contrary to the predictions of Merton's hypothesis. study showed that, in a voluntary movement, muscle
vation does not lag but leads the spindle disch
contrary to the predictions of Merton's hypothesis.
In addition to the experimental findings desc In the spindle discharges,
In addition to the experimental findings described
over the idea that biological movements may be carried

In addition to the experimental findings described above, the idea that biological movements may be carried In addition to the experimental findings described
above, the idea that biological movements may be carried
out by feedback mechanism has been challenged based on
consideration about limb stability and reflex delays. It above, the idea that biological movements may be carried
out by feedback mechanism has been challenged based on
consideration about limb stability and reflex delays. It
takes more than 40 ms before a signal generated by th out by feedback mechanism has been challenged based on
consideration about limb stability and reflex delays. It
takes more than 40 ms before a signal generated by the
muscle spindles may reach the supraspinal motor centres consideration about limb stability and reflex delays. It
takes more than 40 ms before a signal generated by the
muscle spindles may reach the supraspinal motor centres
and it takes $40-60$ ms more before a motor command takes more than 40 ms before a signal generated by the muscle spindles may reach the supraspinal motor centres and it takes $40-60 \text{ ms}$ more before a motor command may be transformed into a measurable contraction of and it takes $40-60 \text{ ms}$ more before a motor command
may be transformed into a measurable contraction of the and it takes $40-60$ ms more before a motor command
may be transformed into a measurable contraction of the
muscles. These transmission delays may cause instability
(Hogan *et al.* 1987) The effects of delays are even gre may be transformed into a measurable contraction of the muscles. These transmission delays may cause instability (Hogan *et al.* 1987). The effects of delays are even greater when the limb interacts with the environment Fo muscles. These transmission delays may cause instability
(Hogan *et al.* 1987). The effects of delays are even greater
when the limb interacts with the environment. For
example if a robotic arm were to contact a rigid sur (Hogan *et al.* 1987). The effects of delays are even greater when the limb interacts with the environment. For example, if a robotic arm were to contact a rigid surface, a delay of 30 ms would initiate a bouncing mot when the limb interacts with the environment. For
example, if a robotic arm were to contact a rigid surface,
a delay of 30 ms would initiate a bouncing motion also
known as 'chattering' instability. This instability is aga example, if a robotic arm were to contact a rigid surface,
a delay of 30 ms would initiate a bouncing motion also
known as 'chattering' instability. This instability is again
due to the fact that the control system could d a delay of 30 ms would initiate a bouncing motion also
known as 'chattering' instability. This instability is again
due to the fact that the control system could detect the
contact only after it has occurred. This would ca known as 'chattering' instability. This instability is again
due to the fact that the control system could detect the
contact only after it has occurred. This would cause a
hack-un motion that would move the arm away from due to the fact that the control system could detect the
contact only after it has occurred. This would cause a
back-up motion that would move the arm away from the
surface. Then, the controller would move again towards contact only after it has occurred. This would cause a
back-up motion that would move the arm away from the
surface. Then, the controller would move again towards
the surface and so on in a repeated bouncing motion back-up motion that would move the arm away from the surface. Then, the controller would move again towards the surface and so on in a repeated bouncing motion.

4. SOLUTIONS BASED ON FEED-FORWARD

An alternative to feedback control would be for the CNS to pre-programme the torques that the muscles must An alternative to feedback control would be for the
CNS to pre-programme the torques that the muscles must
generate for moving the limbs along the desired trajec-
tories. This method is often referred to as 'feed-forward CNS to pre-programme the torques that the muscles must
generate for moving the limbs along the desired trajec-
tories. This method is often referred to as 'feed-forward
control'. The torques needed to move the arm can only generate for moving the limbs along the desired trajectories. This method is often referred to as 'feed-forward
control'. The torques needed to move the arm can only be
computed after the angular motions of the shoulder tories. This method is often referred to as 'feed-forward
control'. The torques needed to move the arm can only be
computed after the angular motions of the shoulder,
elbow and wrist have been derived from the desired control'. The torques needed to move the arm can only be
computed after the angular motions of the shoulder,
elbow and wrist have been derived from the desired
movement of the hand—that is after an inverse kinecomputed after the angular motions of the shoulder, elbow and wrist have been derived from the desired movement of the hand—that is after an inverse kinematics problem has been solved. Investigations in robot movement of the hand—that is after an inverse kine-
matics problem has been solved. Investigations in robot
control in the late 1970s and early 1980s showed that both
the inverse kinematic and inverse dynamic problems may matics problem has been solved. Investigations in robot
control in the late 1970s and early 1980s showed that both
the inverse kinematic and inverse dynamic problems may
be efficiently implemented in a digital computer for control in the late 1970s and early 1980s showed that both
the inverse kinematic and inverse dynamic problems may
be efficiently implemented in a digital computer for many
robot geometries (Brady *et al.* 1982). On the ba the inverse kinematic and inverse dynamic problems may
be efficiently implemented in a digital computer for many
robot geometries (Brady *et al.* 1982). On the basis of these
studies Hollerbach & Elash (1982) put forward t be efficiently implemented in a digital computer for many
robot geometries (Brady *et al.* 1982). On the basis of these
studies, Hollerbach & Flash (1982) put forward the
hypothesis that the brain may be carrying out inver robot geometries (Brady *et al.* 1982). On the basis of these \overline{H} studies, Hollerbach & Flash (1982) put forward the hypothesis that the brain may be carrying out inverse \bigcup kinematic and dynamic computations when moving the hypothesis that the brain may be carrying out inverse
kinematic and dynamic computations when moving the
arm in a purposeful way. Their experimental investigation
of arm-reaching movements combined with inverse kinematic and dynamic computations when moving the
arm in a purposeful way. Their experimental investigation
of arm-reaching movements, combined with inverse
dynamics calculations showed that all components of the arm in a purposeful way. Their experimental investigation
of arm-reaching movements, combined with inverse
dynamics calculations, showed that all components of the
ioint torque played a critical role in the generation of t % of arm-reaching movements, combined with inverse
dynamics calculations, showed that all components of the
joint torque played a critical role in the generation of the
observed hand trajectories. In particular, Hollerbac dynamics calculations, showed that all components of the
joint torque played a critical role in the generation of the
observed hand trajectories. In particular, Hollerbach &
Elash found that while executing reaching moveme Figure 5 in the generation of the observed hand trajectories. In particular, Hollerbach & Flash found that while executing reaching movements the subjects were accurately compensating for the dynamic observed hand trajectories. In particular, Hollerbach &
Flash found that while executing reaching movements the
subjects were accurately compensating for the dynamic
interactions between shoulder and elbow joints Flash found that while executing reaching mover
subjects were accurately compensating for the
interactions between shoulder and elbow joints.
Evidence that the brain is carefully compensed

bjects were accurately compensating for the dynamic
eractions between shoulder and elbow joints.
Evidence that the brain is carefully compensating for
a interaction torques was further provided by more interactions between shoulder and elbow joints.
Evidence that the brain is carefully compensating for
the interaction torques was further provided by more
recent studies of Gbez and of Thach and their co-workers Evidence that the brain is carefully compensating for
the interaction torques was further provided by more
recent studies of Ghez and of Thach and their co-workers.
Sainburg et al. (1993) studied the movements of subjects the interaction torques was further provided by more
recent studies of Ghez and of Thach and their co-workers.
Sainburg *et al.* (1993) studied the movements of subjects
suffering from a rare peripheral neuronathy. A conse recent studies of Ghez and of Thach and their co-workers.
Sainburg et al. (1993) studied the movements of subjects
suffering from a rare peripheral neuropathy. A conse-

bination of primitives F. A. Mussa-Ivaldi and E. Bizzi 1757
quence of this disease is the complete loss of proprioceptive information from the upper and lower limbs. These quence of this disease is the complete loss of proprioceptive information from the upper and lower limbs. These investigators found that the abnormal motions observed in these subjects could be accounted for by lack of tive information from the upper and lower limbs. These
investigators found that the abnormal motions observed
in these subjects could be accounted for by lack of
compensation for the joint interaction torques. A similar investigators found that the abnormal motions observed
in these subjects could be accounted for by lack of
compensation for the joint interaction torques. A similar
conclusion was reached later by Bastian *et al* (1996) ab in these subjects could be accounted for by lack of compensation for the joint interaction torques. A similar conclusion was reached later by Bastian *et al.* (1996) about the movements produced by patients suffering from cereconclusion was reached later by Bastian et al. (1996) about
the movements produced by patients suffering from cere-
bellar lesions. In summary, a substantial body of evidence
suggests that the CNS generates motor command the movements produced by patients suffering from cerebellar lesions. In summary, a substantial body of evidence
suggests that the CNS generates motor commands that
effectively represent the complex dynamics of multiioint bellar lesions. In summary, a substantial body of evidence
suggests that the CNS generates motor commands that
effectively represent the complex dynamics of multijoint
limbs. However, there are different ways for achieving suggests that the CNS generates motor commands that effectively represent the complex dynamics of multijoint limbs. However, there are different ways for achieving this representation. limbs. However, there are different ways for achieving

5. MEMORY-BASED COMPUTATIONS

A rather direct way for a robot to compute inverse dynamics is based on carrying out explicitly the algebraic A rather direct way for a robot to compute inverse
dynamics is based on carrying out explicitly the algebraic
operations after representing variables such as positions,
velocity, acceleration, torque, and inertia. Somethin dynamics is based on carrying out explicitly the algebraic
operations after representing variables such as positions,
velocity acceleration, torque and inertia. Something
similar to this approach had been first proposed by velocity acceleration, torque and inertia. Something
similar to this approach had been first proposed by velocity acceleration, torque and inertia. Something
similar to this approach had been first proposed by
Raibert (1978). He started from the observation that
inverse dynamic can be represented as the operation of a similar to this approach had been first proposed by
Raibert (1978). He started from the observation that
inverse dynamic can be represented as the operation of a
memory that associates a vector of ioint torques to each Raibert (1978). He started from the observation that
inverse dynamic can be represented as the operation of a
memory that associates a vector of joint torques to each
value of joint angles, angular velocities and angular inverse dynamic can be represented as the operation of a
memory that associates a vector of joint torques to each
value of joint angles, angular velocities and angular accelerations. A brute-force approach to dynamics would value of joint angles, angular velocities and angular
accelerations. A brute-force approach to dynamics would
simply be to store a value of torque for each possible value
of position, velocity and acceleration—a computatio accelerations. A brute-force approach to dynamics would
simply be to store a value of torque for each possible value
of position, velocity and acceleration—a computational
device that computer scientists call a 'look-up ta simply be to store a value of torque for each possible value
of position, velocity and acceleration—a computational
device that computer scientists call a 'look-up table'. This
approach is extremely simple and in fact look of position, velocity and acceleration—a computational
device that computer scientists call a 'look-up table'. This
approach is extremely simple and in fact look-up tables
were implicit in early models of motor learning su device that computer scientists call a 'look-up table'. This
approach is extremely simple and in fact look-up tables
were implicit in early models of motor learning, such as
those proposed by Albus (1971) and Marr (1969) approach is extremely simple and in fact look-up tables
were implicit in early models of motor learning, such as
those proposed by Albus (1971) and Marr (1969).
However a closer look at the demands for memory size in were implicit in early models of motor learning, such as
those proposed by Albus (1971) and Marr (1969).
However, a closer look at the demands for memory size in
a reasonable biological context shows that the look-up those proposed by Albus (1971) and Marr (1969).
However, a closer look at the demands for memory size in
a reasonable biological context shows that the look-up
table approach may be impracticable However, a closer look at the demands for memory size in
a reasonable biological context shows that the look-up
table approach may be impracticable.
The number of entries in a look-up table grows expoa reasonable biological context shows that the look-up

table approach may be impracticable.
The number of entries in a look-up table grows expo-
nentially with the number of independent components
that define each table entry. Being well, aware of this The number of entries in a look-up table grows exponentially with the number of independent components
that define each table entry. Being well aware of this
problem. Raibert suggested splitting the arm dynamics nentially with the number of independent components
that define each table entry. Being well aware of this
problem, Raibert suggested splitting the arm dynamics
computations in a combination of smaller subtables: one that define each table entry. Being well aware of this
problem, Raibert suggested splitting the arm dynamics
computations in a combination of smaller subtables: one
can obtain the net torque by adding (i) a term that problem, Raibert suggested splitting the arm dynamics
computations in a combination of smaller subtables: one
can obtain the net torque by adding (i) a term that
denends on the joint angles and on the angular acceleracomputations in a combination of smaller subtables: one
can obtain the net torque by adding (i) a term that
depends on the joint angles and on the angular accelerations to (ii) a term that depends on the joint angles and on the angular velocities. These two terms may be stored tions to (ii) a term that depends on the joint angles and
on the angular velocities. These two terms may be stored
in separate tables. Assuming a resolution of only ten
values per variable the control of a two-joint limb w on the angular velocities. These two terms may be stored
in separate tables. Assuming a resolution of only ten
values per variable, the control of a two-joint limb would
require two tables with 10^4 entries each. For a in separate tables. Assuming a resolution of only ten
values per variable, the control of a two-joint limb would
require two tables with 10^4 entries each. For a more
complete arm model with seven-joint coordinates each values per variable, the control of a two-joint limb would
require two tables with 10^4 entries each. For a more
complete arm model, with seven-joint coordinates, each
table would have 10^{14} entries. These are still require two tables with 10^4 entries each. For a more complete arm model, with seven-joint coordinates, each table would have 10^{14} entries. These are still exceedingly large numbers. A method for reducing the size o complete arm model, with seven-joint coordinates, each table would have 10^{14} entries. These are still exceedingly large numbers. A method for reducing the size of look-up tables was suggested by Raibert $\&$ Horn (197 table would have 10^{14} entries. These are still exceedingly
large numbers. A method for reducing the size of look-up
tables was suggested by Raibert & Horn (1978), who
represented the dynamic problem as a sum of three large numbers. A method for reducing the size of look-up
tables was suggested by Raibert & Horn (1978), who
represented the dynamic problem as a sum of three
elements each one requiring a table that depended only tables was suggested by Raibert & Horn (1978), who represented the dynamic problem as a sum of three elements, each one requiring a table that depended only on the joint angles. Thus, the two-joint limb involved represented the dynamic problem as a sum of three
elements, each one requiring a table that depended only
on the joint angles. Thus, the two-joint limb involved elements, each one requiring a table that depended only
on the joint angles. Thus, the two-joint limb involved
tables with 100 entries and the seven-joint limb tables
with 10^7 entries on the joint ang
tables with 100°
with 10^7 entries. with 10^7 entries.
6. THE EQUILIBRIUM-POINT HYPOTHESIS

The work of Raibert (1978) and Hollerbach (1980) showed that inverse dynamics of complex limbs may be The work of Raibert (1978) and Hollerbach (1980)
showed that inverse dynamics of complex limbs may be
computed with a reasonable number of operations and
with reasonable memory requirements. However, this showed that inverse dynamics of complex limbs may be computed with a reasonable number of operations and with reasonable memory requirements. However, this work did not provide any direct evidence that the brain is computed with a reasonable number of operations and
with reasonable memory requirements. However, this
work did not provide any direct evidence that the brain is

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ever engaged in such computations. Furthermore, on a
nurely theoretical basis explanations based on computing ever engaged in such computations. Furthermore, on a
purely theoretical basis, explanations based on computing
inverse dynamics are unsatisfactory because there is no ever engaged in such computations. Furthermore, on a
purely theoretical basis, explanations based on computing
inverse dynamics are unsatisfactory because there is no
allowance for the inevitable mechanical vagaries assopurely theoretical basis, explanations based on computing
inverse dynamics are unsatisfactory because there is no
allowance for the inevitable mechanical vagaries asso-
ciated with any interaction with the environment. For inverse dynamics are unsatisfactory because there is no
allowance for the inevitable mechanical vagaries asso-
ciated with any interaction with the environment. For
instance if an external force perturbs the trajectory of allowance for the inevitable mechanical vagaries asso-
ciated with any interaction with the environment. For
instance, if an external force perturbs the trajectory of the ciated with any interaction with the environment. For
instance, if an external force perturbs the trajectory of the
arm, dramatic consequences may follow. When we pick
up a glass of water we must undate the pattern of torq instance, if an external force perturbs the trajectory of the
arm, dramatic consequences may follow. When we pick
up a glass of water, we must update the pattern of torques
that our muscles must apply to generate a movemen up a glass of water, we must update the pattern of torques
that our muscles must apply to generate a movement of up a glass of water, we must update the pattern of torques
that our muscles must apply to generate a movement of
the arm. When we open a door, we must deal with a
constraint the hinge whose location in space is only that our muscles must apply to generate a movement of
the arm. When we open a door, we must deal with a
constraint, the hinge, whose location in space is only
approximately known. One may say that most of our the arm. When we open a door, we must deal with a constraint, the hinge, whose location in space is only approximately known. One may say that most of our actions are executed upon a poorly predictable mechanconstraint, the hinge, whose location in space is only
approximately known. One may say that most of our
actions are executed upon a poorly predictable mechan-
ical environment. It would then be erroneous to suggest approximately known. One may say that most of our
actions are executed upon a poorly predictable mechan-
ical environment. It would then be erroneous to suggest
that a stored pattern of neuromuscular activations correactions are executed upon a poorly predictable mechanical environment. It would then be erroneous to suggest
that a stored pattern of neuromuscular activations corre-
sponds to some particular movement. Instead, the moveical environment. It would then be erroneous to suggest
that a stored pattern of neuromuscular activations corre-
sponds to some particular movement. Instead, the move-
ment that arises from that pattern is determined by t that a stored pattern of neuromuscular activations corresponds to some particular movement. Instead, the movement that arises from that pattern is determined by the interaction of the muscle forces with the dynamics of the sponds to some particular movement. Instead, the movement that arises from that pattern is determined by the interaction of the muscle forces with the dynamics of the environment \bullet _{environment.} eraction of the muscle forces with the dynamics of the
vironment.
Hogan (1985*a*) developed this concept in a theory
own as impedance control. Hogan's ideas relate to

known as impedance control. Hogan's ideas relate to Hogan $(1985a)$ developed this concept in a theory
known as impedance control. Hogan's ideas relate to
earlier experiments of Feldman (1966) and Bizzi and co-
workers In one of these experiments Polit & Bizzi (1979) known as impedance control. Hogan's ideas relate to
earlier experiments of Feldman (1966) and Bizzi and co-
workers. In one of these experiments, Polit & Bizzi (1979)
trained monkeys to execute movements of the forearm earlier experiments of Feldman (1966) and Bizzi and co-
workers. In one of these experiments, Polit & Bizzi (1979) m
trained monkeys to execute movements of the forearm by
towards a visual target. The monkeys could not see workers. In one of these experiments, Polit & Bizzi (1979)
trained monkeys to execute movements of the forearm
towards a visual target. The monkeys could not see their
moving arm nor could they perceive it as their proprio trained monkeys to execute movements of the forearm
towards a visual target. The monkeys could not see their
moving arm nor could they perceive it as their proprio-
centive inflow had been surgically interrunted by the towards a visual target. The monkeys could not see their
moving arm nor could they perceive it as their proprio-
ceptive inflow had been surgically interrupted by the
transection of cranial and thoracic dorsal roots—a moving arm nor could they perceive it as their propriotation of cranial and thoracic dorsal roots—a electron of cranial and thoracic dorsal roots—a electron contraction. Surprisingly, Polit & line Rizzi found that despite transection of cranial and thoracic dorsal roots—a
procedure called 'deafferentation'. Surprisingly, Polit &
Bizzi found that, despite such radical deprivation of procedure called 'deafferentation'. Surprisingly, Polit &
Bizzi found that, despite such radical deprivation of
sensory information, the monkeys could successfully
reach the visual targets What was more unexpected was Bizzi found that, despite such radical deprivation of
sensory information, the monkeys could successfully
reach the visual targets. What was more unexpected was
that the monkeys could reach the intended target even sensory information, the monkeys could successfully
reach the visual targets. What was more unexpected was
that the monkeys could reach the intended target even
when their arm had been displaced from the initial reach the visual targets. What was more unexpected was
that the monkeys could reach the intended target even
when their arm had been displaced from the initial
location just prior to the initiation of an arm movement. that the monkeys could reach the intended target even This result did not seem to be compatible either with the idea that goal-directed movements are executed by a preprogrammed sequence of joint torques or with the idea that goal-directed movements are executed by a pre-
programmed sequence of joint torques or with the
hypothesis that sensory feedback is essential to reach the
desired limb position programmed sequence
hypothesis that sensory
desired limb position.
The performance of pothesis that sensory feedback is essential to reach the
sired limb position.
The performance of the deafferented monkey can be
counted for by the hypothesis that the centrally gener-

desired limb position.
The performance of the deafferented monkey can be
accounted for by the hypothesis that the centrally generated motor commands modulate the stiffness and restlength of muscles that act as flexors and extensors about ated motor commands modulate the stiffness and rest-
length of muscles that act as flexors and extensors about
the elbow joint. As a consequence, the elastic behaviour
of the muscles, like that of an opposing spring, defin length of muscles that act as flexors and extensors about
the elbow joint. As a consequence, the elastic behaviour
of the muscles, like that of an opposing spring, defines a
single equilibrium position of the forearm. A po the elbow joint. As a consequence, the elastic behaviour
of the muscles, like that of an opposing spring, defines a
single equilibrium position of the forearm. A position that
ultimately is reached in spite of externally a • of the muscles, like that of an opposing spring, defines a
single equilibrium position of the forearm. A position that
ultimately is reached in spite of externally applied pertur-
bations, without need for feedback corre \Box single equilibrium position of the forearm. A position that ultimately is reached in spite of externally applied perturbations, without need for feedback corrections. This result
led to a question concerning the execution of target-
directed movements. Are these movements executed bations, without need for feedback corrections. This result
led to a question concerning the execution of target-
directed movements. Are these movements executed just
by setting the equilibrium point of a limb to the fina led to a question concerning the execution of target-
directed movements. Are these movements executed just
by setting the equilibrium point of a limb to the final
target? Or does the descending motor command specify directed movements. Are these movements executed just
by setting the equilibrium point of a limb to the final
target? Or does the descending motor command specify
an entire trajectory as a smooth shift of the same equili-

by setting the equilibrium point of a limb to the final
target? Or does the descending motor command specify
an entire trajectory as a smooth shift of the same equili-
brium point? Bizzi et al. (1984) addressed this quest target? Or does the descending motor command specify
an entire trajectory as a smooth shift of the same equili-
brium point? Bizzi *et al.* (1984) addressed this question in
another experiment. If as suggested by the first an entire trajectory as a smooth shift of the same equili-
brium point? Bizzi *et al.* (1984) addressed this question in
another experiment. If, as suggested by the first hypothbrium point? Bizzi et al. (1984) addressed this question in another experiment. If, as suggested by the first hypothesis, there is a sudden jump of the limb's equilibrium to the target location, an elastic force driving the hand towards the target would appear from the onset of the esis, there is a sudden jump of the limb's equilibrium to
the target location, an elastic force driving the hand
towards the target would appear from the onset of the
movement. This force would be directed all the time the target location, an elastic force driving the hand
towards the target would appear from the onset of the
movement. This force would be directed all the time towards the target would appear from the onset of the
movement. This force would be directed all the time
towards the target. The experiment of Bizzi and co-
workers disproved this hypothesis. As in the work of Polit movement. This force would be directed all the time
towards the target. The experiment of Bizzi and co-
workers disproved this hypothesis. As in the work of Polit
& Bizzi (1979) they instructed deafferented monkeys to towards the target. The experiment of Bizzi and co-
workers disproved this hypothesis. As in the work of Polit
& Bizzi (1979), they instructed deafferented monkeys to *Phil. Trans. R. Soc. Lond.* B (2000)

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execute arm movements towards a visual target but with
the vision of the arm blocked by an opaque screen. As execute arm movements towards a visual target but with
the vision of the arm blocked by an opaque screen. As
soon as the EMG activity indicated the opset of a moveexecute arm movements towards a visual target but with
the vision of the arm blocked by an opaque screen. As
soon as the EMG activity indicated the onset of a move-
ment a motor drove the arm right on the target. If this the vision of the arm blocked by an opaque screen. As
soon as the EMG activity indicated the onset of a move-
ment, a motor drove the arm right on the target. If this
were the equilibrium position specified by the muscle soon as the EMG activity indicated the onset of a move-
ment, a motor drove the arm right on the target. If this
were the equilibrium position specified by the muscle
commands at that time the arm should have remained in ment, a motor drove the arm right on the target. If this were the equilibrium position specified by the muscle commands at that time, the arm should have remained in were the equilibrium position specified by the muscle
commands at that time, the arm should have remained in
place. On the contrary, the experimenters could observe
an evident motion backward towards the starting position commands at that time, the arm should have remained in
place. On the contrary, the experimenters could observe
an evident motion backward towards the starting position
followed by a forward motion towards the target. This place. On the contrary, the experimenters could observe
an evident motion backward towards the starting position
followed by a forward motion towards the target. This
finding indicate that the muscular activation does not an evident motion backward towards the starting position followed by a forward motion towards the target. This finding indicate that the muscular activation does not specify a force or a torque, as suggested by the inverse dynamic models, nor a final target position. Instead, the finding indicate that the muscular activation does not
specify a force or a torque, as suggested by the inverse
dynamic models, nor a final target position. Instead, the
response to the initial displacement suggests that t specify a force or a torque, as suggested by the inverse
dynamic models, nor a final target position. Instead, the
response to the initial displacement suggests that the acti-
vation of the muscles produces a gradual shift response to the initial displacement suggests that the activation of the muscles produces a gradual shift of the response to the initial displacement suggests that the activation of the muscles produces a gradual shift of the limb's equilibrium from the start to end location. Accord-
ingly at all times the limb is attracted by an ela vation of the muscles produces a gradual shift of the
limb's equilibrium from the start to end location. Accord-
ingly, at all times the limb is attracted by an elastic force
towards the instantaneous equilibrium point. If limb's equilibrium from the start to end location. Accordingly, at all times the limb is attracted by an elastic force towards the instantaneous equilibrium point. If during a goal-directed movement the limb is forcefully ingly, at all times the limb is attracted by an elastic force
towards the instantaneous equilibrium point. If during a
goal-directed movement, the limb is forcefully moved
ahead towards the target, the elastic force will d towards the instantaneous equilibrium point. If during a goal-directed movement, the limb is forcefully moved
ahead towards the target, the elastic force will drive it
towards the lagging equilibrium point as observed in t goal-directed movement, the limb is forcefully moved
ahead towards the target, the elastic force will drive it
towards the lagging equilibrium point, as observed in the experiment. wards the lagging equilibrium point, as observed in the
periment.
The sequence of equilibrium positions produced during
pyement by all the muscular activations has been called

experiment.
The sequence of equilibrium positions produced during
movement by all the muscular activations has been called
by Hogan (1985b) a 'virtual trajectory'. The virtual trajec-The sequence of equilibrium positions produced during
movement by all the muscular activations has been called
by Hogan (1985*b*) a 'virtual trajectory'. The virtual trajec-
tory is a sequence of points where the elastic f movement by all the muscular activations has been called
by Hogan (1985*b*) a 'virtual trajectory'. The virtual trajec-
tory is a sequence of points where the elastic forces gener-
ated by all the muscles cancel each other by Hogan (1985*b*) a 'virtual trajectory'. The virtual trajectory is a sequence of points where the elastic forces generated by all the muscles cancel each other. By contrast, the actual trajectory is the result of the int tory is a sequence of points where the elastic forces generated by all the muscles cancel each other. By contrast, the actual trajectory is the result of the interaction of these elastic forces with other dynamic component ated by all the muscles cancel each other. By contrast, the actual trajectory is the result of the interaction of these elastic forces with other dynamic components such as limb inertia muscle velocity–tension properties a actual trajectory is the result of the interaction of these
elastic forces with other dynamic components such as
limb inertia, muscle velocity–tension properties and joint
viscosity To intuitively illustrate this distincti elastic forces with other dynamic components such as
limb inertia, muscle velocity–tension properties and joint
viscosity. To intuitively illustrate this distinction, consider
a hall attached to a rubber band. When the ban limb inertia, muscle velocity–tension properties and joint viscosity. To intuitively illustrate this distinction, consider a ball attached to a rubber band. When the band is displaced from its equilibrium position, a restoring force a ball attached to a rubber band. When the band is
displaced from its equilibrium position, a restoring force
is generated with amplitude proportional to the displace-
ment. If we move the free end of the rubber band, we displaced from its equilibrium position, a restoring force
is generated with amplitude proportional to the displace-
ment. If we move the free end of the rubber band, we
control the equilibrium position. As we move the rub is generated with amplitude proportional to the displacement. If we move the free end of the rubber band, we control the equilibrium position. As we move the rubber band along a trajectory the ball will follow a trajectory ment. If we move the free end of the rubber band, we control the equilibrium position. As we move the rubber band along a trajectory, the ball will follow a trajectory that results from the interaction of the elastic force control the equilibrium position. As we move the rubber
band along a trajectory, the ball will follow a trajectory
that results from the interaction of the elastic force with
the mass of the ball band along a trajecto
that results from the
the mass of the ball.
The idea of a virtu at results from the interaction of the elastic force with
e mass of the ball.
The idea of a virtual trajectory provides a new unified
repective for dealing with (i) the mechanics of muscles

the mass of the ball.
The idea of a virtual trajectory provides a new unified
perspective for dealing with (i) the mechanics of muscles,
(ii) the stability of movement, and (iii) the solution of the The idea of a virtual trajectory provides a new unified
perspective for dealing with (i) the mechanics of muscles,
(ii) the stability of movement, and (iii) the solution of the
inverse dynamic problem. In fact, a strictly perspective for dealing with (i) the mechanics of muscles, (ii) the stability of movement, and (iii) the solution of the inverse dynamic problem. In fact, a strictly necessary and (ii) the stability of movement, and (iii) the solution of the inverse dynamic problem. In fact, a strictly necessary and sufficient condition for a virtual trajectory to exist is that the motor commands directed to the mus inverse dynamic problem. In fact, a strictly necessary and
sufficient condition for a virtual trajectory to exist is that
the motor commands directed to the muscle define a
sequence of stable equilibrium positions. If this sufficient condition for a virtual trajectory to exist is that
the motor commands directed to the muscle define a
sequence of stable equilibrium positions. If this require-
ment is met then there exists a single well-defin the motor commands directed to the muscle define a
sequence of stable equilibrium positions. If this require-
ment is met, then there exists a single well-defined trans-
formation from the high-dimensional representation o sequence of stable equilibrium positions. If this requirement is met, then there exists a single well-defined transformation from the high-dimensional representation of
the control signal as a collection of muscle activations, to
a low-dimensional sequence of equilibrium points. formation from the high-dimensional representation of
the control signal as a collection of muscle activations, to
a low-dimensional sequence of equilibrium points. An
advantage of this low-dimensional representation is th a low-dimensional sequence of equilibrium points. An advantage of this low-dimensional representation is that, a low-dimensional sequence of equilibrium points. An advantage of this low-dimensional representation is that, unlike muscle activations, the virtual trajectory may be directly compared with the actual movement of the limb advantage of this low-dimensional representation is that,
unlike muscle activations, the virtual trajectory may be
directly compared with the actual movement of the limb.
The relationship between actual and virtual traject like muscle activations, the virtual trajectory may be
rectly compared with the actual movement of the limb.
The relationship between actual and virtual trajectory
determined by the dynamics of the system and by the

directly compared with the actual movement of the limb.
The relationship between actual and virtual trajectory
is determined by the dynamics of the system and by the
stiffness which transforms a displacement from the equi-The relationship between actual and virtual trajectory
is determined by the dynamics of the system and by the
stiffness, which transforms a displacement from the equi-
librium into a restoring force. In the limit of infini is determined by the dynamics of the system and by the stiffness, which transforms a displacement from the equilibrium into a restoring force. In the limit of infinite stiffness the actual trajectory would match exactly th stiffness, which transforms a displacement from the equilibrium into a restoring force. In the limit of infinite stiffness, the actual trajectory would match exactly the virtual trajectory. On the other end, with low stiff librium into a restoring force. In the limit of infinite stiffness, the actual trajectory would match exactly the virtual trajectory. On the other end, with low stiffness values, the difference between virtual and actual t ness, the actual trajectory would match exactly the virtual trajectory. On the other end, with low stiffness
values, the difference between virtual and actual trajec-
tory may become quite large. In a work that combined
observations of band movements and computer simulavalues, the difference between virtual and actual trajectory may become quite large. In a work that combined
observations of hand movements and computer simula-
tions. Elash (1987) tested the hypothesis that multiioint tory may become quite large. In a work that combined
observations of hand movements and computer simula-
tions, Flash (1987) tested the hypothesis that multijoint
arm movements are obtained by the CNS shifting the observations of hand movements and computer simulations, Flash (1987) tested the hypothesis that multijoint arm movements are obtained by the CNS shifting the

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equilibrium position of the hand along a straight and
rectilinear motion from the start to end position. As equilibrium position of the hand along a straight and
rectilinear motion from the start to end position. As
shown by Morasso (1981), approximately straight hand equilibrium position of the hand along a straight and
rectilinear motion from the start to end position. As
shown by Morasso (1981), approximately straight hand
naths characterize planar hand movements between pairs rectilinear motion from the start to end position. As
shown by Morasso (1981), approximately straight hand
paths characterize planar hand movements between pairs
of targets If the same movements are analysed at a finer shown by Morasso (1981), approximately straight hand
paths characterize planar hand movements between pairs
of targets. If the same movements are analysed at a finer
level of detail however the paths present certain degree paths characterize planar hand movements between pairs
of targets. If the same movements are analysed at a finer
level of detail, however, the paths present certain degrees
of inflection and curvature, depending on the dir of targets. If the same movements are analysed at a finer
level of detail, however, the paths present certain degrees
of inflection and curvature, depending on the direction of
movement and on the work-space location. In t level of detail, however, the paths present certain degrees
of inflection and curvature, depending on the direction of
movement and on the work-space location. In the simula-
tions. Flash, made, the assumption, that, the h of inflection and curvature, depending on the direction of
movement and on the work-space location. In the simula-
tions Flash made the assumption that the hand
equilibrium trajectories (but not necessarily the actual movement and on the work-space location. In the simulations Flash made the assumption that the hand
equilibrium trajectories (but not necessarily the actual
trajectories) are invariantly strajoht. In addition, she tions Flash made the assumption that the hand
equilibrium trajectories (but not necessarily the actual
trajectories) are invariantly straight. In addition, she
assumed that the equilibrium trajectory had a unimodal equilibrium trajectories (but not necessarily the actual
trajectories) are invariantly straight. In addition, she
assumed that the equilibrium trajectory had a unimodal
velocity profile. The results obtained from the simul trajectories) are invariantly straight. In addition, she
assumed that the equilibrium trajectory had a unimodal
velocity profile. The results obtained from the simulation captured the subtle in£ections and the curvatures of the velocity profile. The results obtained from the simulation
captured the subtle inflections and the curvatures of the
actual trajectories. Moreover, the direction of curvature
in different work-space, locations, and with di captured the subtle inflections and the curvatures of the actual trajectories. Moreover, the direction of curvature in different work-space locations and with different movement directions matched quite closely the observe actual trajectories. Moreover, the direction of curvature
in different work-space locations and with different
movement directions matched quite closely the observed
movements movements. movement directions matched quite closely the observed
movements.
It must be stressed that the stiffness values used in this

It must be stressed that the stiffness values used in this
simulation were taken from measurements that had been
performed not during movements but while subjects were
maintaining their arm at rest in different locations simulation were taken from measurements that had been simulation were taken from measurements that had been
performed not during movements but while subjects were
maintaining their arm at rest in different locations
(Mussa-Ivaldi *et al.* 1985). Katayama & Kawato (1993) performed not during movements but while subjects were
maintaining their arm at rest in different locations
(Mussa-Ivaldi *et al.* 1985). Katayama & Kawato (1993)
and then Gomi & Kawato (1997) repeated Elash's simulamaintaining their arm at rest in different locations (Mussa-Ivaldi *et al.* 1985). Katayama & Kawato (1993) and then Gomi & Kawato (1997) repeated Flash's simula-为 and then Gomi & Kawato (1997) repeated Flash's simulation using lower values of stiffness and found, not surprisingly, that in order to reproduce the actual trajectory of the hand the virtual trajectory had to follow a muc tion using lower values of stiffness and found, not surpristion using lower values of stiffness and found, not surprisingly, that in order to reproduce the actual trajectory of the hand, the virtual trajectory had to follow a much more complicated pathway. The results obtained by ingly, that in order to reproduce the actual trajectory of
the hand, the virtual trajectory had to follow a much
more complicated pathway. The results obtained by Gomi
& Kawato are at variance with those of Won & Hogan the hand, the virtual trajectory had to follow a much
more complicated pathway. The results obtained by Gomi
& Kawato are at variance with those of Won & Hogan
(1995) who were able to show that for relatively slow and more complicated pathway. The results obtained by Gomi & Kawato are at variance with those of Won & Hogan (1995), who were able to show that for relatively slow and low-amplitude arm trajectories the virtual equilibrium & Kawato are at variance with those of Won & Hogan stimulation of the interneuronal circuitry in the lumbar (1995), who were able to show that for relatively slow and spinal cord of frogs and rats has been shown to impose (1995), who were able to show that for relatively slow and
low-amplitude arm trajectories the virtual equilibrium
point was close to the actual trajectory. Clearly, the
complexity of the virtual trajectory depends critical low-amplitude arm trajectories the virtual equilibrium
point was close to the actual trajectory. Clearly, the
complexity of the virtual trajectory depends critically
upon the elastic field surrounding the equilibrium point point was close to the actual trajectory. Clearly, the complexity of the virtual trajectory depends critically upon the elastic field surrounding the equilibrium point.
Experimental estimates of the elastic field under sta complexity of the virtual trajectory depends critically
upon the elastic field surrounding the equilibrium point.
Experimental estimates of the elastic field under static Experimental estimates of the elastic field under static conditions have shown that the local stiffness, i.e. the ratio of force and displacement, changes at different distances from the equilibrium point (Shadmebr *et al* conditions have shown that the local stiffness, i.e. the ratio of force and displacement, changes at different distances from the equilibrium point (Shadmehr *et al.* 1993) Specifically it was found that the stiffness conditions have shown that the local stiffness, i.e. the ratio of force and displacement, changes at different distances from the equilibrium point (Shadmehr *et al.* 1993). Specifically, it was found that the stiffness decreased with this distance This is a nonlinear feature of distances from the equilibrium point (Shadmehr *et al.* 1993). Specifically, it was found that the stiffness decreased with this distance. This is a nonlinear feature of the elastic field. Accordingly if as in Gomi $\&$ K 1993). Specifically, it was found that the stiffness
decreased with this distance. This is a nonlinear feature of
the elastic field. Accordingly if, as in Gomi & Kawato
(1997) one attempted to derive the equilibrium point decreased with this distance. This is a nonlinear feature of
the elastic field. Accordingly if, as in Gomi & Kawato
(1997), one attempted to derive the equilibrium point the elastic field. Accordingly if, as in Gomi & Kawato (1997), one attempted to derive the equilibrium point using a linear estimate based on the stiffness at the current position, one would overestimate the distance (1997), one attempted to derive the equilibrium point using a linear estimate based on the stiffness at the current position, one would overestimate the distance between current and equilibrium position. At present using a linear estimate based on the stiffness at the current position, one would overestimate the distance between current and equilibrium position. At present, however, there is not vet an acceptable technique for current position, one would overestimate the distance
between current and equilibrium position. At present,
however, there is not yet an acceptable technique for
measuring the elastic force field generated by the muscles between current and equilibrium position. At present,
however, there is not yet an acceptable technique for
measuring the elastic force field generated by the muscles
during movement But if the shape of the virtual trajechowever, there is not yet an acceptable technique for measuring the elastic force field generated by the muscles during movement. But, if the shape of the virtual trajectory is a complex path as in Gomi $\&$ Kawato's simu The measuring the elastic force field generated by the muscles $\overline{11}$ during movement. But, if the shape of the virtual trajectory is a complex path, as in Gomi & Kawato's simulatory is a complex path, as in Gomi & Kawato's simulations, then the apparent computational simplicity of the earlier formulation of the equilibrium-point hypothesis is lost \bigcup tions, then the apparent computational simplicity of the rlier formulation of the equilibrium-point hypothesis is
t.
Another challenge to the equilibrium-point hypothesis
mes from the work of Lackner & Dizio (1994) who \bullet lost.

lost.
Another challenge to the equilibrium-point hypothesis
comes from the work of Lackner & Dizio (1994) who
asked subjects to execute reaching hand movements while Another challenge to the equilibrium-point hypothesis
comes from the work of Lackner & Dizio (1994) who
asked subjects to execute reaching hand movements while
sitting at the centre of a slowly rotating room. Because of comes from the work of Lackner & Dizio (1994) who asked subjects to execute reaching hand movements while sitting at the centre of a slowly rotating room. Because of this rotation a Coriolis force proportional to the speed asked subjects to execute reaching hand movements while
sitting at the centre of a slowly rotating room. Because of
this rotation, a Coriolis force proportional to the speed of
the band perturbs the subject's arm. The Cori sitting at the centre of a slowly rotating room. Because of
this rotation, a Coriolis force proportional to the speed of
the hand perturbs the subject's arm. The Coriolis force
acts perpendicularly to the direction of moti this rotation, a Coriolis force proportional to the speed of
the hand perturbs the subject's arm. The Coriolis force
acts perpendicularly to the direction of motion. Lackner
 $\frac{1}{2}$. Dizio, found that, under this conditi the hand perturbs the subject's arm. The Coriolis force
acts perpendicularly to the direction of motion. Lackner
& Dizio found that, under this condition, there is a
systematic residual error at the final position in the d acts perpendicularly to the direction of motion. Lackner & Dizio found that, under this condition, there is a systematic residual error at the final position in the direction of the Coriolis force. This finding seems incom & Dizio found that, under this condition, there is a systematic residual error at the final position in the direction of the Coriolis force. This finding seems incompatible with the equilibrium-point physothesis because th systematic residual error at the final position in the direction of the Coriolis force. This finding seems incompatible with the equilibrium-point hypothesis because the

hand position. Therefore, it should not alter the location Coriolis force depends upon hand velocity but not upon
hand position. Therefore, it should not alter the location
of the final equilibrium point. However, the experimental
results of Lackner & Dizio are in apparent contras hand position. Therefore, it should not alter the location
of the final equilibrium point. However, the experimental
results of Lackner & Dizio are in apparent contrast with
other experimental findings obtained with simila of the final equilibrium point. However, the experimental
results of Lackner & Dizio are in apparent contrast with
other experimental findings obtained with similar force
fields. In particular, Shadmehr & Mussa-Ivaldi (199 results of Lackner & Dizio are in apparent contrast with
other experimental findings obtained with similar force
fields. In particular, Shadmehr & Mussa-Ivaldi (1994) used an instrumented manipulandum for applying a fields. In particular, Shadmehr & Mussa-Ivaldi (1994)
used an instrumented manipulandum for applying a
velocity-dependent field to the hand of the subjects. In
this paradigm the perturbation acted specifically on the used an instrumented manipulandum for applying a
velocity-dependent field to the hand of the subjects. In
this paradigm the perturbation acted specifically on the
arm dynamics and did not affect in any way other velocity-dependent field to the hand of the subjects. In
this paradigm the perturbation acted specifically on the
arm dynamics and did not affect in any way other
systems, such as the vestibular apparatus. Shadmebr & this paradigm the perturbation acted specifically on the arm dynamics and did not affect in any way other systems, such as the vestibular apparatus. Shadmehr & Mussa-Ivaldi, as well as Gandolfo *et al.* (1996) found that arm dynamics and did not affect in any way other
systems, such as the vestibular apparatus. Shadmehr &
Mussa-Ivaldi, as well as Gandolfo *et al.* (1996) found that
the final position of the movement was not substantially systems, such as the vestibular apparatus. Shadmehr &
Mussa-Ivaldi, as well as Gandolfo *et al.* (1996) found that
the final position of the movement was not substantially
affected by the presence of velocity-dependent fie Mussa-Ivaldi, as well as Gandolfo *et al.* (1996) found that
the final position of the movement was not substantially
affected by the presence of velocity-dependent fields, in
full agreement with the equilibrium-point hypo the final position of the movement was not substantially affected by the presence of velocity-dependent fields, in full agreement with the equilibrium-point hypothesis.
The cause of the discrepancy between these results an affected by the presence of velocity-dependent fields, in
full agreement with the equilibrium-point hypothesis.
The cause of the discrepancy between these results and
those of Lackner & Dizio (1994) has yet to be deterfull agreement with the equilibrium-point hypothesis.
The cause of the discrepancy between these results and
those of Lackner & Dizio (1994) has yet to be determined.

7. BUILDING BLOCKS FOR COMPUTATION OF DYNAMICS: SPINAL FORCE FIELDS

Recent electrophysiological studies of the spinal cord of frogs and rats by Bizzi and co-workers (Bizzi *et al.* 1991; Recent electrophysiological studies of the spinal cord of frogs and rats by Bizzi and co-workers (Bizzi *et al.* 1991; Giszter *et al.* 1993; Mussa-Ivaldi *et al.* 1990; Tresch & Bizzi 1999) suggest a new theoretical frame frogs and rats by Bizzi and co-workers (Bizzi *et al.* 1991; Giszter *et al.* 1993; Mussa-Ivaldi *et al.* 1990; Tresch & Bizzi 1999) suggest a new theoretical framework that combines some features of inverse dynamic comput 1999) suggest a new theoretical framework that combines some features of inverse dynamic computations with the 1999) suggest a new theoretical framework that combines
some features of inverse dynamic computations with the
equilibrium-point hypothesis. In these studies, electrical
stimulation of the interneuronal circuitry in the lu some features of inverse dynamic computations with the equilibrium-point hypothesis. In these studies, electrical stimulation of the interneuronal circuitry in the lumbar spinal cord of froms and rats has been shown to imp equilibrium-point hypothesis. In these studies, electrical
stimulation of the interneuronal circuitry in the lumbar
spinal cord of frogs and rats has been shown to impose a
specific balance of muscle activation. The evoked specific balance of muscle activation. The evoked synerspinal cord of frogs and rats has been shown to impose a
specific balance of muscle activation. The evoked syner-
gistic contractions generate forces that direct the
hindlimb towards an equilibrium point in space (figure 1 specific balance of muscle activation. The evoked syner-
gistic contractions generate forces that direct the
hindlimb towards an equilibrium point in space (figure 1).
To measure the mechanical responses of the activated gistic contractions generate forces that direct the
hindlimb towards an equilibrium point in space (figure 1).
To measure the mechanical responses of the activated
muscles Bizzi et al. (1991) Gizzter et al. (1993) and Mus hindlimb towards an equilibrium point in space (figure 1).
To measure the mechanical responses of the activated
muscles, Bizzi *et al.* (1991), Giszter *et al.* (1993) and Mussa-Ivaldi *et al.* (1990) attached the right ankle of the frog to muscles, Bizzi *et al.* (1991), Giszter *et al.* (1993) and Mussa-Ivaldi *et al.* (1990) attached the right ankle of the frog to a force transducer. To record the spatial variations of the force vectors generated by the l Ivaldi *et al.* (1990) attached the right ankle of the frog to
a force transducer. To record the spatial variations of the
force vectors generated by the leg muscles, they placed
the frog's leg at a location within the leg a force transducer. To record the spatial variations of the force vectors generated by the leg muscles, they placed the frog's leg at a location within the leg's work-space. Then, they stimulated a site in the spinal cord force vectors generated by the leg muscles, they placed
the frog's leg at a location within the leg's work-space.
Then, they stimulated a site in the spinal cord and
recorded the direction and amplitude of the elicited the frog's leg at a location within the leg's work-space.
Then, they stimulated a site in the spinal cord and
recorded the direction and amplitude of the elicited
isometric force at the ankle This stimulation procedure Then, they stimulated a site in the spinal cord and recorded the direction and amplitude of the elicited isometric force at the ankle. This stimulation procedure recorded the direction and amplitude of the elicited
isometric force at the ankle. This stimulation procedure
was repeated with the ankle placed at each of nine to 16
locations spanning a large portion of the leg's work-sp isometric force at the ankle. This stimulation procedure
was repeated with the ankle placed at each of nine to 16
locations spanning a large portion of the leg's work-space.
The collection of the measured forces correspond was repeated with the ankle placed at each of nine to 16
locations spanning a large portion of the leg's work-space.
The collection of the measured forces corresponded to a
well-structured spatial pattern, called a vector locations spanning a large portion of the leg's work-space.
The collection of the measured forces corresponded to a well-structured spatial pattern, called a vector field. In most instances, the spatial variation of the me The collection of the measured forces corresponded to a
well-structured spatial pattern, called a vector field. In
most instances, the spatial variation of the measured force
vectors resulted in a field that was at all tim well-structured spatial pattern, called a vector field. In
most instances, the spatial variation of the measured force
vectors resulted in a field that was at all times both
convergent and characterized by a single equilib vectors resulted in a field that was at all times both convergent and characterized by a single equilibrium point. In general, the activation of a region within the spinal
In general, the activation of a region within the spinal
rd does not produce a stationary force field. Instead

point.
In general, the activation of a region within the spinal
cord does not produce a stationary force field. Instead,
following, the onset of stimulation, the force vector cord does not produce a stationary force field. Instead, following the onset of stimulation, the force vector cord does not produce a stationary force field. Instead, following the onset of stimulation, the force vector measured at each limb location changes continuously with time (figure 2). As the force vectors elicited by a following the onset of stimulation, the force vector
measured at each limb location changes continuously
with time (figure 2). As the force vectors elicited by a
stimulus change so does the equilibrium position: the measured at each limb location changes continuously
with time (figure 2). As the force vectors elicited by a
stimulus change, so does the equilibrium position: the
sites occupied by the equilibrium position at subsequent with time (figure 2). As the force vectors elicited by a stimulus change, so does the equilibrium position: the sites occupied by the equilibrium position at subsequent stimulus change, so does the equilibrium position: the sites occupied by the equilibrium position at subsequent instants of times define a spatial trajectory. The time-
varying field is the expression of a mechanical wave sites occupied by the equilibrium position at subsequent
instants of times define a spatial trajectory. The time-
varying field is the expression of a mechanical wave that
summarizes the combined action of the muscles that instants of times define a spatial trajectory. The time-
varying field is the expression of a mechanical wave that
summarizes the combined action of the muscles that are
affected by the stimulation. Mechanical waves of the varying field is the expression of a mechanical wave that
summarizes the combined action of the muscles that are
affected by the stimulation. Mechanical waves of the
same kind can be used to describe the operation of centr summarizes the combined action of the muscles that are
affected by the stimulation. Mechanical waves of the
same kind can be used to describe the operation of central
pattern generators, and of other patural structures affected by the stimulation. Mechanical waves of the same kind can be used to describe the operation of central pattern generators and of other natural structures

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Figure 1. Force fields induced by microstimulation of the spinal cord in spinalized frogs. (From Bizzi *et al.* 1991.) (*a*) The hindlimh was placed at a number of locations on the borizontal plane (indicated by the dots). Figure 1. Force fields induced by microstimulation of the spinal cord in spinalized frogs. (From Bizzi *et al.* 1991.) (*a*) The hindlimb was placed at a number of locations on the horizontal plane (indicated by the dots) hindlimb was placed at a number of locations on the horizontal plane (indicated by the dots). At each location a stimulus
was derived at a fixed site in the lumbar spinal cord. The ensuing force was measured by a six-axes force vectors recorded at the nine locations shown in (*a*). (*c*) The work-space of the hindlimb was partitioned into a set of was derived at a fixed site in the lumbar spinal cord. The ensuing force was measured by a six-axes force transducer. (b) Peak
force vectors recorded at the nine locations shown in (a). (c) The work-space of the hindlimb force vectors recorded at the nine locations shown in (a) . (c) The work-space of the hindlinear interpolation, the forces in the interior of the triangle. (d) Interpolated force field.

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involved in the control of motor behaviour. At all lateninvolved in the control of motor behaviour. At all latencies after the onset of stimulation, the force field converges towards an equilibrium position. The temporal involved in the control of motor behaviour. At all latencies after the onset of stimulation, the force field converges towards an equilibrium position. The temporal sequence of these equilibrium positions provides us with cies after the onset of stimulation, the force field
converges towards an equilibrium position. The temporal
sequence of these equilibrium positions provides us with
an image of a virtual trajectory as in the sequence of converges towards an equilibrium position. The temporal
sequence of these equilibrium positions provides us with
an image of a virtual trajectory, as in the sequence of
frames of figure 2. Sometimes we found that the virtu sequence of these equilibrium positions provides us with
an image of a virtual trajectory, as in the sequence of
frames of figure 2. Sometimes we found that the virtual
trajectories observed after electrical stimulation fo an image of a virtual trajectory, as in the sequence of
frames of figure 2. Sometimes we found that the virtual
trajectories observed after electrical stimulation followed
circular pathways starting and ending at the same frames of figure 2. Sometimes we found that the virtual
trajectories observed after electrical stimulation followed
circular pathways starting and ending at the same point
(Mussa-Ivaldi *et al.* 1990) In contrast, the vir trajectories observed after electrical stimulation followed
circular pathways starting and ending at the same point
(Mussa-Ivaldi *et al.* 1990). In contrast, the virtual trajec-
tories inferred by Elash (1987) and Won & H circular pathways starting and ending at the same point (Mussa-Ivaldi *et al.* 1990). In contrast, the virtual trajectories inferred by Flash (1987) and Won & Hogan (1995) (Mussa-Ivaldi *et al.* 1990). In contrast, the virtual trajectories inferred by Flash (1987) and Won & Hogan (1995) from reaching arm movements followed rectilinear and smooth nathways from start to final position of the tories inferred by Flash (1987) and Won & Hogan (1995)
from reaching arm movements followed rectilinear and
smooth pathways, from start to final position of the hand.
This is not a surprising discrepancy given the great di from reaching arm movements followed rectilinear and
smooth pathways, from start to final position of the hand.
This is not a surprising discrepancy given the great differ-
ence in experimental conditions limb mechanics an smooth pathways, from start to final position of the hand.
This is not a surprising discrepancy given the great difference in experimental conditions, limb mechanics and
neural structures involved in these studies. Despite This is not a surprising discrepancy given the great difference in experimental conditions, limb mechanics and neural structures involved in these studies. Despite these differences however it is remarkable that the essent ence in experimental conditions, limb mechanics and
neural structures involved in these studies. Despite these
differences, however, it is remarkable that the essential
biomechanics of the moving limb is the same for the he neural structures involved in these studies. Despite these
differences, however, it is remarkable that the essential
biomechanics of the moving limb is the same for the
hindlimb of the spinalized frog and for the arm of differences, however, it is remarkable that the essential
biomechanics of the moving limb is the same for the
hindlimb of the spinalized frog and for the arm of the
human subject. In both cases, movement is described as a biomechanics of the moving limb is the same for the
hindlimb of the spinalized frog and for the arm of the
human subject. In both cases, movement is described as a
smooth temporal evolution of a convergent force field hindlimb of the spinalized frog and for the arm of the human subject. In both cases, movement is described as a smooth temporal evolution of a convergent force field human subject. In both cases, movement is described as a smooth temporal evolution of a convergent force field produced by the spring-like properties of the neuro-
muscular apparatus smooth temporal evo
produced by the spr
muscular apparatus.
In the spinal frog 6 oduced by the spring-like properties of the neuro-
Iscular apparatus.
In the spinal frog, different groups of leg muscles were
tivated as the stimulating electrodes were moved to

muscular apparatus.
In the spinal frog, different groups of leg muscles were
activated as the stimulating electrodes were moved to
different loci of the lumbar spinal cord in the rostro-In the spinal frog, different groups of leg muscles were
activated as the stimulating electrodes were moved to
different loci of the lumbar spinal cord in the rostro-
caudal and mediolateral direction. After manning most o activated as the stimulating electrodes were moved to different loci of the lumbar spinal cord in the rostrocaudal and mediolateral direction. After mapping most of the premotor regions in the lumbar cord with the techdifferent loci of the lumbar spinal cord in the rostro-
caudal and mediolateral direction. After mapping most of
the premotor regions in the lumbar cord with the techcaudal and mediolateral direction. After mapping most of
the premotor regions in the lumbar cord with the tech-
nique of electrical microstimulation, Bizzi *et al.* (1991)
reached the conclusion that there were at least fo the premotor regions in the lumbar cord with the technique of electrical microstimulation, Bizzi *et al.* (1991) reached the conclusion that there were at least four areas from which distinct types of convergent force fie mique of electrical microstimulation, Bizzi *et al.* (1991) reached the conclusion that there were at least four areas from which distinct types of convergent force fields were elicited. These results were confirmed by Sa reached the conclusion that there were at least four areas from which distinct types of convergent force fields were elicited. These results were confirmed by Saltiel *et al.* from which distinct types of convergent force fields were
elicited. These results were confirmed by Saltiel *et al.*
(1998) with the more selective method of chemical micro-
stimulation N-methyl-D-aspartate iontophoresis a elicited. These results were confirmed by Saltiel *et al.* (1998) with the more selective method of chemical microstimulation. N-methyl-D-aspartate iontophoresis applied to a large number of sites of the lumbar spinal cor (1998) with the more selective method of chemical microstimulation. N-methyl-D-aspartate iontophoresis applied
to a large number of sites of the lumbar spinal cord
revealed a man comparable with that obtained with elecstimulation. N-methyl-D-aspartate iontophoresis applied
to a large number of sites of the lumbar spinal cord
revealed a map comparable with that obtained with elec-
trical microstimulation. to a large number of sites of the lumbar spinal cord

of the spinal cord in frogs and rats was the discovery that Perhaps the most interesting aspect of the investigation
of the spinal cord in frogs and rats was the discovery that
the fields induced by the focal activation of the cord
follow a principle of vectorial summation (forme % of the spinal cord in frogs and rats was the discovery that
the fields induced by the focal activation of the cord
follow a principle of vectorial summation (figure 3).
Specifically Mussa-Ivaldi et el. (1994) developed the fields induced by the focal activation of the cord
follow a principle of vectorial summation (figure 3).
Specifically, Mussa-Ivaldi *et al.* (1994) developed an
experimental paradigm involving the simultaneous follow a principle of vectorial summation (figure 3).
Specifically, Mussa-Ivaldi *et al.* (1994) developed an experimental paradigm involving the simultaneous stimulation of two distinct sites in the frog's spinal cord Specifically, Mussa-Ivaldi *et al.* (1994) developed an experimental paradigm involving the simultaneous stimulation of two distinct sites in the frog's spinal cord. They found that the simultaneous stimulation of two sit experimental paradigm involving the simultaneous
stimulation of two distinct sites in the frog's spinal cord.
They found that the simultaneous stimulation of two sites
led to vector summation at the ankle of the forces gen stimulation of two distinct sites in the frog's spinal cord.
They found that the simultaneous stimulation of two sites
led to vector summation at the ankle of the forces gener-They found that the simultaneous stimulation of two sites
led to vector summation at the ankle of the forces gener-
ated by each site separately. When the pattern of forces
recorded at the ankle following co-stimulation we recorded to vector summation at the ankle of the forces generated by each site separately. When the pattern of forces
recorded at the ankle following co-stimulation were
compared with those computed by summation of the two ated by each site separately. When the pattern of forces
recorded at the ankle following co-stimulation were
compared with those computed by summation of the two
individual fields. Muses-Ivaldi *et al.* (1994) found that ' recorded at the ankle following co-stimulation were
compared with those computed by summation of the two
individual fields, Mussa-Ivaldi *et al.* (1994) found that `co-
stimulation fields' and 'summation fields' were equiv individual fields, Mussa-Ivaldi *et al.* (1994) found that 'co-
U stimulation fields' and 'summation fields' were equivalent individual fields, Mussa-Ivaldi *et al.* (1994) found that 'co-
stimulation fields' and 'summation fields' were equivalent
in more than 87% of cases. Similar results have been
obtained by Tresch & Bizzi (1999) by stimulat stimulation fields' and 'summation fields' were equivalent
in more than 87% of cases. Similar results have been
obtained by Tresch & Bizzi (1999) by stimulating the
spinal cord of the rat. Recently, Kargo & Gizzter (2000) in more than 87% of cases. Similar results have been
obtained by Tresch & Bizzi (1999) by stimulating the
spinal cord of the rat. Recently, Kargo & Giszter (2000)
showed that force field summation underlies the control of obtained by Tresch & Bizzi (1999) by stimulating the spinal cord of the rat. Recently, Kargo & Giszter (2000) showed that force field summation underlies the control of limb trajectories in the frog spinal cord of the rat. Recent
showed that force field summa
limb trajectories in the frog.
Vector, summation, of for Note that force field summation underlies the control of
the trajectories in the frog.
Vector summation of force fields implies that the
mplex poplinearity that characterizes the interactions

limb trajectories in the frog.
Vector summation of force fields implies that the
complex nonlinearity that characterizes the interactions
both among neurons and between neurons and muscles is Vector summation of force fields implies that the
complex nonlinearity that characterizes the interactions
both among neurons and between neurons and muscles is
in some way eliminated More importantly this result has complex nonlinearity that characterizes the interactions
both among neurons and between neurons and muscles is
in some way eliminated. More importantly, this result has
led to a novel hypothesis for explaining movement and both among neurons and between neurons and muscles is is consistent with the empirical observation that the
in some way eliminated. More importantly, this result has pattern of force orientation of spinal fields remained
l in some way eliminated. More importantly, this result has
led to a novel hypothesis for explaining movement and
posture based on combinations of a few basic elements.
The few active force fields stored in the spinal cord m led to a novel hypothesis for explaining movement and
posture based on combinations of a few basic elements.
The few active force fields stored in the spinal cord may
be viewed as representing motor primitives from which posture based on combinations of a few basic elements.
The few active force fields stored in the spinal cord may
be viewed as representing motor primitives from which, *Phil. Trans. R. Soc. Lond.* B (2000) *Phil. Trans. R. Soc. Lond.* B (2000)

Figure 3. Spinal force fields add vectorially. Fields A and B
were obtained in response to stimulations delivered to two
different spinal sites. The & field was obtained by stimulating Figure 3. Spinal force fields add vectorially. Fields A and B
were obtained in response to stimulations delivered to two
different spinal sites. The & field was obtained by stimulating
simultaneously the same two sites. I were obtained in response to stimulations delivered to two different spinal sites. The & field was obtained by stimulation simultaneously the same two sites. It matches closely (correlation coefficient larger than 0.9) th different spinal sites. The & field was obtained by stimulating
simultaneously the same two sites. It matches closely
(correlation coefficient larger than 0.9) the force field in +,
which was derived by adding pairwise the (correlation coefficient larger than 0.9) the force field in $+$,
which was derived by adding pairwise the vectors in A and
in B. This highly linear behaviour was found to apply to
more than 87% of dual stimulation e which was derived by adding pairwise the vectors in A and
in B. This highly linear behaviour was found to apply to
more than 87% of dual stimulation experiments. (From
Mussa-Ivaldi et al. 1994) in B. This highly linear beha
more than 87% of dual stim
Mussa-Ivaldi *et al*. 1994.)

cal microstimulation.

Perhaps the most interesting aspect of the investigation

Perhaps the most interesting aspect of the investigation

the spinal cord in frogs and rats was the discovery that

Giszter (1992) and Mussathrough superposition, a vast number of movements can
be fashioned by impulses conveyed by supraspinal paththrough superposition, a vast number of movements can
be fashioned by impulses conveyed by supraspinal path-
ways. Through computational analysis. Mussa-Ivaldi. & through superposition, a vast number of movements can
be fashioned by impulses conveyed by supraspinal pathways. Through computational analysis, Mussa-Ivaldi &
Giszter (1992) and Mussa-Ivaldi (1997) verified that this be fashioned by impulses conveyed by supraspinal pathways. Through computational analysis, Mussa-Ivaldi & Giszter (1992) and Mussa-Ivaldi (1997) verified that this view of the generation of movement and posture has the ways. Through computational analysis, Mussa-Ivaldi &
Giszter (1992) and Mussa-Ivaldi (1997) verified that this
view of the generation of movement and posture has the
competence required for controlling a wide repertoire of Giszter (1992) and Mussa-Ivaldi (1997) verified that this
view of the generation of movement and posture has the
competence required for controlling a wide repertoire of
motor behaviours view of the generation
competence require
motor behaviours.
The fields genera mpetence required for controlling a wide repertoire of
otor behaviours.
The fields generated by focal activation of the spinal
rd are nonlinear functions of limb position, velocity

motor behaviours.
The fields generated by focal activation of the spinal
cord are nonlinear functions of limb position, velocity The fields generated by focal activation of the spinal
cord are nonlinear functions of limb position, velocity
and time: $\phi_i(q, \dot{q}, t)$ (figure 2). Consistent with the obser-
vation that these fields add vectorially one m cord are nonlinear functions of limb position, velocity
and time: $\phi_i(q, \dot{q}, t)$ (figure 2). Consistent with the obser-
vation that these fields add vectorially, one may modify
the formulation of the inverse dynamic probl and time: $\phi_i(q, \dot{q}, t)$ (figure 2). Consistent with the observation that these fields add vectorially, one may modify the formulation of the inverse dynamic problem by replacing the generic torque function $\tau(t)$ with a vation that these fields add vectorially, one may modify
the formulation of the inverse dynamic problem by repla-
cing the generic torque function, $\tau(t)$, with a superposi-
tion of spinal fields: the formulation of the inverse dynamic problem by replacing the generic torque function, $\tau(t)$, with a superposition of spinal fields:

$$
D(q, \dot{q}, \ddot{q}) = \sum_{i=1}^{K} c_i \phi_i(q, \dot{q}, t).
$$
 (2)

Here, each spinal field is tuned by a (non-negative) scalar Here, each spinal field is tuned by a (non-negative) scalar coefficient, c_i , that represents a descending supraspinal command. We should stress, that in this model, the Here, each spinal field is tuned by a (non-negative) scalar coefficient, c_i , that represents a descending supraspinal command. We should stress that in this model, the descending commands do not alter the shape of the coefficient, c_i , that represents a descending supraspinal
command. We should stress that in this model, the
descending commands do not alter the shape of the
fields—that is their dependence upon state and time. This command. We should stress that in this model, the descending commands do not alter the shape of the fields—that is their dependence upon state and time. This descending commands do not alter the shape of the fields—that is their dependence upon state and time. This
is consistent with the empirical observation that the
pattern of force orientation of spinal fields remained fields—that is their dependence upon state and time. This
is consistent with the empirical observation that the
pattern of force orientation of spinal fields remained
invariant in time and with different intensities of sti invariant in time and with different intensities of stimulapattern of force orientation of spinal fields remained
invariant in time and with different intensities of stimula-
tion (Giszter *et al.* 1993). Thus, it is plausible to assume
that the sunraspinal signals select the spin invariant in time and with different intensities of stimulation (Giszter *et al.* 1993). Thus, it is plausible to assume that the supraspinal signals select the spinal fields by determining how much each one contributes t tion (Giszter *et al.* 1993). Thus, it is plausible to assume that the supraspinal signals select the spinal fields by determining how much each one contributes to the total

Figure 4. A simplified model of limb dynamics. The mechanics of the arm in the horizontal plane are approximated by a two-joint mechanism (*a*). Shoulder and elbow are mechanics of the arm in the horizontal plane are approximated by a two-joint mechanism (a) . Shoulder and elbow are modelled as two revolute joints with angles q_1 (with respect to the torso) and q_1 (with respect to mated by a two-joint mechanism (*a*). Shoulder and elbow are
modelled as two revolute joints with angles q_1 (with respect to
the torso) and q_2 (with respect to the forearm), respectively.
(*b*) The dynamics are desc modelled as two revolute joints with angles q_1 (with respect to
the torso) and q_2 (with respect to the forearm), respectively.
(*b*) The dynamics are described by two nonlinear equations
that relate the joint torque the torso) and q_2 (with respect to the forearm), respectively.
(*b*) The dynamics are described by two nonlinear equations that relate the joint torques at the shoulder (*D*₁) and at the (*b*) The dynamics are described by two nonlinear equations
that relate the joint torques at the shoulder (D_1) and at the
elbow (D_2) to the angular position velocity and acceleration
of both joints. The parameters t that relate the joint torques at the shoulder (D_1) and at the
elbow (D_2) to the angular position velocity and acceleration
of both joints. The parameters that appear in these expressions
are the lengths of the two seg elbow (D_2) to the angular position velocity and acceleration
of both joints. The parameters that appear in these expression
are the lengths of the two segments $(l_1 \text{ and } l_2)$; their masses
 $(m_1 \text{ and } m)$: and their moment of both joints. The parameters that appear in these expression
are the lengths of the two segments $(l_1 \text{ and } l_2)$; their masses
 $(m_1 \text{ and } m_2)$; and their moments of inertia $(l_1 \text{ and } l_2)$. The
numerical values used in the are the lengths of the two segments $(l_1 \text{ and } l_2)$; their masses $(m_1 \text{ and } m_2)$; and their moments of inertia $(I_1 \text{ and } I_2)$. The numerical values used in the simulations are the same as those listed in Shadmehr & Mussa-I $(m_1 \text{ and } m_2)$; and their moments of inertia $(I_1 \text{ and } I_2)$. The
numerical values used in the simulations are the same as
those listed in Shadmehr & Mussa-Ivaldi (1994, table1) and corresp ond to values estimated from an experimental subject. those listed in Shadmehr & Mussa-Ivaldi (1994, table1) and
correspond to values estimated from an experimental subject.
The terms β_1 and β_2 describe the viscoelastic behaviour of the
resting arm. They are simulate correspond to values estimated from an experimental subject.
The terms β_1 and β_2 describe the viscoelastic behaviour of the resting arm. They are simulated here by linear stiffness and viscosity matrices resting arm. They are simulated here by linear stiffness and
viscosity matrices.

%ecosity matrices.

field. The computational model of equation (2) is simply

a reformulation of inverse dynamics, with the additional field. The computational model of equation (2) is simply
a reformulation of inverse dynamics, with the additional
constraint that ioint torque is produced by the modulation The computational model of equation (2) is simply (1997). Briefly, for each desired movement in figure 6b,

a reformulation of inverse dynamics, with the additional one derives the corresponding joint angle trajectory,

C a reformulation of inverse dynamics, with the additional constraint that joint torque is produced by the modulation of a set of pre-defined primitives, the fields $\phi_i(q, \dot{q}, t)$.
How does the nervous system derive the tun constraint that joint torque is produced by the modulation
of a set of pre-defined primitives, the fields $\phi_i(q, \dot{q}, t)$.
How does the nervous system derive the tuning coeffi-
cients ϵ , from the specification of a desi of a set of pre-defined primitives, the fields $\phi_i(q, \dot{q}, t)$.
How does the nervous system derive the tuning coefficients, c_i , from the specification of a desired movement?
We do not yet have an answer to this question How does the nervous system derive the tuning coefficients, c_i , from the specification of a desired movement?
We do not yet have an answer to this question. However,
a simple mathematical applyies demonstrates that the cients, c_i , from the specification of a desired movement?
We do not yet have an answer to this question. However,
a simple mathematical analysis demonstrates that the
model is connectent to generate movements similar to We do not yet have an answer to this question. However,
a simple mathematical analysis demonstrates that the
model is competent to generate movements similar to
those observed in experimental studies. In particular, the a simple mathematical analysis demonstrates that the model is competent to generate movements similar to those observed in experimental studies. In particular, the superposition of few stereotyped fields is sufficient to model is competent to generate movements similar to
those observed in experimental studies. In particular, the
superposition of few stereotyped fields is sufficient to
control the movements of the two-joint arm shown in those observed in experimental studies. In particular, the
superposition of few stereotyped fields is sufficient to
control the movements of the two-joint arm shown in
figure 4. To demonstrate this we begin by defining a s superposition of few stereotyped fields is sufficient to control the movements of the two-joint arm shown in figure 4. To demonstrate this, we begin by defining a set of control the movements of the two-joint arm shown in
figure 4. To demonstrate this, we begin by defining a set of
force fields that capture the main qualitative features of
the spinal force fields. Here we focus on two spec figure 4. To demonstrate this, we begin by defining a set of force fields that capture the main qualitative features of the spinal force fields. Here we focus on two specific features: (i) the convergence of the field tow force fields that capture the main qualitative features of
the spinal force fields. Here we focus on two specific
features: (i) the convergence of the field towards a single features: (i) the convergence of the field towards a single
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equilibrium point, and (ii) the tendency of muscle forces
to grow reach a neak and then smoothly decrease when a equilibrium point, and (ii) the tendency of muscle forces
to grow, reach a peak and then smoothly decrease when a
muscle is stretched. A simple way to capture both features equilibrium point, and (ii) the tendency of muscle forces
to grow, reach a peak and then smoothly decrease when a
muscle is stretched. A simple way to capture both features
is to represent the force fields as gradients of to grow, reach a peak and then smoothly decrease when a
muscle is stretched. A simple way to capture both features
is to represent the force fields as gradients of Gaussian
potential functions. Each field in this model (fi muscle is stretched. A simple way to capture both features
is to represent the force fields as gradients of Gaussian
potential functions. Each field in this model (figure 5*a*) is
centred at an arm configuration $a0$ and g is to represent the force fields as gradients of Gaussian
potential functions. Each field in this model (figure $5a$) is
centred at an arm configuration, $q0$ and generates a joint potential functions. Each field in this model (figure 5*a*) is
centred at an arm configuration, $q0$ and generates a joint
torque that depends upon the distance of the limb from
this configuration: centred at an arm cotorque that depends
this configuration:

$$
\chi(q, \dot{q}) = K(q - q0) e^{-(q - q0)^T K(q - q0)} + B\dot{q}.
$$
\n(3)

 $\chi(q, \dot{q}) = K(q - q0) e^{-(q - q0)^T K(q - q0)} + B\dot{q}.$ (3)
The exponential term ensures that the joint torques do
not keen growing as the limb moves away from the equili-The exponential term ensures that the joint torques do
not keep growing as the limb moves away from the equili-
brium point. The last term $R\ddot{a}$ represents a viscous dissi-The exponential term ensures that the joint torques do
not keep growing as the limb moves away from the equili-
brium point. The last term, $B\dot{q}$, represents a viscous dissi-
native component in its simplest form not keep growing as the limb moves awa
brium point. The last term, $B\dot{q}$, represent
pative component in its simplest form.
The field $\chi(a, \dot{a})$ depends upon the ium point. The last term, $B\dot{q}$, represents a viscous dissitive component in its simplest form.
The field $\chi(q, \dot{q})$ depends upon the state of motion of e limb but not upon time. In contrast, it is reasonable to

pative component in its simplest form.
The field $\chi(q, \dot{q})$ depends upon the state of motion of
the limb but not upon time. In contrast, it is reasonable to
assume that the modules implemented by the neural The field $\chi(q, \dot{q})$ depends upon the state of motion of
the limb but not upon time. In contrast, it is reasonable to
assume that the modules implemented by the neural
circuits in the spinal cord have well-defined timing the limb but not upon time. In contrast, it is reasonable to assume that the modules implemented by the neural circuits in the spinal cord have well-defined timing properties, established for example by recurrent patterns of circuits in the spinal cord have well-defined timing properties, established for example by recurrent patterns of interconnections. A simple way to introduce stereotyped temporal features in our model is to express each fo erties, established for example by recurrent patterns of
interconnections. A simple way to introduce stereotyped
temporal features in our model is to express each force
field as a product of the constant viscoelastic term interconnections. A simple way to introduce stereotyped
temporal features in our model is to express each force
field as a product of the constant viscoelastic term, χ , and
a time function $f(t)$: temporal features in
field as a product of t
a time function $f(t)$:

$$
\phi(q, \dot{q}, t) = f(t) \times \chi(q, \dot{q}). \tag{4}
$$

The separation of time and state dependence is also The separation of time and state dependence is also
consistent with the observation that the forces generated
by electrical stimulation of the spinal cord maintain a The separation of time and state dependence is also
consistent with the observation that the forces generated
by electrical stimulation of the spinal cord maintain a
relatively constant orientation while the overall field relatively consistent with the observation that the forces generated
by electrical stimulation of the spinal cord maintain a
relatively constant orientation while the overall field
amplitude changes in time following each by electrical stimulation of the spinal cord maintain a relatively constant orientation while the overall field amplitude changes in time following each stimulus relatively constant orientation while the overall field
amplitude changes in time following each stimulus
(Giszter *et al.* 1993). Always for sake of simplicity, here we
consider only time-functions that have the form of a amplitude changes in time following each stimulus (Giszter *et al.* 1993). Always for sake of simplicity, here we consider only time-functions that have the form of a smooth step (figure 5*b c*) and its first derivative ((Giszter *et al.* 1993). Always for sake of simplicity, here we consider only time-functions that have the form of a smooth step (figure $5b,c$) and its first derivative (figure $5d e$) (a smooth 'pulse') consider only time-func
smooth step (figure $5b, c$)
 $5d,e$) (a smooth 'pulse').
This model provides u mooth step (figure $5b,c$) and its first derivative (figure ζ_e) (a smooth pulse').
This model provides us with a way to design a family stereotyped force fields with features that are qualita-

 $5d,e$) (a smooth 'pulse').
This model provides us with a way to design a family
of stereotyped force fields with features that are qualita-This model provides us with a way to design a family
of stereotyped force fields with features that are qualita-
tively consistent with empirical observations. Here we
have derived a small family of eight fields by combini of stereotyped force fields with features that are qualitatively consistent with empirical observations. Here we have derived a small family of eight fields by combining the four fields of figure fig with each of the timetively consistent with empirical observations. Here we
have derived a small family of eight fields by combining
the four fields of figure 6*a* with each of the time-functions
of figure 5. In the end, we have a model of an have derived a small family of eight fields by combining
the four fields of figure $6a$ with each of the time-functions
of figure 5. In the end, we have a model of an arm that the four fields of figure 6*a* with each of the time-functions
of figure 5. In the end, we have a model of an arm that
may only be operated by specifying eight positive
numbers the coefficients ϵ of equation (2). The s of figure 5. In the end, we have a model of an arm that
may only be operated by specifying eight positive
numbers, the coefficients c_i of equation (2). The simula-
tion results in figure 6c show that by modulating these may only be operated by specifying eight positive
numbers, the coefficients c_i of equation (2). The simula-
tion results in figure 6*c* show that by modulating these
eight numbers it is possible to approximate the minim numbers, the coefficients c_i of equation (2). The simulation results in figure 6c show that by modulating these eight numbers it is possible to approximate the minimum-
jerk movements of figure 6b. The procedure for det tion results in figure 6*c* show that by modulating these eight numbers it is possible to approximate the minimum-
jerk movements of figure 6*b*. The procedure for deter-
mining the coefficients is described in Mussa-Ivald eight numbers it is possible to approximate the minimumfigure 6*b*. The procedure for determining the coefficients is described in Mussa-Ivaldi (1997). Briefly, for each desired movement in figure 6*b*, one derives the corresponding joint angle trajectory, $a_{\ell}(t)$. Then the (1997). Briefly, for each desired movement in figure 6*b*, one derives the corresponding joint angle trajectory, $q_p(t)$. Then, the dynamics equation (2) is projected on each field evaluated along the desired trajectory. T one derives the corresponding joint angle trajectory, $q_D(t)$. Then, the dynamics equation (2) is projected on each field, evaluated along the desired trajectory. The result of this operation is a system of eight algebraic $q_D(t)$. Then, the dynamics equation (2) is projected on each field, evaluated along the desired trajectory. The result of this operation is a system of eight algebraic equations in the eight unknowns c_i : result of this operation is a system of eight algebraic equa-

$$
\sum_{i=1}^{8} \Phi_{j,i} c_i = \Lambda_j \qquad (j = 1, \ldots, 8),
$$
\n(5)

with

$$
\begin{cases}\n\Phi_{l,m} = \int \phi_l(q_D(t), \dot{q}_D(t), t) \bullet \phi_m(q_D(t), \dot{q}_D(t), t) dt \\
\Lambda_j = \int \phi_j(q_D(t), \dot{q}_D(t), t) \bullet D(q_D(t), \dot{q}_D(t), \ddot{q}(t)) dt\n\end{cases} (6)
$$

 -0.5 0 0.5 -0.5 0 0.5 -0.5 0 0.5 -0.5 0 0.5 0 0.5
Figure 5. A simplified model of spinal force fields. The force field in (*a*) is the gradient of a Gaussian potential function defined
over the angular coordinates Figure 5. A simplified model of spinal force fields. The force field in (a) is the gradient of a Gaussian potential function define
over the angular coordinates of the mechanism in figure 4. The force vectors converge to over the angular coordinates of the mechanism in figure 4. The force vectors converge towards a stable equilibrium point
indicated by the small cross. Gaussian potentials are smooth functions defined over the entire limb w over the angular coordinates of the mechanism in figure 4. The force vectors converge towards a stable equilibrium point
indicated by the small cross. Gaussian potentials are smooth functions defined over the entire limb w indicated by the small cross. Gaussian potentials are smooth functions defined over the entire limb work-space. The gradient
defines a stable equilibrium and the forces grow in amplitude within a region defined by the vari

defines a stable equilibrium and the forces grow in amplitude within a region defined by the variance of the Gaussian poten
This behaviour simulates the tendency of muscle-generated forces to grow until a critical amount This behaviour simulates the tendency of muscle-generated forces to grow until a critical amount of stretch is reached. At that
point the forces yield and then begin to decline. It is worth observing that in this mechanic point the forces yield and then begin to decline. It is worth observing that in this mechanical context, the variance of the
Gaussian potential has the dimension of compliance (the inverse of stiffness). The functions of Gaussian potential has the dimension of compliance (the inverse of stiffness). The functions of time in (b) and (d) are a smooth step and a smooth pulse, respectively. When they multiply the field in (a) they generate step and a smooth pulse, respectively. When they multiply the field in (a) they generate the wave functions depicted in (c) and (e). The time corresponding to each frame is indicated by the shaded areas in (b) and (d). Th

A standard non-negative least-squares method is used to derive the coefficients with the additional requirement that these are greater than or equal to zero. This is an impor-A standard non-negative least-squares method is used to
derive the coefficients with the additional requirement that
these are greater than or equal to zero. This is an impor-
tant condition reflecting the fact that muscle derive the coefficients with the additional requirement that
these are greater than or equal to zero. This is an impor-
tant condition reflecting the fact that muscles cannot push. tant condition reflecting the fact that muscles cannot push.
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unibrium position. The pulse field is a transient response that emulates the response to spinal stimulation shown in figure 2.
A standard non-negative least-squares method is used to The same condition is also sufficient t The same condition is also sufficient to ensure the stability
of posture and movement by imposing that the forces
generated by each field converge towards the equilibrium The same condition is also sufficient to ensure the stability
of posture and movement by imposing that the forces
generated by each field converge towards the equilibrium
point. Another significant issue, from a computatio of posture and movement by imposing that the forces
generated by each field converge towards the equilibrium
point. Another significant issue, from a computational

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Figure 6. The vectorial superposition of few force fields is competent to reproduce the kinematics and dynamics of arm
movements. These movement simulations have been obtained by combining step and pulse fields generated movements. These movement simulations have been obtained by combining step and pulse fields generated by four Gaussian potentials. The gradients of these potentials are shown in (a) . The least-squares procedure defined b movements. These movement simulations have been obtained by combining step and pulse fields generated by four Gaussian
potentials. The gradients of these potentials are shown in (*a*). The least-squares procedure defined potentials. The gradients of these potentials are shown in (*a*). The least-squares procedure defined by equations (3) and (4)—described in more detail in Mussa-Ivaldi (1997)—was used to approximate the desired trajectori the procedure is a set of constant coefficients that modulate a linear combination of the step and pulse fields (equation (2)). The trajectories generated by these linear combinations are shown in (c) . When the arm dyn the procedure is a set of constant coefficients that modulate a linear combination of the step and pulse fields (equation (2)). Trajectories generated by these linear combinations are shown in (c) . When the arm dynamics trajectories generated by these linear combinations are shown in (c) . When the arm dynamics are perturbed by the application of
the force field shown in figure 7*b*, the resulting hand movement are distorted as shown in the force field shown in figure 7*b*, the resulting hand mo
obtained by applying the same coefficients as in (c) . The
experimentally observed responses shown in figure 7*d*.

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Experimentally observed responses shown in light n .
standpoint, is to ensure that equation (5) may be inverted.
We know from elementary algebra that this is contingent standpoint, is to ensure that equation (5) may be inverted.
We know from elementary algebra that this is contingent
upon the matrix Φ being full rank, a condition that is met standpoint, is to ensure that equation (5) may be inverted.
We know from elementary algebra that this is contingent
upon the matrix Φ being full rank, a condition that is met
by the class of nonlinear force fields used We know from elementary algebra that this is contingent
upon the matrix Φ being full rank, a condition that is met
by the class of nonlinear force fields used here (Poggio & m
Girosi 1990: Mussa-Ivaldi & Giszter 1999) upon the matrix Φ being full rank, a conditi
by the class of nonlinear force fields used he
Girosi 1990; Mussa-Ivaldi & Giszter 1992).
Remarkably, the simulation results of t

Girosi 1990; Mussa-Ivaldi & Giszter 1992).
Remarkably, the simulation results of this extremely simplified example are not only consistent with the kine-Remarkably, the simulation results of this extremely
simplified example are not only consistent with the kine-
matics of reaching, but also with the responses observed
(figure $7d$) when unexpected mechanical perturbation simplified example are not only consistent with the kine-
matics of reaching, but also with the responses observed
(figure 7*d*) when unexpected mechanical perturbations
(figure 7*h*) are imposed upon the moving hand. In matics of reaching, but also with the responses observed
(figure 7*b*) when unexpected mechanical perturbations
(figure 7*b*) are imposed upon the moving hand. In this
case, the trajectories executed by experimental subje (figure 7*d*) when unexpected mechanical perturbations \Box (figure 7*b*) are imposed upon the moving hand. In this case, the trajectories executed by experimental subjects \bigcup display a distinctive pattern of deflections. The same case, the trajectories executed by experimental subjects
display a distinctive pattern of deflections. The same
pattern was produced by the simulation (figure 6*d*) when
the same perturbing field was added to the dynamics display a distinctive pattern of deflections. The same
pattern was produced by the simulation (figure $6d$) when
the same perturbing field was added to the dynamics of
the model arm with the same coefficients used to gene pattern was produced by the simulation (figure $6d$) when
the same perturbing field was added to the dynamics of
the model arm with the same coefficients used to generate
the reaching movements of figure $6c$ The same perturbing field was added to the dynamics of
the model arm with the same coefficients used to generate
the reaching movements of figure 6*c*.
Obviously, the repertoire of behaviours generated by
equation (2) depe

the reaching movements of figure 6*c*.

Obviously, the repertoire of behaviours generated by

equation (2) depends on the functional form of the fields

that, at present, still needs to be accurately determined Obviously, the repertoire of behaviours generated by
equation (2) depends on the functional form of the fields
that, at present, still needs to be accurately determined.
In the current model we have strongly simplified the Equation (2) depends on the functional form of the fields
that, at present, still needs to be accurately determined.
In the current model we have strongly simplified the
velocity-dependent forces by neglecting the known that, at present, still needs to be accurately determined.
In the current model we have strongly simplified the
velocity-dependent forces by neglecting the known
poplinear features of muscle force versus velocity In the current model we have strongly simplified the
velocity-dependent forces by neglecting the known
nonlinear features of muscle force versus velocity
dependence Instead here we are focusing on the convervelocity-dependent forces by neglecting the known
nonlinear features of muscle force versus velocity
dependence. Instead, here we are focusing on the conver-
rent features of the static fields reperated by the spinal nonlinear features of muscle force versus velocity
dependence. Instead, here we are focusing on the conver-
gent features of the static fields generated by the spinal
cord A particularly significant feature of this field i dependence. Instead, here we are focusing on the convergent features of the static fields generated by the spinal
cord. A particularly significant feature of this field is that *Phil. Trans. R. Soc. Lond.* B (2000)

they have a broad but limited region where they exert an influence. This feature is cantured by the variance of the they have a broad but limited region where they exert an influence. This feature is captured by the variance of the
Gaussian potentials, and, may be characterized as the they have a broad but limited region where they exert an influence. This feature is captured by the variance of the Gaussian potentials and may be characterized as the motor counternart of a receptive field. A computationa influence. This feature is captured by the variance of the Gaussian potentials and may be characterized as the motor counterpart of a receptive field. A computational Gaussian potentials and may be characterized as the
motor counterpart of a receptive field. A computational
analysis by Schaal & Atkeson (1998) indicated that on-
line learning of complex behaviours is successful only motor counterpart of a receptive field. A computational
analysis by Schaal & Atkeson (1998) indicated that on-
line learning of complex behaviours is successful only
when the receptive fields of the motor primitives are su analysis by Schaal & Atkeson (1998) indicated that on-
line learning of complex behaviours is successful only
when the receptive fields of the motor primitives are suffi-
ciently small. If each primitive had a large region line learning of complex behaviours is successful only
when the receptive fields of the motor primitives are suffi-
ciently small. If each primitive had a large region of influwhen the receptive fields of the motor primitives are sufficiently small. If each primitive had a large region of influence, the tuning of its parameters might interfere
disruptively with neighbouring regions. Remarkably, ciently small. If each primitive had a large region of influ-
ence, the tuning of its parameters might interfere
disruptively with neighbouring regions. Remarkably, the
force fields elicited by stimulation of muscles and m ence, the tuning of its parameters might interfere
disruptively with neighbouring regions. Remarkably, the
force fields elicited by stimulation of muscles and spinal
cord have consistently large domains of action disruptively with neighbouring regions. Remarkably, the force fields elicited by stimulation of muscles and spinal cord have consistently large domains of action. The vector fields elicited by stimulation of muscles and spinal rd have consistently large domains of action.
The vector fields generated by the spinal cord offer a
rear example of the impedance control that has been

The vector fields generated by the spinal cord offer a clear example of the impedance control that has been discussed in $\S 6$. The experiments suggest that the circuitry clear example of the impedance control that has been
discussed in $\S 6$. The experiments suggest that the circuitry
in the spinal cord—and perhaps also in other areas of the
nervous system—is organized in independent unit discussed in §6. The experiments suggest that the circuitry
in the spinal cord—and perhaps also in other areas of the
nervous system—is organized in independent units, or
modules While each module generates a specific fiel in the spinal cord—and perhaps also in other areas of the
nervous system—is organized in independent units, or
modules. While each module generates a specific field,
more complex behaviours may be easily produced by nervous system- is organized in independent units, or modules. While each module generates a specific field, more complex behaviours may be easily produced by superposition of the fields generated by concurrently active modules. Thus, we may regard these force fields as indemore complex behaviours may be easily produced by superposition of the fields generated by concurrently active modules. Thus, we may regard these force fields as independent elements of a representation of dynamics. Recent superposition of the fields generated by concurrently active modules. Thus, we may regard these force fields as independent elements of a representation of dynamics. Recent
simulation studies (Mussa-Ivaldi 1997) have demonstrated
that by using this modular representation, that is by pendent elements of a representation of dynamics. Recent
simulation studies (Mussa-Ivaldi 1997) have demonstrated
that by using this modular representation, that is by
adding convergent force fields, the CNS may learn to simulation studies (Mussa-Ivaldi 1997) have demonstrated
that by using this modular representation, that is by
adding convergent force fields, the CNS may learn to

Figure 7. Adaptation to external force fields. (a) Sketch of the experimental apparatus. Subjects executed planar arm movement
while holding the handle of an instrumented manipulandum. A monitor (not shown) placed in front Figure 7. Adaptation to external force fields. (a) Sketch of the experimental apparatus. Subjects executed planar arm movem
while holding the handle of an instrumented manipulandum. A monitor (not shown) placed in front of while holding the handle of an instrumented manipulandum. A monitor (not shown) placed in front of the subjects and above
the manipulandum displayed the location of the handle as well as targets of reaching movements. The equipped with two computer-controlled torque motors, two joint-angle encoders and a six-axes force transducer mounted on the *handle.* (b) Velocity-dependent force field corresponding to the expression

$$
\mathbf{F} = B \cdot \mathbf{v} \text{ with } B = \begin{bmatrix} -10.1 & -11.2 \\ -11.2 & 11.1 \end{bmatrix} \text{ N} \times \text{s m}^{-1}.
$$

 $\mathbf{F} = B \cdot \mathbf{v}$ with $B = \begin{bmatrix} 1 & 0.1 & 11.2 \\ -11.2 & 11.1 \end{bmatrix} N \times s m^{-1}$.
The manipulandum was programmed to generate a force **F** that was linearly related to the velocity of the hand, $\mathbf{v} = [\mathbf{v}_x, \mathbf{v}_y]$.
Note tha The manipulandum was programmed to generate a force **F** that was linearly related to the velocity of the hand, $v = [v_x, v_y]$.
Note that the matrix B has a negative and a positive eigenvalue. The negative eigenvalue induces Note that the matrix *B* has a negative and a positive eigenvalue. The negative eigenvalue induces a viscous damping at 23°
whereas the positive eigenvalue induces an assistive destabilizing force at 113° . (*c*) Unpe whereas the positive eigenvalue induces an assistive destabilizing force at 113° . (*c*) Unperturbed reaching trajectories executed by a subject when the manipulandum was not producing disturbing forces (null field). 1994.)

1994.)
reproduce and control the dynamics of a multijoint limb
counled with the dynamics of the environment reproduce and control the dynamics of a multij
coupled with the dynamics of the environment. **8. EVIDENCE FOR INTERNAL MODELS**

The findings on the spinal cord suggest that the CNS is **EXECT OR INTERNAL MODELS**
The findings on the spinal cord suggest that the CNS is
capable of representation is an internal model. The term The findings on the spinal cord suggest that the CNS is
capable of representing the dynamic properties of the
limbs. This representation is an internal model. The term
"internal model" refers to two distinct mathematical capable of representing the dynamic properties of the
limbs. This representation is an internal model. The term
'internal model' refers to two distinct mathematical
transformations: (i) the transformation from a motor limbs. This representation is an internal model. The term
'internal model' refers to two distinct mathematical
transformations: (i) the transformation from a motor
command to the consequent behaviour and (ii) the trans-'internal model' refers to two distinct mathematical
transformations: (i) the transformation from a motor
command to the consequent behaviour, and (ii) the trans-
formation from a desired behaviour to the corresponding transformations: (i) the transformation from a motor
command to the consequent behaviour, and (ii) the trans-
formation from a desired behaviour to the corresponding
motor command (Jordan & Bumelbart 1992 Kawato & command to the consequent behaviour, and (ii) the trans-
formation from a desired behaviour to the corresponding
motor command (Jordan & Rumelhart 1992; Kawato & internal models. Their experimental subjects were asked
Wolp formation from a desired behaviour to the corresponding
motor command (Jordan & Rumelhart 1992; Kawato &
Wolpert 1998; McIntyre *et al.* 1998). A model of the first
kind is called a 'forward model' Forward models provide motor command (Jordan & Rumelhart 1992; Kawato & Wolpert 1998; McIntyre *et al.* 1998). A model of the first kind is called a 'forward model'. Forward models provide the controller with the means not only to predict the Wolpert 1998; McIntyre *et al.* 1998). A model of the first
kind is called a 'forward model'. Forward models provide
the controller with the means not only to predict the
expected outcome of a command, but also to estimate kind is called a 'forward model'. Forward models provide
the controller with the means not only to predict the
expected outcome of a command, but also to estimate the
current state in the presence of feedback delays (Mial the controller with the means not only to predict the
expected outcome of a command, but also to estimate the
current state in the presence of feedback delays (Miall &
Wohert 1996) A representation of the mapping from expected outcome of a command, but also to estimate the (ficurrent state in the presence of feedback delays (Miall & m
Wolpert 1996). A representation of the mapping from fo *Phil. Trans. R. Soc. Lond.* B (2000)
Phil. Trans. R. Soc. Lond. B (2000)

planned actions to motor commands is called an 'inverse
model', Studies by Wolpert et al. (1998) proposed that the planned actions to motor commands is called an 'inverse model'. Studies by Wolpert *et al.* (1998) proposed that the neural structures within the cerebellum perform sensoriplanned actions to motor commands is called an 'inverse model'. Studies by Wolpert *et al.* (1998) proposed that the neural structures within the cerebellum perform sensori-
motor operations equivalent to a combination of model'. Studies by Wolpert *et al.* (1998) proposed that the neural structures within the cerebellum perform sensorimotor operations equivalent to a combination of multiple forward and inverse models. Strong experimental evidence for the biological and behavioural relevance of forward and inverse models. Strong experimental
evidence for the biological and behavioural relevance of
internal models has been offered by numerous recent
experiments (Brasbers-Krug et al. 1996; Flanagan & evidence for the biological and behavioural relevance of
internal models has been offered by numerous recent
experiments (Brashers-Krug *et al.* 1996; Flanagan &
Wing 1997: Flash & Gurevich 1999: Gottlieb 1996: Sabes internal models has been offered by numerous recent
experiments (Brashers-Krug *et al.* 1996; Flanagan &
Wing 1997; Flash & Gurevich 1992; Gottlieb 1996; Sabes
et al. 1998: Shadmehr & Mussa-Ivaldi 1994). In particular experiments (Brashers-Krug *et al.* 1996; Flanagan & Wing 1997; Flash & Gurevich 1992; Gottlieb 1996; Sabes *et al.* 1998; Shadmehr & Mussa-Ivaldi 1994). In particular, the experimental results obtained by Shadmehr & Wing 1997; Flash & Gurevich 1992; Gottlieb 1996; Sabes
et al. 1998; Shadmehr & Mussa-Ivaldi 1994). In particular,
the experimental results obtained by Shadmehr &
Mussa-Ivaldi (1994) demonstrate clearly the formation of et al. 1998; Shadmehr & Mussa-Ivaldi 1994). In particular, the experimental results obtained by Shadmehr &
Mussa-Ivaldi (1994) demonstrate clearly the formation of
internal models. Their experimental subjects were asked
to make reaching movements in the presence of externally Mussa-Ivaldi (1994) demonstrate clearly the formation of
internal models. Their experimental subjects were asked
to make reaching movements in the presence of externally
imposed forces. These forces were produced by a robo internal models. Their experimental subjects were asked
to make reaching movements in the presence of externally
imposed forces. These forces were produced by a robot whose free end-point was held as a pointer by the subjects imposed forces. These forces were produced by a robot
whose free end-point was held as a pointer by the subjects
(figure 7). The subjects were asked to execute reaching
movements towards a number of visual targets. Since t whose free end-point was held as a pointer by the subjects
(figure 7). The subjects were asked to execute reaching
movements towards a number of visual targets. Since the
force field produced by the robot significantly cha (figure 7). The subjects were asked to execute reaching
movements towards a number of visual targets. Since the
force field produced by the robot significantly changed

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Figure 8. Time-course of adaptation. Average and standard deviation of hand trajectories executed during the training period in the force field of figure $7b$. Performance is plotted during the (a) first, (b) second, (c) third and the training period in the force field of figure 7*b*. Performance
is plotted during the (*a*) first, (*b*) second, (*c*) third and
(*d*) final set of 250 movements. All trajectories shown here
were under no-visual feedba is plotted during the (*a*) first, (*b*) second, (*c*) third and (*d*) final set of 250 movements. All trajectories shown here were under no-visual feedback condition. (From Shadmehr & Mussa-Ivaldi 1994) (d) final set of 250 moven
were under no-visual feed
& Mussa-Ivaldi 1994.)

the dynamics of the reaching movements, the subjects'
movements initially were grossly distorted when the dynamics of the reaching movements, the subjects' movements, initially, were grossly distorted when the dynamics of the reaching movements, the subjects' movements, initially, were grossly distorted when compared with the undisturbed movements. However, with practice the subjects' hand trajectories in the force movements, initially, were grossly distorted when
compared with the undisturbed movements. However,
with practice, the subjects' hand trajectories in the force
field converged to a path similar to that produced in compared with the undisturbed movements. However,
with practice, the subjects' hand trajectories in the force
field converged to a path similar to that produced in
absence of any perturbing force (figure 8) field converged to a path similar to that produced in absence of any perturbing force (figure 8). Id converged to a path similar to that produced in
sence of any perturbing force (figure 8).
Subjects' recovery of performance is due to learning.
ter the training had been established, the force field

Absence of any perturbing force (figure 8).

Subjects' recovery of performance is due to learning.

After the training had been established, the force field

was unexpectedly removed for the duration of a single Subjects' recovery of performance is due to learning.
After the training had been established, the force field
was unexpectedly removed for the duration of a single
hand movement. The resulting trajectories (figure 9) After the training had been established, the force field was unexpectedly removed for the duration of a single hand movement. The resulting trajectories (figure 9), was unexpectedly removed for the duration of a single
hand movement. The resulting trajectories (figure 9),
named after-effects, were approximately mirror images of
those that the same subjects produced when they had hand movement. The resulting trajectories (figure 9),
named after-effects, were approximately mirror images of
those that the same subjects produced when they had
initially been exposed to the force field. The emergence of named after-effects, were approximately mirror images of
those that the same subjects produced when they had
initially been exposed to the force field. The emergence of
after-effects indicates that the CNS had composed an those that the same subjects produced when they had
initially been exposed to the force field. The emergence of
after-effects indicates that the CNS had composed an
internal model of the external field. The internal model initially been exposed to the force field. The emergence of after-effects indicates that the CNS had composed an internal model of the external field. The internal model was generating patterns of force that effectively an after-effects indicates that the CNS had composed an internal model of the external field. The internal model
was generating patterns of force that effectively anticipated
the disturbing forces that the moving hand was enc internal model of the external field. The internal model
 \Box was generating patterns of force that effectively anticipated
— the disturbing forces that the moving hand was encoun- \bigcup tering. The fact that these learned forces compensated for the disturbing forces that the moving hand was encountering. The fact that these learned forces compensated for the disturbances applied by the robotic arm during the subjects' reaching movements indicates that the CNS tering. The fact that these learned forces compensated for
the disturbances applied by the robotic arm during the
subjects' reaching movements indicates that the CNS
programmes these forces in advance. The after-effects the disturbances applied by the robotic arm during the subjects' reaching movements indicates that the CNS programmes these forces in advance. The after-effects demonstrate that these forces are not the products of some subjects' reaching movements indicates that the CNS
programmes these forces in advance. The after-effects
demonstrate that these forces are not the products of some
reflex compensation of the disturbing field programmes these forces in advance. The
demonstrate that these forces are not the pro-
reflex compensation of the disturbing field.
It is of interest to ask what are the promonstrate that these forces are not the products of some
dex compensation of the disturbing field.
It is of interest to ask what are the properties of the
rernal model, and in particular, whether, the model

reflex compensation of the disturbing field.
It is of interest to ask what are the properties of the
internal model, and in particular whether the model
could generalize to regions of the state space where the It is of interest to ask what are the properties of the
internal model, and in particular whether the model
could generalize to regions of the state space where the
disturbing forces were not experienced Recent experiinternal model, and in particular whether the model
could generalize to regions of the state space where the
disturbing forces were not experienced. Recent experi-
ments by Gandolfo et al. (1996) were designed to test the could generalize to regions of the state space where the
disturbing forces were not experienced. Recent experi-
ments by Gandolfo *et al.* (1996) were designed to test the
generalization of motor admittion to regions where disturbing forces were not experienced. Recent experiments by Gandolfo *et al.* (1996) were designed to test the generalization of motor adaptation to regions where training had not occurred. In these experiments subjects ments by Gandolfo *et al.* (1996) were designed to test the generalization of motor adaptation to regions where training had not occurred. In these experiments, subjects were asked to execute point-to-point planar movement generalization of motor adaptation to regions where
training had not occurred. In these experiments, subjects
were asked to execute point-to-point planar movements

Figure 9. After-effects of adaptation. Average and standard Figure 9. After-effects of adaptation. Average and standard
deviations of hand trajectories executed at the end of training
in the field when the field was unexpectedly removed on Figure 9. After-effects of adaptation. Average and standard
deviations of hand trajectories executed at the end of trainir
in the field when the field was unexpectedly removed on
random trials. Compare these trajectories w in the field when the field was unexpectedly removed on random trials. Compare these trajectories with the in the field when the field was unexpectedly removed on
random trials. Compare these trajectories with the
initial-exposure movements of figure 7*d*. (From Shadmehr
& Mussa-Ivaldi 1994) random trials. Compare t
initial-exposure movemen
& Mussa-Ivaldi 1994.)

between targets placed in one section of the work-space. between targets placed in one section of the work-space.
Their hand grasped the handle of the robot, which was
used to record and perturb their trajectories. Again, as in between targets placed in one section of the work-space.
Their hand grasped the handle of the robot, which was
used to record and perturb their trajectories. Again, as in
the experiments of Shadmehr & Mussa-Ivaldi (1994) Their hand grasped the handle of the robot, which was
used to record and perturb their trajectories. Again, as in
the experiments of Shadmehr & Mussa-Ivaldi (1994),
adaptation was quantified by the amount of the afterused to record and perturb their trajectories. Again, as in
the experiments of Shadmehr & Mussa-Ivaldi (1994),
adaptation was quantified by the amount of the after-
effects observed when the perturbing forces were disconthe experiments of Shadmehr & Mussa-Ivaldi (1994), adaptation was quantified by the amount of the after-
effects observed when the perturbing forces were discontinued. Fects observed when the perturbing forces were discon-

As a way of establishing the generalization of motor

arning Gandolfo *et al.* (1996) perturbed only the trajection

tinued.
As a way of establishing the generalization of motor
learning, Gandolfo *et al.* (1996) perturbed only the trajec-
tories made to a subset of the targets and searched for As a way of establishing the generalization of motor
learning, Gandolfo *et al.* (1996) perturbed only the trajec-
tories made to a subset of the targets and searched for
after-effects in movements that had not been expos learning, Gandolfo *et al.* (1996) perturbed only the trajectories made to a subset of the targets and searched for after-effects in movements that had not been exposed to perturbations. The amount of the after-effect made tories made to a subset of the targets and searched for
after-effects in movements that had not been exposed to
perturbations. The amount of the after-effect made it
possible to quantify the force field that the subjects after-effects in movements that had not been exposed to
perturbations. The amount of the after-effect made it
possible to quantify the force field that the subjects
expected to encounter during their movements in the perturbations. The amount of the after-effect made it
possible to quantify the force field that the subjects
expected to encounter during their movements in the
trained as well as in the novel directions. The same invespossible to quantify the force field that the subjects
expected to encounter during their movements in the
trained as well as in the novel directions. The same inves-
tigators found that the after-effects were present as expected to encounter during their movements in the
trained as well as in the novel directions. The same inves-
tigators found that the after-effects were present, as
expected along the trained directions but the magnitude trained as well as in the novel directions. The same investigators found that the after-effects were present, as
expected, along the trained directions, but the magnitude
of the after-effects decayed smoothly with increasi tigators found that the after-effects were present, as
expected, along the trained directions, but the magnitude
of the after-effects decayed smoothly with increasing
distance from the trained directions. This finding indi expected, along the trained directions, but the magnitude
of the after-effects decayed smoothly with increasing
distance from the trained directions. This finding indi-
cates that the ability of the CNS to compensate for of the after-effects decayed smoothly with increasing distance from the trained directions. This finding indicates that the ability of the CNS to compensate for external forces is restricted to those regions of state space cates that the ability of the CNS to compensate for cates that the ability of the CNS to compensate for external forces is restricted to those regions of state space where the perturbations have been experienced by the moving arm. However, most importantly subjects were external forces is restricted to those regions of state space
where the perturbations have been experienced by the
moving arm. However, most importantly, subjects were
also able to compensate to some extent for forces expe where the perturbations have been experienced by the
moving arm. However, most importantly, subjects were
also able to compensate to some extent for forces experi-
enced at neighbouring work-space locations. There is a moving arm. However, most importantly, subjects were
also able to compensate to some extent for forces experi-
enced at neighbouring work-space locations. There is a
remarkable degree of consistency between these results o also able to compensate to some extent for forces experienced at neighbouring work-space locations. There is a
remarkable degree of consistency between these results on
dynamic admitation and some studies of the remonses t enced at neighbouring work-space locations. There is a
remarkable degree of consistency between these results on
dynamic adaptation and some studies of the responses to
perturbations in the perceived kinematics. For exampl remarkable degree of consistency between these results on
dynamic adaptation and some studies of the responses to
perturbations in the perceived kinematics. For example,
Ghahramani et al. (1996) exposed subjects to a local dynamic adaptation and some studies of the responses to
perturbations in the perceived kinematics. For example,
Ghahramani *et al.* (1996) exposed subjects to a localized
shift in the visual presentation of a target and ob perturbations in the perceived kinematics. For example,
Ghahramani *et al.* (1996) exposed subjects to a localized
shift in the visual presentation of a target and observed
the adaptive changes in reaching movements of the Ghahramani *et al.* (1996) exposed subjects to a localized shift in the visual presentation of a target and observed the adaptive changes in reaching movements of the hand induced by this shift at a number of surrounding shift in the visual presentation of a target and observed
the adaptive changes in reaching movements of the hand
induced by this shift at a number of surrounding loca-
tions. They found that the adaptive responses decayed the adaptive changes in reaching movements of the hand
induced by this shift at a number of surrounding loca-
tions. They found that the adaptive responses decayed
smoothly with distance from the training location, where induced by this shift at a number of surrounding locations. They found that the adaptive responses decayed smoothly with distance from the training location, where the visual information was presented. In a different set o smoothly with distance from the training location, where the visual information was presented. In a different set of smoothly with distance from the training location, where
the visual information was presented. In a different set of
experiments, Martin *et al.* (1996) trained subjects to
throw a ball at a visual target while wearing pr the visual information was presented. In a different set of experiments, Martin *et al.* (1996) trained subjects to throw a ball at a visual target, while wearing prism spec-
tacles that displayed the visual field. They f experiments, Martin *et al.* (1996) trained subjects to throw a ball at a visual target, while wearing prism spectacles that displayed the visual field. They found that learning did not generalize between right and left h throw a ball at a visual target, while wearing prism spectacles that displayed the visual field. They found that learning did not generalize between right and left hand. tacles that displayed the visual field. They found that learning did not generalize between right and left hand.
However, they could occasionally, although rarely, observe generalization across different throwing patterns learning did not generalize between right and left hand.
However, they could occasionally, although rarely,
observe generalization across different throwing patterns
executed with the same hand. A somewhat contrasting However, they could occasionally, although rarely,
observe generalization across different throwing patterns
executed with the same hand. A somewhat contrasting
result was recently obtained by Vetter et al. (1999) who observe generalization across different throwing patterns executed with the same hand. A somewhat contrasting result was recently obtained by Vetter *et al.* (1999), who did not observe a decay in generalization after rema result was recently obtained by Vetter $et \ al.$ (1999), who

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Figure 10. Evidence of motor memory consolidation. The left
panels show the learning curves for three groups of subjects.
Learning in a perturbing force field was quantified by a corre-Figure 10. Evidence of motor memory consolidation. The left
panels show the learning curves for three groups of subjects.
Learning in a perturbing force field was quantified by a corre-
lation coefficient between the traje panels show the learning curves for three groups of subjects.
Learning in a perturbing force field was quantified by a correlation coefficient between the trajectories in the field and the
average trajectory before any per Learning in a perturbing force field was quantified by a correlation coefficient between the trajectories in the field and the average trajectory before any perturbation had been applied.
On the right are the mean performa lation coefficient between the trajectories in the field and the
average trajectory before any perturbation had been applied.
On the right are the mean performances in experiment days 1
and 2. Subjects in the control grou average trajectory before any perturbation had been applied.
On the right are the mean performances in experiment days 1
and 2. Subjects in the control group (*a*) practised reaching
movements against a force field (task A On the right are the mean performances in experiment days 1
and 2. Subjects in the control group (a) practised reaching
movements against a force field (task A) in the first day and
then were tested again in the same fie and 2. Subjects in the control group (a) practised reaching
movements against a force field (task A) in the first day and
then were tested again in the same field during the second
day. Subjects in the no-break group (b) movements against a force field (task A) in the first day and
then were tested again in the same field during the second
day. Subjects in the no-break group (b) during the first day
practised movements in the field of ta then were tested again in the same field during the seconday. Subjects in the no-break group (b) during the first depractised movements in the field of task A. Then they immediately practised movements in a different fie day. Subjects in the no-break group (b) during the first day
practised movements in the field of task A. Then they
immediately practised movements in a different field (task B).
On the second day they practised again in practised movements in the field of task A. Then they
immediately practised movements in a different field (task B).
On the second day they practised again in the field of task A.
Finally, subjects of the 4.h break group (immediately practised movements in a different field (task B).
On the second day they practised again in the field of task A.
Finally, subjects of the 4 h break group (c) during the first day
were exposed to the fields o On the second day they practised again in the field of task A.
Finally, subjects of the 4 h break group (c) during the first day
were exposed to the fields of tasks A and B but with a breaking
interval of 4 h between the Finally, subjects of the 4 h break group (c) during the first
were exposed to the fields of tasks A and B but with a brea
interval of 4 h between the two. Their performance was
measured on task A in day 2. Learning curve were exposed to the fields of tasks A and B but with a breakinductival of 4 h between the two. Their performance was measured on task A in day 2. Learning curves and mean performance were significantly bigher in day 2 both interval of 4 h between the two. Their performance was
measured on task A in day 2. Learning curves and mean
performance were significantly higher in day 2 both for the
control group and for the 4 h break group. In contra measured on task A in day 2. Learning curves and mean
performance were significantly higher in day 2 both for t
control group and for the 4 h break group. In contrast,
subjects in the no-break group did not display any dif performance were significantly higher in day 2 both for the
control group and for the 4 h break group. In contrast,
subjects in the no-break group did not display any difference
in performance from day 1 to day 2. (From Br control group and for the 4 h break group. In contrast,
subjects in the no-break group did not display any difference
in performance from day 1 to day 2. (From Brashers-Krug
 $et al. 1996$) subjects in the
in performanc
et al. 1996.)

of the target location in a pointing paradigm similar to
that of Ghahramani et al. (1996) of the target location in a pointin
that of Ghahramani *et al.* (1996).
The experiments on dynamic the target location in a pointing paradigm similar to
at of Ghahramani *et al.* (1996).
The experiments on dynamic adaptation have shown
at subjects adapt to a new environment by forming a

that of Ghahramani *et al.* (1996).
The experiments on dynamic adaptation have shown
that subjects adapt to a new environment by forming a
representation of the external force field that they The experiments on dynamic adaptation have shown
that subjects adapt to a new environment by forming a
representation of the external force field that they
encounter when making reaching movements. Does this representation of the external force field that they encounter when making reaching movements. Does this representation of the external force field that they
encounter when making reaching movements. Does this
representation form an imprint in long-term memory?
Brashers-Krug et al. (1996) investigated this question by encounter when making reaching movements. Does this
representation form an imprint in long-term memory?
Brashers-Krug *et al.* (1996) investigated this question by
exposing their subjects to perturbing force fields that representation form an imprint in long-term memory?
Brashers-Krug et al. (1996) investigated this question by
exposing their subjects to perturbing force fields that exposing their subjects to perturbing force fields that *Phil. Trans. R. Soc. Lond.* B (2000)

interfered with the execution of reaching movements
(figure 10) After practising reaching movements these interfered with the execution of reaching movements
(figure 10). After practising reaching movements, these
subjects were able to compensate for the imposed forces interfered with the execution of reaching movements
(figure 10). After practising reaching movements, these
subjects were able to compensate for the imposed forces
(task A) and were able to quide the cursor accurately to (figure 10). After practising reaching movements, these
subjects were able to compensate for the imposed forces
(task A) and were able to guide the cursor accurately to
the targets despite the disturbing forces. This grou (task A) and were able to guide the cursor accurately to the targets despite the disturbing forces. This group of subjects, which was tested $24h$ later with the same the targets despite the disturbing forces. This group of disturbing forces, demonstrated not only retention of the subjects, which was tested 24h later with the same
disturbing forces, demonstrated not only retention of the
acquired motor skill, but also additional learning.
Surprisingly they performed at a significantly higher disturbing forces, demonstrated not only retention of the
acquired motor skill, but also additional learning.
Surprisingly, they performed at a significantly higher
level on day 2 than they had on day 1. A second group of acquired motor skill, but also additional learning.
Surprisingly, they performed at a significantly higher
level on day 2 than they had on day 1. A second group of
subjects was trained on day 1 with a different pattern of Surprisingly, they performed at a significantly higher
level on day 2 than they had on day 1. A second group of
subjects was trained on day 1 with a different pattern of
forces (task B), immediately after performing task A level on day 2 than they had on day 1. A second group of
subjects was trained on day 1 with a different pattern of
forces (task B), immediately after performing task A. In
task B the manipulandum produced forces opposite i subjects was trained on day 1 with a different pattern of
forces (task B), immediately after performing task A. In
task B the manipulandum produced forces opposite in
direction to those applied during task A. When this forces (task B), immediately after performing task A. In task B the manipulandum produced forces opposite in direction to those applied during task A. When this second group of subjects was tested for retention of task A. task B the manipulandum produced forces opposite in
direction to those applied during task A. When this
second group of subjects was tested for retention of task A
on day 2 the investigators found that the subjects did not direction to those applied during task A. When this
second group of subjects was tested for retention of task A
on day 2, the investigators found that the subjects did not
retain any of the skills that had been learned ear second group of subjects was tested for retention of task A on day 2, the investigators found that the subjects did not retain any of the skills that had been learned earlier. This on day 2, the investigators found that the subjects did not
retain any of the skills that had been learned earlier. This
phenomenon is known as retrograde interference. Next,
 $Brsabers-Kruq$, et , al , (1996) , investigated, w retain any of the skills that had been learned earlier. This
phenomenon is known as retrograde interference. Next,
Brashers-Krug *et al.* (1996) investigated whether the
susceptibility to retrograde interference decreased phenomenon is known as retrograde interference. Next,
Brashers-Krug *et al.* (1996) investigated whether the
susceptibility to retrograde interference decreased with
time. They found that retrograde interference decreased Brashers-Krug *et al.* (1996) investigated whether the susceptibility to retrograde interference decreased with time. They found that retrograde interference decreased monotonically with time as the interval between task susceptibility to retrograde interference decreased with
time. They found that retrograde interference decreased
monotonically with time as the interval between task A
and B increased (figure 10) When 4 h passed before tas time. They found that retrograde interference decreased monotonically with time as the interval between task A and B increased (figure 10). When 4 h passed before task B was learned, the skill learned in task A was complet monotonically with time as the interval between task A and B increased (figure 10). When 4 h passed before task
B was learned, the skill learned in task A was completely
retained—the initial learning had consolidated. What is
remarkable in these results is that motor memory is B was learned, the skill learned in task A was completely
retained—the initial learning had consolidated. What is
remarkable in these results is that motor memory is trans-
formed with the passage of time and in absence of retained—the initial learning had consolidated. What is
remarkable in these results is that motor memory is trans-
formed with the passage of time and in absence of further
practice from an initial fragile state to a more remarkable in these results is that motor memory is transformed with the passage of time and in absence of further practice, from an initial fragile state to a more solid state. practice, from an initial fragile state to a more solid state.
9. CORTICAL PRIMITIVES

While the internal representation of limb's dynamics **based on modules is of central importance for the execu-**
based on modules is of central importance for the execu-
tion of motor tasks, voluntary movements are often speci-While the internal representation of limb's dynamics
based on modules is of central importance for the execu-
tion of motor tasks, voluntary movements are often speci-
fied and planned in terms of mals. Recordings of cell based on modules is of central importance for the execution of motor tasks, voluntary movements are often specified and planned in terms of goals. Recordings of cell activity from primates' premotor areas of the frontal lo tion of motor tasks, voluntary movements are often specified and planned in terms of goals. Recordings of cell
activity from primates' premotor areas of the frontal lobe fied and planned in terms of goals. Recordings of cell
activity from primates' premotor areas of the frontal lobe
have revealed the presence of neurons active during
various forms of grasping. Each neuron is selectively activity from primates' premotor areas of the frontal lobe
have revealed the presence of neurons active during
various forms of grasping. Each neuron is selectively
active for a specific type of grasping. Rizzolatti et al. have revealed the presence of neurons active during
various forms of grasping. Each neuron is selectively
active for a specific type of grasping. Rizzolatti *et al.*
(1990) interpreted their findings as an indication of a various forms of grasping. Each neuron is selectively
active for a specific type of grasping. Rizzolatti *et al.*
(1990) interpreted their findings as an indication of a
"vocabulary of actions" The words of the vocabulary active for a specific type of grasping. Rizzolatti *et al.* (1990) interpreted their findings as an indication of a 'vocabulary of actions'. The words of the vocabulary are represented by neuronal populations, each of which Specifies a given motor act. It is of the vocabulary are
represented by neuronal populations, each of which
specifies a given motor act. It is of interest that these
neurons are active not only during the act of grasning represented by neuronal populations, each of which
specifies a given motor act. It is of interest that these
neurons are active not only during the act of grasping,
but also when the primate simply looks at the objects specifies a given motor act. It is of interest that these
neurons are active not only during the act of grasping,
but also when the primate simply looks at the objects
that eventually will be picked up. Neurons with simila neurons are active not only during the act of grasping,
but also when the primate simply looks at the objects
that, eventually, will be picked up. Neurons with similar
visuomotor properties have been found in the parietal but also when the primate simply looks at the objects
that, eventually, will be picked up. Neurons with similar
visuomotor properties have been found in the parietal
lobe where neurons selectively active during manipulathat, eventually, will be picked up. Neurons with similar visuomotor properties have been found in the parietal
lobe where neurons selectively active during manipula-
tions are present in the anterior intraparietal area visuomotor properties have been found in the parietal
lobe where neurons selectively active during manipula-
tions are present in the anterior intraparietal area
(Sakata et al. 1995) (b) lobe where neurons
tions are present is
(Sakata *et al.* 1995). tions are present in the anterior intraparietal area
(Sakata *et al.* 1995). Cells active prior and during reaching moments were
also found in the parietal lobe by Mountcastle *et al.* (1975)

Cells active prior and during reaching moments were and in the frontal motor area by Georgopoulos *et al.* also found in the parietal lobe by Mountcastle *et al.* (1975) and in the frontal motor area by Georgopoulos *et al.* (1988). However, unlike the cells representing grasping, directionally tuned arm-reaching neurons displ and in the frontal motor area by Georgopoulos *et al.* (1988). However, unlike the cells representing grasping, directionally tuned arm-reaching neurons display contin-
neurons display continuous parameterization of direct (1988). However, unlike the cells representing gredirectionally tuned arm-reaching neurons display
uous parameterization of directional movements.
While the significance and the functional directionally tuned arm-reaching neurons display continuous parameterization of directional movements.
While the significance and the functional role of

nous parameterization of directional movements.
While the significance and the functional role of
distributed and categorical cortical codes remains to be
investigated a question of great importance is to While the significance and the functional role of distributed and categorical cortical codes remains to be investigated, a question of great importance is to understand how the codes representing reaching and investigated, a question of great importance is to understand how the codes representing reaching and investigated, a question of great importance is to understand how the codes representing reaching and manipulation may be combined with each other by the brain to span a repertoire of purposeful behaviours. At understand how the codes representing reaching and
manipulation may be combined with each other by the
brain to span a repertoire of purposeful behaviours. At
present we know that spinal force fields implementing manipulation may be combined with each other by the
brain to span a repertoire of purposeful behaviours. At
present, we know that spinal force fields implementing

the execution of motor commands are combined by vectorial superp osition. However, we do not know the the execution of motor commands are combined by
vectorial superposition. However, we do not know the
rules that govern the combination of reaching and manip-
ulation goals. If there is a system of high-order primitives vectorial superposition. However, we do not know the
rules that govern the combination of reaching and manip-
ulation goals. If there is a system of high-order primitives
that code for goals, then it remains to be establis rules that govern the combination of reaching and manipulation goals. If there is a system of high-order primitives
that code for goals, then it remains to be established how
these goals may be combined and translated into ulation goals. If there is a system of high-order primitives
that code for goals, then it remains to be established how
these goals may be combined and translated into movethat code for goals, then it remains to be established how these goals may be combined and translated into movements so that their concurrent activation leads to mean-ingful results. ments so that their concurrent activation leads to mean-

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10. CONCLUSION

In this paper we have shown that the problem of plan- \blacktriangleright ning and execution of a visuomotor task can be divided into a set of subprocesses. Actions are ¢rst planned in reference to the objects and the geometry of the into a set of subprocesses. Actions are first planned in
reference to the objects and the geometry of the
surrounding environment. Then, once a movement is
specified in the environment it must be translated into reference to the objects and the geometry of the
surrounding environment. Then, once a movement is
specified in the environment, it must be translated into
motions of multiple body segments. Finally the execution surrounding environment. Then, once a movement is
specified in the environment, it must be translated into
motions of multiple body segments. Finally, the execution
phase requires the solution of an inverse dynamic specified in the environment, it must be translated into
motions of multiple body segments. Finally, the execution
phase requires the solution of an inverse dynamic
problem Various schemes have been proposed in order to motions of multiple body segments. Finally, the execution
phase requires the solution of an inverse dynamic
problem. Various schemes have been proposed in order to
represent and solve the complex dynamics of the multiphase requires the solution of an inverse dynamic
problem. Various schemes have been proposed in order to
represent and solve the complex dynamics of the multi-
ioint apparatus: look-up tables equilibrium-point trajec-

problem. Various schemes have been proposed in order to
represent and solve the complex dynamics of the multi-
joint apparatus: look-up tables, equilibrium-point trajec-
tory combination of spinal cord modules and the represent and solve the complex dynamics of the multi-
joint apparatus: look-up tables, equilibrium-point trajec-
tory, combination of spinal cord modules and the
formation of internal models of dynamics joint apparatus: look-up tables, equilibrium-point trajectory, combination of spinal cord modules and the \bigcap formation of internal models of dynamics.

Motor patterns come into fragments or modules. These formation of internal models of dynamics.
Motor patterns come into fragments or modules. These
modules find their ultimate expression in the force fields
generated by the concurrent activation of multiple Motor patterns come into fragments or modules. These
modules find their ultimate expression in the force fields
generated by the concurrent activation of multiple
muscles. Our current understanding of the spinal cord modules find their ultimate expression in the force fields
generated by the concurrent activation of multiple
muscles. Our current understanding of the spinal cord
suggests that this structure provides the brain with a fir generated by the concurrent activation of multiple
muscles. Our current understanding of the spinal cord
suggests that this structure provides the brain with a first
vocabulary of such synergistic force fields What we foun muscles. Our current understanding of the spinal cord
suggests that this structure provides the brain with a first
vocabulary of such synergistic force fields. What we found
to be remarkable is that there seems to be only suggests that this structure provides the brain with a first
vocabulary of such synergistic force fields. What we found
to be remarkable is that there seems to be only a handful vocabulary of such synergistic force fields. What we found
to be remarkable is that there seems to be only a handful
of words in this vocabulary in spite of all the muscle
combinations that could be realized. It will certa to be remarkable is that there seems to be only a handful
of words in this vocabulary in spite of all the muscle
combinations that could be realized. It will certainly be
important to understand what are the origin and the of words in this vocabulary in spite of all the muscle
combinations that could be realized. It will certainly be
important to understand what are the origin and the
rationale for this particular choice of spinal force fiel combinations that could be realized. It will certainly be
important to understand what are the origin and the
rationale for this particular choice of spinal force fields.
By focusing on the mechanics of force fields we hav important to understand what are the origin and the rationale for this particular choice of spinal force fields.
By focusing on the mechanics of force fields we have not
only found a system of modules but also a very simple
syntax: fields can be literally added with each ot By focusing on the mechanics of force fields we have not
only found a system of modules but also a very simple
syntax: fields can be literally added with each other to
generate a rich repertoire of behaviours. This additiv only found a system of modules but also a very simple
syntax: fields can be literally added with each other to
generate a rich repertoire of behaviours. This additive
property is likely to be the basis for our ability to syntax: fields can be literally added with each other to
generate a rich repertoire of behaviours. This additive
property is likely to be the basis for our ability to
compensate complex patterns of force disturbances as it generate a rich repertoire of behaviours. This additive
property is likely to be the basis for our ability to
compensate complex patterns of force disturbances, as it
has been seen in many of the experiments that we have property is likely to be the basis for our ability to compensate complex patterns of force disturbances, as it has been seen in many of the experiments that we have compensate complex patterns of force disturbances, as it
has been seen in many of the experiments that we have
reviewed. And, ultimately, the internal model of a limb's
dynamics is nothing else than another field which rel has been seen in many of the experiments that we have
reviewed. And, ultimately, the internal model of a limb's
dynamics is nothing else than another field which relates
the forces generated by the muscular apparatus to th reviewed. And, ultimately, the internal model of a limb's
dynamics is nothing else than another field which relates
the forces generated by the muscular apparatus to the
state of motion of the limb dynamics is nothing else than another field which relates
the forces generated by the muscular apparatus to the
state of motion of the limb.

state of motion of the limb.
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NS3567 to F.A.M.-I., NS 09343 to E.B. and 5 P50 MH48185 to
both authors This work was
NS3567 to F.A.
both authors.

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