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HANDBOOK OF PSYCHOPHYSIOLOGY

SECOND EDITION

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MOTOR PREPARATION

C. H. M. BRUNIA & G. J. M. VAN BOXTEL

Prologue

OVERVIEW

Motor preparation is part of anticipatory behavior. It is an expression of a change in the state of the organism aimed at a better adaptation to expected changes in the environment upon which an adequate response must be given. The setting of the organism implies both the perceptual input and the motor output. In this chapter we will argue that it is impossible to exclusively discuss motor processes without taking into account the related perception. After all, much of our behavior is triggered by changes in our environment, which must therefore be monitored continuously. From the available information in our environment, the relevant part has to be selected and processed further in order to provide an appropriate action.

HISTORICAL BACKGROUND

Information processing takes time because it is based upon physical processes in the central nervous system. For us this is so obvious that it is hard to imagine that the best-known physiologist of the first half of the nineteenth century, Johannes Müller, was convinced that the time needed for an excited nerve to produce a muscle contraction was instantaneous, of the order of the speed of light (Donders 1868/1969). Sensory and motor nerves were considered different but passive channels for the animal spirits since the days of Galen. Bell (1811) and Magendie (1822) discovered that the sensory fibers entered the spinal cord via the dorsal roots, whereas the motor fibers left it via the ventral roots. This became the basis for a distinction between sensory and motor processes – between sensation and movement (Boring 1950). In contrast to the opinion of Müller, his pupil Helmholtz demonstrated in 1850 that the

conduction velocity of a motor nerve in the frog was of the order of a hundred feet per second (Donders 1868/1969). In other words, processes preceding the activation of a muscle had become measurable. The minutes of a meeting of the Dutch Royal Academy of Arts and Sciences in 1865 mention that Donders presented experiments (of his student de Jaeger and himself) about measuring the speed of mental processes. Some years later, he wrote his first publication, entitled "On the Speed of Mental Processes," which also appeared in a French and German translation (Donders 1868/1969). The kind of experiments he performed became known as "reaction" experiments, a term coined by Exner (1873).

The basic idea was that information processing is based upon a number of constituent processes, such as "discrimination" or "choice," each taking a circumscribed amount of time. Donders distinguished between the well-known A-, B-, and C-type responses. The A-response was found in a simple reaction time (RT) task in which the subject had to repeat the stimulus word "ki" as quickly as possible. In the B-task, five different stimulus words were used, each of which had to be repeated as quickly as possible. The B-response presumably included discriminative attention and a response choice. In the C-task, only one of the five stimulus words had to be repeated; here a discrimination was needed, but no choice. Presuming that the time needed for a complicated response was that of the simple response plus that of the additional central process, subtraction of A from B or C would provide the time needed for the higher process involved. Donders' method was systematically applied in Wundt's laboratory (Wundt 1893). It became clear that the C-response implied a choice, too – that is, between a Go and a No-Go response. Thus the D-response was added, which required two different responses for two different stimuli (Wundt 1893, pp. 386–9). The notion of "attention" was also needed to explain

the experimental results; it was used by Lange (1888) to describe a difference between sensorial and muscular reactions. If attention was directed to a fast response (muscular reaction), then one had a shorter RT than when attention was directed toward analyzing the stimulus (sensory reaction). Although in later years the method became more and more criticized, it marked the emergence of experimental psychology from a physiological background.

The reaction time method became combined with a technique that stemmed from the philosophical background of psychology – namely, introspection. This was practiced systematically at the Würzburger school. Külpe contributed to the mental chronometry by an important study of bimanual RTs. He demonstrated the facilitation of the hand toward which attention is directed, supporting the attentional theory of RT (Boring 1950). Yet he soon came to the conclusion that the subtraction method was not justified because it could not be maintained that, in different experimental conditions, just one subprocess was changed. Külpe explained the experimental results of Lange (1888) by a difference in predisposition, in what later became called "attitude." A major topic of the Würzburger school was thinking, a function to be analyzed by the introspective method. Thus, Watt (1904) investigated how associations were brought about by asking his subjects to produce a superordinate for a subordinate or a part for a whole. A crucial conception in this line of research became the *Aufgabe*, the instruction given to a subject to start a thinking process. The instruction was supposed to evoke an *Linstellung* – a "set," as we would say (Boring 1950). So the concept of *set* – a preparedness to cope with a future situation – originated from association psychology. It emerged from experiments in which subjects observed and analyzed their own behavior by systematic experimental introspection. Another notion relevant for preparation is the determining tendency in the formation of associations (Ach 1905). If several associations between different items are of equal strength, the response a subject comes up with might be influenced by an earlier *Aufgabe*. If that instruction predetermines a subject so that even a weaker associative tendency is activated instead of one that is normally stronger, then a determining tendency is operating: a tendency to respond.

In the nineteenth century, psychologists talked about "attention" when the effective tendency was fully conscious and about "expectation" when this was less so. Both were supposed to influence perception and (re)action. It was even suggested that reaction time could be diminished to zero if expectation was optimal by always giving a warning signal at a fixed interval prior to the response stimulus (Boring 1950, p. 715). Too fast, as it happens, since Helmholtz discovered that some time is needed for an excited nerve to activate a muscle. Yet the notion that some form of preparation would result in a faster response was in line with the prevailing way of thinking. It is inter-

esting to note that Külpe supposed that expectancy effects upon perception were based upon spirits entering the sensory fibers from the senses to be later reflected to the muscles. It was said, in other words, that anticipatory behavior was characterized by changes in both the sensory and the motor domain.

It would take some decennia before psychologists would try to measure the physiological changes underlying anticipatory behavior. First the days of introspection came to an end, and behaviorism tried to expel notions like attention and consciousness from the field of scientific psychology. Stimulus and response became the crucial variables. Yet it was clear that psychology could not miss attention, attitude, expectancy, hypothesis, intention, vector, need, perseveration, and preoccupation – all of which were considered to be related to set (Gibson 1941). What these notions had in common was the view of behavior as determined by something other than the immediately preceding sensory stimulation. "It does not deny the importance of the immediate stimulus, it does deny that sensory stimulation is everything in behavior" (Hebb 1949). A new interest emerged in the "central process which seems relatively independent of afferent stimuli." In the same year that Hilgard and Marquis (1940) used this characterization, Davis (1940) published his paper on set and muscular tension. These first psychophysiological results showed a systematic increase in electromyographic (EMG) activity in arm muscles preceding a response stimulus. Two decades later, the first direct recordings of anticipatory brain activity took place. Walter and colleagues (1964) discovered the contingent negative variation, and Kornhuber and Deecke (1965) discovered the *Bereitschaftspotential* or readiness potential. Systematic anticipatory changes were demonstrated not only in the electroencephalogram (EEG), they proved to be present in the electrocardiogram (ECG) as well. The deceleration in heart rate prior to the presentation of an imperative stimulus (Lacey & Lacey 1970), together with other changes in autonomic responses, suggested that anticipatory behavior is reflected in a number of response systems.

Physical Context

INTRODUCTION

Any study of overt behavior is based upon the measurement of some form of movement. Movements are either triggered by some kind of external stimuli or stem from within the organism. It is plausible that both types of movement originate from different brain areas (Passingham 1987). However different the origin, the movement itself can only be brought about via the activation of the relevant motoneurons in brainstem and spinal cord. These constitute the starting point for the final common path (Sherrington 1906/1947) for all movements. The execution of a movement is based upon the contraction of muscles

following an excitation of the relevant motoneurons that is sufficiently strong to make them fire. A classical opinion holds that the posterior part of the cerebral cortex is involved in perception and the anterior part in motricity (Luria 1973). We will see later on that this distinction cannot be maintained. Certain neurons in the posterior cortex fire only if a movement is to follow a stimulus presentation, and cells in the anterior cortex fire only after a preceding stimulus presentation. This suggests that, even from a functional anatomical point of view, it is not always easy to define an area as stimulus-bound or response-bound. We will further see that the motor system is really a distributed system in which many cortical and subcortical areas of the central nervous system participate.

The final result of all information processing is the execution of some movement. This chapter is aimed at the discussion of motor preparation, that is, the processes preceding the execution of the movement in question. The notion of preparation implies that there is at least prior knowledge about the necessity of a response, although there might be a temporal uncertainty and an event uncertainty. In experimental circumstances, anticipatory behavior starts with the presentation of a warning stimulus, indicating to the subjects that – after a known or unknown time – a stimulus might be presented, which must be responded to and which might or might not ask for a choice between several response alternatives. Although motor preparation is aimed at the processes at the end of this chain of stages, it is always accompanied by an anticipatory attention to instruction stimuli and possible cues that may or may not be present and that may or may not have behavioral significance. In the actual behavior it is rather artificial to insist upon a strict separation between anticipatory attention and preparation of the response. Anticipatory processes become manifest in more efficient behavior. In laboratory tasks, this all adds up to a shorter reaction time than would have been found without any antecedent knowledge of the experimental situation.

There are several ways to manipulate the subject's expectancy of the experimental situation. They involve stimulus-response compatibility, the number of stimulus-response alternatives, or the relative frequency of stimulus-response alternatives (Requin, Brenner, & Ring 1991). Expectancy can also be influenced by giving a cue to a subject that indicates which of several possible alternatives may be needed (Rosenbaum 1980). If there is uncertainty about several variables in a movement at the same time (e.g., the distance that must be bridged, the side at which the response must be made, the finger that must be used), then partial advance information ameliorates the chance that a correct response will be made earlier in time than without that information (Rosenbaum 1985). Although the final result is a shorter RT, this effect hides a number of different mechanisms that might be responsible for it. In a strictly behavioral analysis it is certainly possible to separate some

of the underlying processes. Yet their implementation in the central nervous system remains unknown. Psychophysiology can offer techniques that can help unravel these underlying mechanisms and suggest their possible relation to circumscribed brain areas.

In the following text we will see how psychophysiological variables such as event-related potentials (ERPs) or reflexes can be used to improve the behavioral analysis. However helpful, the ERPs themselves are in general a reflection of cortical activity, since the EEG itself is. From animal and clinical work we know that anticipatory behavior cannot exhaustively be described in terms of cortical processes. Rather, we know that behavior in general is based upon the timely activation of a number of different neural structures, many of which are subcortical. Yet with the exception of some clinical studies, we are generally unable to investigate electrophysiological activity in subcortical human brain areas. Brain imaging studies might be helpful here, but animal studies are also still relevant. If we accept that there are many commonalities between the functioning of the human brain and that of the monkey, this gap in our knowledge can be partly bridged by the study of unit recordings in the nonhuman primate. In this chapter we will try to understand motor preparation as a part of anticipatory behavior, which itself can be described from structural and functional points of view. To appreciate the relevance of the unit recordings in nonhuman primates, an implicit knowledge of the functional neuroanatomy of anticipatory behavior is mandatory; hence we will also provide information about the presumed neuroanatomy of anticipatory behavior.

HOW TO UNDERSTAND BEHAVIOR: BOTTOM-UP OR TOP-DOWN?

The most simple involuntary movement is the *reflex*: an innate obligatory response upon an adequate stimulus. A reflex can be elicited by a proprioceptive stimulus, as is the case with the Achilles tendon reflex or the knee jerk, or by an exteroceptive stimulus, as with the flexion reflex or the blink reflex. The underlying wiring is different: the proprioceptive reflex is the most simple, because it is largely monosynaptic; the exteroceptive reflex is polysynaptic. The Achilles tendon reflex and the knee jerk have similar wiring but at a different level of the spinal cord. In both cases the essential stimulus is the stretching of the muscle by the tap on the tendon. This causes the intrafusal fibers of the muscle spindle to stretch as well, and this is the very trigger for the Ia afferents to send action potentials to the motoneurons in the spinal cord. The Ia afferents excite the alpha-motoneurons via their largely monosynaptic connection and cause these neurons to fire. This results in the obligatory contraction of the triceps surae muscles (in the case of the Achilles tendon reflex) or the quadriceps femoris muscle (in the knee jerk).

These reflexes are an example of a segmental organization of the motor system in the spinal cord: both the reflex afferents and efferents arrive at or leave from the same level. The reflex circuitry itself is under supraspinal control, both from the brainstem and the cortical level. Efferent fibers from brainstem and cortex influence the state of activity of the motoneuron pool. That is what makes the reflex modifiable and so enables its use as a tool to study response preparation (Bonner, Requin, & Semjen 1981; Brunia & Boelhouwer 1988). If the fibers impinging upon the pool are inhibitory, then the membrane potential of the neurons in the pool moves away from the firing threshold. Thus, fewer elements in the pool will be apt to fire if the adequate stimulus is presented and, consequently, the reflex will show a smaller amplitude. From the other side, if the membrane potential of the motoneurons is moved nearer to the threshold by an excitatory supraspinal influence, then a larger number of them will fire if the adequate stimulus is presented, and the amplitude of the reflex becomes larger than in the absence of that influence. The latency of the reflex remains constant; it is mainly determined by the length of the muscle fibers involved in the reflex (e.g., leg length in the case of the Achilles tendon reflex).

The exteroceptive reflexes, which are evoked by skin stimulation, are determined by similar mechanisms. However, their afferents do not reach the agonist motoneurons directly but rather via interneurons. Hence, the exteroceptive reflexes are polysynaptic. They are also organized at different levels of the spinal cord and the brainstem. In contrast to the monosynaptic reflexes, there is a simultaneous activation of different muscles whose motoneurons are at different levels of the spinal cord. If one steps with naked foot on a drawing pin, an immediate flexion of the leg follows. Now neurons of different pools of flexor muscles of the foot, the limb, and the hip are excited, leading to a coordinated movement away from the stimulus. Exteroceptive reflexes are mostly defense responses.

The blink reflex is a brainstem reflex. Its circuitry is more complex and is not restricted to just one level of the brainstem. It is a polysynaptic reflex with a multimodal direct access for auditory, visual, and somatosensory stimuli. This makes it an interesting tool for studying attentional processes in different modalities (Dawson et al. 1997; Graham & Hackley 1991). The blink reflex is part of a defensive response pattern known as the startle reflex (Landis & Hunt 1939); it has therefore become also a tool for the study of emotional and motivational processes (Lang, Bradley, & Cuthbert 1990; Lang, Simons, & Balaban 1997). Finally, motor preparation has been studied also with the electrically evoked blink reflexes (Boelhouwer 1982; Brunia & Boelhouwer 1988).

The very existence of reflexes suggested to Sherrington (1906/1947) that our complete behavior might be built from reflex chains. The response in one reflex might be the trigger for the next, and so on. Thus, chains of reflexes are

brought about by feedback to the central nervous system. This is a clear example of a "bottom up" organization in behavior. Quite early in this century it had already become clear that deafferentation does not prevent the execution of complicated movements. In 1917, Lashley pointed to the behavior of a patient with a gunshot wound in his spinal cord. The lesion caused a complete anaesthesia for movements of the knee joint. Yet the patient was able to control the extent and speed of flexion and extension movements of the knee like normal people (Lashley 1917). Lashley returned to that finding in a famous paper in which he remarked that a competent musician can play a series of keystrokes at rates too fast to allow feedback to the central nervous system (Lashley 1951). Although the details of that argument do not seem to hold any longer, the interest in the "top-down" organization of the motor system was born; with that, the response-chaining hypothesis came to an end.

In Keele's (1968) notion of a motor program, the possibility for feedback to correct a sequence of movements is explicitly denied. He defined a motor program as "a set of muscle commands that are structured before a movement sequence begins, and that allows the entire sequence to be carried out uninfluenced by peripheral feedback" (1968, p. 387). The specification of response parameters like force, duration, and complexity must be implemented before the movement can be executed. Thus, it is no surprise that the reaction time to the first of a series of responses increases with the length of the series even though that first movement remains identical (Henry & Rogers 1960). This result cannot be explained by peripheral control from proprioceptive feedback. Further supporting evidence for the existence of motor programs came from studies in which nonhuman primates, deprived from proprioceptive feedback via a neurosurgical intervention, were still able to carry out skillful reaching movements (Taub & Berman 1968). A similar result was reported for humans (Forget & Lamarre 1987). Although this underlines the importance of central processes for the initiative of an action, we do not deny the significance of feedback for our behavior in general.

In a cognitive psychological approach of motor preparation, our point of departure is the central organization responsible for development of behavior. Most movements serve a goal - for instance, keeping one's equilibrium, bridging a distance in walking or running, plying a tool, aiming at a target in any kind of shooting, handling a ball in a game, pointing, and grasping. In order to reach the goal, some kind of perceptual control is necessary, be it visual, somatosensory, or auditory. So even if the plan to address a specific action is made and results in a series of voluntary movements, we should keep in mind that these movements must be carried out within the constraints of the available environment. Thus, as soon as the plan is developed and translated into the preparation and execution

of certain movements, the environment plays its role. In playing a well-known piece of music, violists might close their eyes; they know the music by heart. Putting the fingers of their left hand on the correct place on the string happens under the control of the auditory and somatosensory feedback: the sound, touch, and vibration of the string. We have seen earlier that playing music has been an argument for Lashley (1951) in favor of the existence of motor programs. Rosenbaum (1980) observed that the very existence of anticipatory effects – both in behavioral output and in the concomitant (psycho)physiological phenomena – is a strong argument against the chaining theory and in favor of the existence of motor programs. Accepting a top-down structure as the basis for interpreting behavior, we argue again that anticipation in our behavior determines not only the output of the system but also the input – that is, both perception and action.

THE NEUROANATOMY OF ANTICIPATORY BEHAVIOR

Motor control is in essence the control of the excitatory and inhibitory influences impinging upon the motoneuron cell columns in the spinal cord. Once these cells discharge, there is no way to stop the final response. The efferent volley is transmitted along the motor fibers to the muscles, resulting in some sort of contraction. In contrast to many situations in everyday life, this is not what one aims at when preparing a response in a reaction time task. Here, the final discharge must be produced at the very moment a stimulus is presented. Such experiments are in a certain sense static. The subject is sitting in a chair and waits upon the arrival of an imperative stimulus. There is not much posture control required, and the activation of only some muscles is needed for the crucial timely response. However artificial this situation might look, the analysis of human behavior under these circumstances has implications for all kinds of supervisory tasks in industrial settings. Its ecological validity can be doubted, however, in a number of other situations. Playing tennis is of course a much more dynamic affair and involves the active assessment of one's ability to answer a future attack. Both posture and beginning arm movements are based upon an estimation of the behavior of the opponent. Neither the spot where the ball will arrive, nor the force with which it will be hit, are known. Preparation implies here a setting of posture and movement under active visuomotor control and is much more complicated than in the RT task. Although different in many important ways, the laboratory and real-life situations both involve a coordinated activation of a number of different brain areas. Consequently, the relevant neuroanatomical structures implicated in the organization of a system of descending fibers to the motoneuron cell columns in the spinal cord will now be discussed, albeit in outline form.

We will first describe the general outline of the motor system. Then we will report a number of anatomical structures in which, by any technique, anticipatory phenomena have been recorded. Next we will discuss some aspects of the visual system in order to later discuss visuomotor control in anticipatory behavior. Finally we will address the role of the prefrontal cortex in the executive control of anticipatory behavior. Although our main focus is on discrete hand responses (such as key presses) in the context of RT experiments, much of what follows is applicable to other types of responses and movements as well.

Contractions of muscles take place after an efferent volley from the motoneurons to the muscles. The motoneuron, its axon, and the muscle fibers innervated are together defined as the *motor unit*. Therefore, one could consider the motoneuron "peripheral" in relation to the rest of the motor system. Holstege (1991) divides the motor system in three parts (see Figure 1). The first motor system is formed by the interneuronal projections into the motoneurons (Holstege 1991, p. 89); they are present in the spinal cord, in the caudal brainstem, and in between. The neurons involved receive information from the periphery (via afferent fibers) and from the second and third motor system. The second motor system sends its fibers to a limited extent directly to the motoneurons but largely to the interneurons of the first system. It has a mediolateral organization; that is, it can be divided into a medial and lateral part with different functions (Holstege 1991; Kuypers 1981). The medial part originates from the brainstem and descends in the ventral funiculus of the spinal cord to terminate on the interneurons of the medial motoneuron column. It is involved in eye and neck movements and in axial and proximal body movements. The lateral part descends from the cortex and (to a lesser extent) from the red nucleus to the lateral motoneuron cell column. From here, the distal body muscles are innervated (Holstege 1991; Kuypers 1981). The third motor system has hardly any overlap with the secondary system. Here, too, is a mediolateral division of labor. The medial component originates from the medial hypothalamus and mesencephalon and terminates in the locus coeruleus, the ventral part of the caudal pons, and the medial tegmentum. The latter structures form the final output to the first system. The lateral part originates in the lateral hypothalamus, the central nucleus of the amygdala, and the bed nucleus of the stria terminalis to terminate in the lateral tegmentum (Holstege 1991).

The third system is a rather recent discovery, based upon new tracer techniques in neuroanatomy (Holstege 1991). It is along this system that emotions enter the motor system. This is an interesting example of "discovery" of a system whose existence was taken for granted by clinicians, who knew that emotional influences played a role in the motor system without knowing the crucial pathways (Gellhorn & Loolbourrow 1963). The medial part of the third system has a diffuse influence on the spinal cord via descending

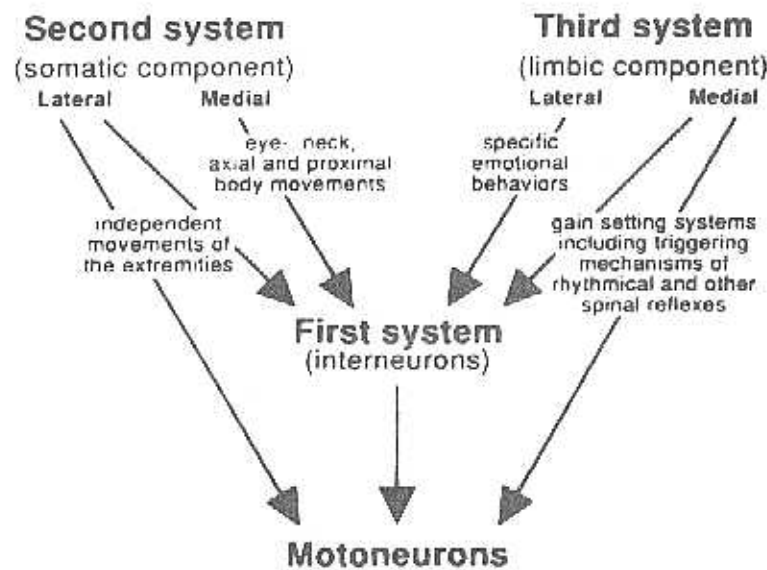


Figure 1. Schematic overview of the three subdivisions of the motor system. Reprinted with permission from Holstege, "Descending motor pathways and the spinal motor system. Limbic and non-limbic components," in Holstege (Ed.), *Role of the Forebrain in Sensation and Behavior* (Progress in Brain Research, vol. 87), pp. 307–421. Copyright 1991 Elsevier Science.

fibers from the locus coeruleus and the raphe nuclei to the motor nuclei and the dorsal horn. The medial part of the third system is activated in the expression of emotions such as laughing or crying; it has the effect of lowering the firing threshold of the motor nuclei of the spinal cord so that their excitation by fibers from the secondary system is facilitated (Holstege 1991). The lateral part of the third motor system projects to the lateral tegmentum, where the interneurons of the primary system are situated. These are involved in rather automatic functions such as respiration, vomiting, swallowing, chewing, and licking.

Structures Involved in Motor Preparation

We will start with a description of relevant cortical structures. The corticalization of the human brain is so impressive that one would be inclined to consider that the prerequisite for any cognitive behavior. This does not imply, however, that we consider behavior to be exclusively a manifestation of cortical processes. Rather, we are convinced of the importance of all kinds of subcortical processes that influence – in a dynamic ongoing gating – the crucial cortical structures. The cortex is certainly involved both in initiating our behavior and in executing all kinds of movements. Yet none of these movements are brought about without the cooperation of the basal ganglia and the cerebellum. These structures handle the information from and to the cortex via different pathways. Both have connections to structures in the brainstem from which the spinal motoneurons are activated.

The Cortex Cerebri. The following parts of the cortex can be considered motor areas (see Figure 2): (1) the precentral gyrus or M1, (2) the premotor cortex, (3) the supplementary motor area, (4) the cingulate motor area, and (5) the frontal eye field.

The precentral gyrus is the motor cortex *sensu strictu*; lying immediately anterior to the central sulcus, it is involved in the execution of voluntary movements. Onset of a movement starts with the discharge of pyramidal tract neurons (Evarts 1968). The firing threshold is lower in the motor cortex than in the premotor or supplementary motor cortex. The activity pattern of a large number of neurons in this area is related to force or speed of a movement. Its cortical sensory input stems for a large part from the adjacent somatosensory areas. Its cortical motor input arrives from the neighboring premotor and supplementary motor areas. Axons of the pyramidal cells descend to the brainstem and spinal motoneurons, either directly or via interneurons. This is the pathway by which discrete skilled movements are realized.

Anterior to the precentral gyrus we find the premotor cortex (PMC), also known as Brodmann's area 6, in which ventral (F4 and F5 in Figure 2) and dorsal (F2 and F7 in Figure 2) parts can be distinguished. The dorsal part of the premotor cortex receives input from the superior parietal lobe, from which sensory information is relayed. A detailed description of the many intricate sensory-motor connections is not possible in this chapter, and the reader is referred to Wise et al. (1997) for more detail. The premotor cortex is better developed in humans than in nonhuman primates. Deiber and associates (1991) asked their subjects to make simple movements with a joystick following the presentation of a tone. In one condition, the movement always had to be made in one direction; in the other condition, a choice had to be made between four possible directions. An increase in regional bloodflow (rCBF), which is an index of increased metabolism, was found in the premotor and supplementary motor cortices in the choice condition, whereas the activity in M1 did not differ between the simple and the choice condition. This suggests that the premotor and supplementary motor cortex are involved in response selection. Recording of unit activity in the PMC suggests that this brain area is also responsible for stimulus-guided movements.

Wiesendanger (1993) summarized the possible functions of the supplementary motor area (SMA). Planning of our behavior is attributed to this brain area. Preparation and initialization of movements seem to be organized here, and the SMA is also involved in the translation of motives and intentions in behavior. Timing of our behavior and the control of the sequencing of behavioral elements are possible functions, as are the organization of posture

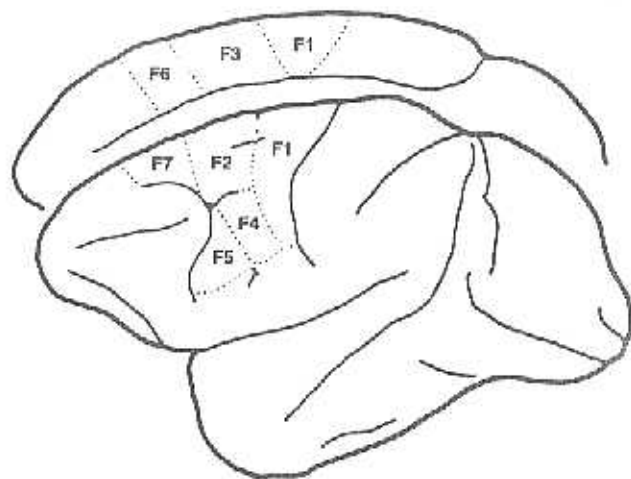


Figure 2. Lateral view of the left hemisphere and medial view of the right hemisphere in the monkey with terminology of Rizzolatti et al. (1996). The primary motor cortex (precentral gyrus, M1, Brodmann's area 4) is designated by F1. The premotor cortex (PMC, Brodmann's area 6) is divided into dorsal (F7 and F2) and ventral (F5 and F4) parts. The supplementary motor area (SMA, Brodmann's mesial area 6) is divided in two different areas: F3 (the SMA proper) and F6 (the pre-SMA), with different cytoarchitectonic structures, different subcortical connections, and different functions. Not shown are the frontal eye field (FEF, Brodmann's area 8), situated between F7 and F5, and the cingulate motor areas (Brodmann's areas 23 and 24), situated below the mesial areas F6, F3, and F1. Reprinted (and relabeled) with permission from Rizzolatti, Luppino, & Matelli, "The classic supplementary motor area is formed by two independent areas," in Liders (Ed.), *Supplementary Sensorimotor Area* (Advances in Neurology, vol. 70), pp. 45-56. Copyright 1996 Lippincott Williams & Wilkins.

during the execution of purposive movements. Furthermore, the control of self-initiated movements is attributed to the SMA. Indeed, the question can be asked whether all this does not point to a supramotor role rather than to a supplementary motor function. It is too early for a definite conclusion, but part of the existing controversy seems to be solved by a paper of Matelli, Luppino, and Rizzolatti (1991; see Figure 2). These authors divide the classic SMA into two parts, the SMA proper (area F3) and, just in front of this, the pre-SMA (area F6). The input to both areas is different: F3 but not F6 is connected to M1. This connection is somatotopically organized (Rizzolatti, Luppino, & Matelli 1996). There are also connections to the dorsal part of the premotor cortex and the cingulate areas. Area F6 is mainly connected to the anterior premotor cortex. It receives an additional input from the prefrontal cortex, which does not hold for F3 (Rizzolatti et al. 1996). The thalamic projections are also different for F3 and F6; F3 gets its major input from the ventrolateral and the posterior ventrolateral nuclei of the thalamus, whereas the input to F6 stems from the dorsomedial and the anterior ventral nucleus of the thalamus.

It is a relatively recent discovery that the cingulate region has a function in motor behavior. As a consequence, this area has not been extensively studied. One of the few

facts known about the cingulate region is that it can be divided in two parts: an anterior and a posterior area, the first of which seems to be related to self-paced motor acts (Rothwell 1995, p. 355).

Area 8 of Brodmann is known as the frontal eye field (FEF). It has strong reciprocal connections to the lateral intraparietal area, situated in the lateral bank of the intraparietal sulcus. Both project to the colliculus superior (Milner & Goodale 1995) and are strongly implicated in the control of saccadic eye movements. The FEF also receives an input from two temporal areas, the medial superior temporal area and the fundus of the superior temporal sulcus (Boussaoud & Wise 1993). These areas seem to be involved in the control of pursuit eye movements (Milner & Goodale 1995). In other words, the control of saccades and of pursuit eye movements seems to be organized into two independent fronto-parietal systems.

The Basal Ganglia. The basal ganglia can be distinguished in the neostriatum. They consist of the caudate nucleus and the putamen, the globus pallidus (pars interna and pars externa), the subthalamic nucleus, and the substantia nigra pars reticulata (Figure 3). Originally, DeLong and Georgopoulos (1981) suggested that there were two loops in which different parts of the basal ganglia are connected to the cortex via different thalamic nuclei: a motor loop and a complex loop. The motor loop directs influences from the sensorimotor and premotor cortices via putamen, pallidum, and thalamus to the premotor cortex. The complex loop connects the association cortex via caudate nucleus, pallidum, and thalamus to the prefrontal cortex. These circuits are independent of each other; they remain segregated, as are the leg and arm representations within the motor loop (DeLong et al. 1984). A couple of years later, Alexander, DeLong, and Strick (1986) suggested the existence of five different circuits between basal ganglia and cortex, all built following the same model. The model itself is discussed further in Alexander and Crutcher (1990) and DeLong (1990), whose description will be followed here. Within the motor loop there are two pathways to the globus pallidus pars interna (GPi) and the substantia nigra pars reticularis (SNr). An indirect pathway passes the globus pallidus pars externa (GPe) and the subthalamic nucleus (STN), and a direct pathway innervates the GPi and SNr monosynaptically. From here is a direct connection to one of the possible thalamic nuclei, which project - depending on which thalamic nucleus was passed - to different cortical areas. The projections from the different cortical areas to the putamen (or the globus pallidus, not depicted here) is excitatory. The direct pathway has an inhibitory connection to the GPe/SNr; in the indirect pathway, two inhibitory connections are followed by one excitatory to the same target (GPe/SNr). From here, there is an inhibitory connection to the thalamus and an excitatory connection to the cortex (Figure 3).

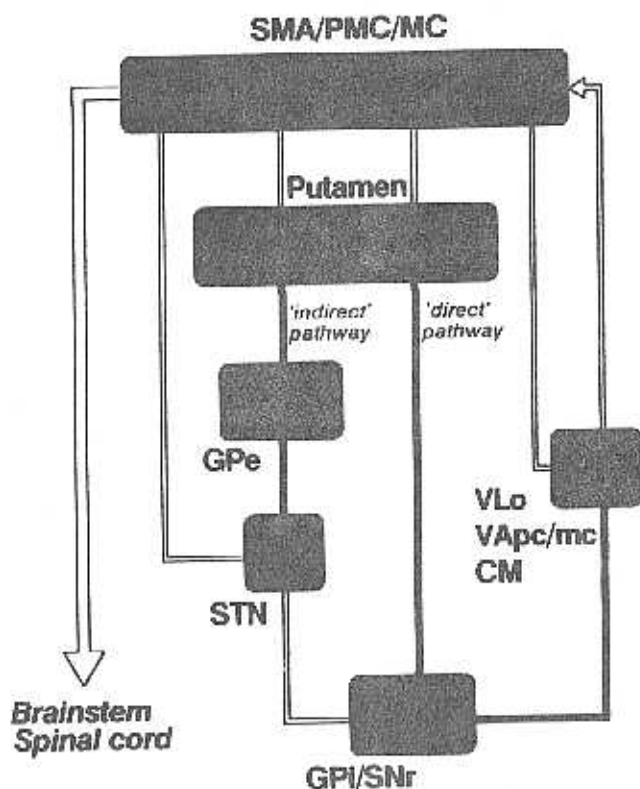


Figure 3. Diagram of the motor circuit in which only the closed loop is depicted. Inhibitory neurons are depicted in black, excitatory neurons in gray. Key: CM, center median; GPe, globus pallidus pars externa; GPI, globus pallidus pars interna; MC, primary motor cortex; PMC, premotor cortex; SMA, supplementary motor cortex; SNr, substantia nigra pars reticularis; STN, subthalamic nucleus; VA, nucleus ventralis anterior; VLo, nucleus ventralis pars oralis. Reprinted with permission from Alexander & Crutcher, "Functional architecture of basal ganglia circuits: Neural substrates of parallel processing," *Trends in Neurosciences*, vol. 13, pp. 266-71. Copyright 1990 Elsevier Science.

Although the basal ganglia seem to be involved in different kinds of cognitive functioning, in the present context we will discuss only their role for motor behavior and, more specifically, motor preparation. Schultz and colleagues (1995) provided arguments for this based upon (1) the behavioral effects of lesions in the basal ganglia in animals and humans, (2) the anatomical targets for the output of the basal ganglia (i.e., the motor cortex and the colliculus superior), and (3) the firing of basal ganglia units in relation to force and direction of movements. It is interesting to note that Schultz et al. (1995) found anticipatory firing of units preceding spontaneous and stimulus-triggered movements – and prior to all kind of stimuli that are of relevance for upcoming behavior. This suggests that an almost simultaneous basal ganglia activity is present during all anticipatory EEG activity that we know about in humans (to be discussed later on).

The Cerebellum. The cerebellum receives ascending input from the spinal cord and descending input from senso-

rimotor cortex via the brainstem. Its output to the cortex runs from the dentate nucleus via the thalamus to MI. In line herewith, Thach (1987) reported preparatory activity in dentate nucleus *prior* to that in MI whereas other cerebellar nuclei only fired *after* movement onset; this suggests that the dentate nucleus is involved in motor preparation, with the other nuclei in control of movement execution. Indeed, lesions in the dentate nucleus in nonhuman primates resulted in the absence of a well-known slow wave, the readiness potential, which can normally be recorded prior to voluntary movements. We will discuss this anticipatory slow wave later on, but here we note that subcortical input to MI seems to be obligatory for the emergence of this slow wave. A more general conclusion is that the activity in the motor cortex is based upon an important subcortical input via the thalamus, which enables modulation of the input relevant for sensory processing and for motor processing in a comparable way. In other words, there is a commonality in the organization of anticipatory attention and motor preparation (Brunia 1997).

Structures Involved in Visuomotor Control

Of the three major modalities, the visual system is presumably the best investigated. We will discuss it here in short because many of our movements are in some way or another coupled to what we see. The optic nerve on its way to the cortex passes the lateral geniculate body, considered a "relay" nucleus for visual information. From here, fibers ascend to the visual cortex and participate in a local intracortical circuit, a cortico-cortical circuit, and a thalamo-cortico-thalamic circuit. The first circuit is excitatory, suggesting that a certain input can have an enduring activity in that column (LaBerge 1995). Cortico-cortical pathways are divided into two main streams for visual information, known as the "what" and the "where" systems (Ungerleider & Mishkin 1982). Fibers returning to the thalamus do so to the lateral geniculate body, but also to the pulvinar. The pulvinar is (among others) connected to the parietal cortex, which plays a role in an attentional network (Mesulam 1981; Posner 1994). Yet it should be kept in mind that 50% of the pulvinar cells do not respond to sensory stimulation, so it is doubtful that the only function of the pulvinar is attentional. The same holds for the parietal cortex, with which it has many reciprocal connections. Many parietal neurons are described as responding upon sensory stimulation *only if* a response has to be generated. Moreover, recent studies in patients with certain parietal lesions suggest that their pathology can be described as "not knowing how to act" rather than as a disturbance in the "where" system (Milner & Goodale 1995). These authors noted that picking up an object requires not only a reaching movement but also that hand and fingers be shaped in such a way that size and orientation of the object are anticipated in order to perform a correct grasping movement. Reaching and grasping are

temporally coupled under normal circumstances, although they seem to be organized independently (Jeannerod 1997). A combined disturbance can be found in patients with optic ataxia following lesions in the posterior parietal cortex: they not only might fail to reach in the right direction, they also fail to orient their hand and form their grasp appropriately (Milner & Goodale 1995, p. 97). This example clarifies that motor preparation is much more than being ready to press a button. Moreover, it illustrates how the posterior part of the cortex is related not only to perceptual processes but also to the organization of action.

Structures Involved in Executive Control

Anatomically, the prefrontal cortex is defined as the projection area of the dorsomedial nucleus of the thalamus. Apart from that input, the prefrontal cortex also receives fibers from the ventral anterior nucleus and the anterior part of the intralaminar nuclei. According to Fuster (1997), behavior is typified as a hierarchical order of elements that are structured in time. He considers the temporal organization of complex behavior to be the main job of this brain area, and he distinguishes three major functions of the prefrontal cortex: (1) preparation for coming events, (2) memory of recent events, and (3) suppression of interference.

As we argued already in the introduction, preparatory behavior is aimed at the setting of relevant motor structures and also of perceptual systems. Perception can be facilitated by attention, a function that is accomplished by the parietal cortex in collaboration with the pulvinar (LaBerge 1995). The attentional network is under the control of the prefrontal cortex; the same holds for the motor cortex and the dorsomedial nucleus. Elsewhere (Brunia 1997) we have claimed that motor preparation and anticipatory attention are realized via comparable networks in which the reticular nucleus of the thalamus plays a crucial role. The reticular nucleus itself is (among others) under the excitatory influence of the prefrontal cortex. Activation of that pathway results in a relative closing of thalamo-cortical channels. In other words, the thalamo-cortical stream of information – be it in the sensory or in the motor route – can still be modulated just before its entrance into the cortex.

An instruction given to a subject must be kept in a working memory circuit together with other relevant information from comparable situations. Fuster and Alexander (1971) recorded unit activity in the prefrontal cortex that they related to a mnemonic process of retaining a cue. Clinical data also suggest that the prefrontal cortex is involved in holding information that is relevant for only a short time. Neuropsychological research in patients with prefrontal lesions shows that they have a deficient response inhibition. The well-known work of B. Milner (1964) with the Wisconsin card-sorting test demonstrates that patients have difficulties in shifting between response strategies. There is much supporting evidence for the notion that the

prefrontal cortex is indeed involved in response inhibition. Fuster (1997) claimed that the medial part of the prefrontal cortex is responsible; Goldman-Rakic (1987) suggested that the function of the prefrontal cortex is initializing, facilitating, or stopping of commands to structures that are involved in motor programming. In other words, the Go-No-Go decision seems to be a function in which the prefrontal cortex participates, as can be concluded from the reports of Sasaki and Gamba (1989; Gamba & Sasaki 1989).

Another function has been suggested by Teuber (1964). In order to distinguish between self-paced movements and externally triggered movements, an organism should be informed about self-initiated movement. Teuber suggested that this is realized via "corollary discharges": a motor command is sent not only to movement-related structures but also to parietal and temporal association areas to inform these areas about the impinging movement. This, too, is an indication of the executive control the prefrontal cortex exerts upon other brain areas. Later on we will see that anticipatory slow waves have a major source in this brain area.

Inferential Context

THE PSYCHOPHYSIOLOGICAL APPROACH TO MOTOR PREPARATION

In the foregoing text we have indicated that, however important the cortex cerebri might be for anticipatory behavior, the role of subcortical structures – the ascending brainstem systems, cerebellum, basal ganglia, and thalamus – must not be forgotten. Much of what happens at the cortical level is, at least partly, a reflection of processes in these structures. As an example we mentioned the well-known anticipatory readiness potential that does not show up if a lesion in the dentate nucleus of the cerebellum is present. This example clarifies the importance of knowledge of subcortical processes for the interpretation of experimental results obtained from the cortex. A real understanding of what happens when a response is prepared and executed must be based upon knowledge of all areas involved. The consequence of this is that we need information from as many different sources as possible.

One psychophysiological approach is to use the EEG (or, more precisely, ERPs) to investigate the relation between behavior and the relevant brain processes. This method can certainly provide results that allow further-reaching conclusions than a strictly behavioral analysis. Yet it should not be forgotten that the EEG and, by implication, most ERPs are a reflection of cortical activity. Changes in this activity that are caused by subcortical processes can certainly be demonstrated in humans, but recordings from subcortical areas can only be obtained in relatively rare clinical cases. Therefore, we also need to know about depth recordings

in monkeys under similar experimental conditions to the ones we are interested in. Such recordings concern mostly cell activity. Electromagnetic brain activity reflects changes in postsynaptic membranes of large numbers of cells in the cortex that are activated more or less simultaneously. If the membrane potentials reach the firing threshold, the cells discharge. Thus, the EEG and the unit firing reflect related but different aspects of the same process. There are relatively few studies in which unit firing and slow potentials have been recorded simultaneously (e.g. Arezzo & Vaughan 1980; Fox & Norman 1968). Monkey studies allow the recording of unit firing at both the cortical and subcortical level. If unit recordings at the cortical level in monkeys show commonalities with the ERP recordings in humans, and if subcortical unit activity in monkeys is related to their cortical unit activity, then we are on relatively safe ground when we consider the whole set of data of importance to our understanding of human behavior.

The study of ERPs or event-related fields (ERFs) provides results of high precision in the time domain, but spatial resolution is a problem. The skin, the skull, and the meninges cause a dispersion of the relevant brain activity owing to their different conduction properties. Recently developed techniques of source localization (see Scherg 1990) provide one possible method to overcome this limitation, but the fact remains that we are unable to record subcortical processes directly from the skull.

This problem does not exist with the technique of positron emission tomography (PET), which provides an image of all areas relevant for the execution of a certain task. This advantage goes along with a loss of precision in time, however. Here a better spatial resolution is obtained, and it is possible to record changes in subcortical activation. The newly developed technique of functional magnetic resonance imaging (fMRI) provides a better temporal resolution than the PET studies, so we can expect more fMRI research to take place on the present topic.

Transcranial magnetic stimulation (TMS; Barker, Jalinous, & Freeston 1985) is a technique by which a short magnetic pulse is applied to the motor cortex via the skull, resulting in a short muscle contraction. The pre-existing excitability of the target motoneurons determines the outcome of the stimulation. If a stimulus is applied during the foreperiod of a reaction time task and if an identical stimulus is applied under control conditions, then comparison of both responses provides an insight into the changes in excitability due to the preparation of a response. This is a comparable (yet dissimilar) approach to the use of reflexes as a probe for studying motor preparation.

If an Achilles tendon reflex (or a Hoffmann reflex) is evoked during the foreperiod of a reaction time task, then the amplitude of the reflex is an expression of the number of alpha-motoneurons that fire as a result of the stimulus strength and the pre-existing excitability of the motoneuron pool. Keeping the stimulus strength constant, changes

in excitability due to the preparation of the movement can be investigated by comparing the amplitudes of the reflexes evoked during preparation with those evoked under control conditions. The changes in amplitude are a peripheral manifestation of supraspinal preparatory processes.

EVENT-RELATED POTENTIALS

The first electroencephalographic measurement related to a human motor act was reported by Bates (1951), who described a negative potential after movement onset that was interpreted as a reafferent sensory evoked potential. The study of preparatory EEG measurements in humans was initiated by the discovery of the contingent negative variation (CNV) by Walter and his colleagues at the Burden Neurological Institute in Bristol, England (Walter et al. 1964). They recorded a sustained negative potential shift of about $-20 \mu\text{V}$ in the 1-sec interval between a warning stimulus (S1, a single click) and an imperative stimulus (S2, repetitive flashes that could be terminated by a button press). The CNV was discernible in the raw EEG traces but became more evident when noise was reduced by calculating averages of twelve successive trials. The CNV reached its maximum amplitude at the presentation of S2 and returned to the baseline level when the response was made.

At about the same time, Kornhuber and Deecke were studying the brain electrical activity that accompanies voluntary motor actions at the University of Freiburg, Germany. They asked their subjects to press a button at intervals of their own choice and recorded the electrical activity from the scalp on magnetic tape. Backward analysis of the tape recording allowed them to study the brain activity preceding the button press. They found a slowly increasing negative potential shift, starting more than 1 sec before the button press (depending on the rate of responding) and increasing up to the instant of the motor act. This negative shift was labeled *Bereitschaftspotential* or readiness potential (RP; Kornhuber & Deecke 1965).

Kornhuber and Deecke (1965) suggested that the neuronal processes underlying the RP and the CNV were similar. The similarities and differences between these slow brain potentials have been the topic of a considerable amount of research, especially in the 1970s and 1980s. Since the CNV is usually larger than the RP, it was thought that the CNV (i) consisted of an RP associated with the motor response but (ii) was recorded on top of another, presumably nonmotor, negativity. This nonmotor negativity was subsequently isolated and termed stimulus-preceding negativity (Brunia 1988).

An interesting psychophysiological tool that can be applied in the study of motor processes is the lateralized readiness potential (see Coles 1989 for an overview). This measure is based on the observation that the amplitude of the RP becomes greater over the hemisphere contralateral to the responding hand than over the ipsilateral hand.

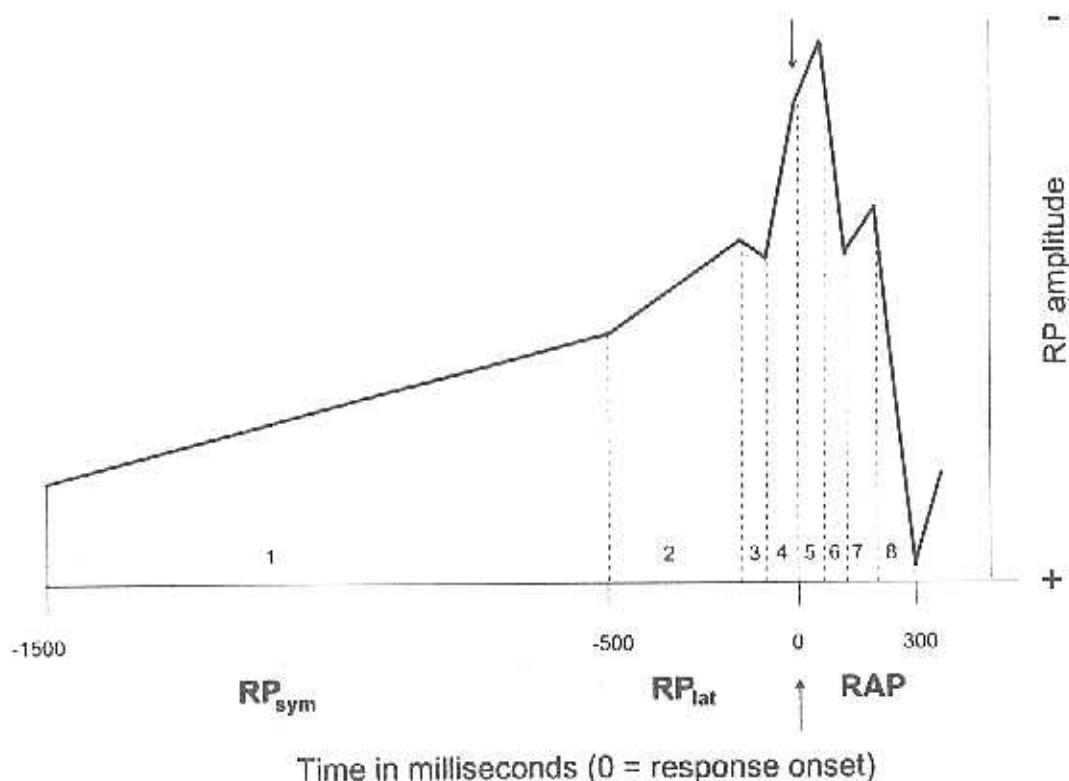


Figure 4. Schematic representation of the eight components of the potentials related to motor acts. The terminology used for the various components is given in Table 1. This representation is a theoretical integration of components that were distinguished based on recordings from various electrode positions; a waveform as depicted in this figure cannot be measured at a single electrode.

Kutas and Donchin (1974) showed that the lateralized portion of the RP could also be measured after an imperative stimulus in a reaction time task if that stimulus indicated the hand with which the response had to be made. The lateralized portion can be isolated by subtracting the ipsilateral from the contralateral potentials, and nonmotor asymmetries in the brain can be removed by subtracting the isolated lateralization for left- and right-hand conditions.

The Readiness Potential

In the original study of Kornhuber and Deecke (1965), four potentials related to the button presses were described: three that occurred before the motor act and one thereafter. By today's standards, one would probably notice that they reported four "components" in the sense of, for instance, Donchin, Ritter, and McCallum (1978). Preceding the button press, Kornhuber and Deecke (1965) distinguished a negative *Bereitschaftspotential*, a premotion positivity, and a negative motor potential. The positive potential complex that followed the button press was designated as a reafferent potential (RAP). In contrast to using names that suggested a functional meaning of these components, other authors preferred to designate the components by polarity and sequence (e.g. Gildea, Vaughan, & Costa 1966) or by polarity and latency (e.g. Shibasaki et al. 1980). Because the number of components studied in various reports has differed somewhat, the naming convention by polarity and sequence has led to some confusion in designating the different components, especially those following the motor act.

Bruma (1987) summarized the most common designations that appeared in the literature up to the mid-1980s. Because no new components have been discovered since that time, the survey is still valid. In Figure 4, a systematic representation of the eight known components is presented; the associated nomenclatures are summarized in Table 1. In the present review, which is focused on the components preceding the motor act, we have adhered as much as possible to the original nomenclature of Kornhuber and Deecke (1965) as a tribute to their seminal work. But we do distinguish between the symmetrical and lateralized portions of the RP, designated by RP_{sym} and RP_{lat} , respectively. The components following the motor act will be referred to using the polarity-latency convention, which is now the most frequently used. These potentials are not reviewed systematically here.

The RP_{sym} starts between one and two seconds prior to the motor act, depending on factors such as the rate at which the motor acts are issued, their nature and complexity, and the limb with which they are issued. The interval between the start of the RP_{sym} and the motor act is shorter at high rates of successive motor acts (Kornhuber & Deecke 1965). Complex motor acts are usually preceded by an

TABLE 1. Terminology Used to Describe Components of Brain Potentials Related to Motor Acts

1	2	3	4	5	6	7	8	Authors
				N				Bates (1951)
← BP →		PMP	MP		←	RAP	→	Kornhuber & Deecke (1965)
← N ₁ →		P ₁	N ₂		P ₂			Gilden, Vaughan, & Costa (1966)
← N ₃ →		P ₁		N ₂	P _{2a}		P _{2b}	Gerbrandt, Goff, & Smith (1973)
← N ₁ →		P ₁	N ₂		P ₂		P ₃	Arezzo & Vaughan (1975)
N _{1a}	N _{1b}	P ₁	N ₂	N ₃	P _{2a}	N ₄	P _{2b}	Gerbrandt (1977)
← N ₁ →				MCP				Papakostopoulos (1978)
← N ₁ →		P ₁		P ₁ , N ₂	P ₂		P ₂	Hazemann, Metral, & Lille (1978)
← N ₁ →		P ₁	N _{2a}	N _{2b}	P _{2a}		P _{2b} , P ₃	Arezzo & Vaughan (1980)
BP	NS	P ₋₃₀	N ₋₁₀	N ₊₃₀	P ₊₉₀	N ₋₁₆₀	P ₋₃₀₀	Shibasaki et al. (1980)
RP I	RP II	—						Libet, Wright, & Gleason (1982)
RP _{sym}	RP _{lat}	PMP	MP	N ₃₀	P ₉₀	N ₁₆₀	P ₃₀₀	This chapter

Note: The sequence numbers of the components refer to Figure 4; arrows indicate the range of the definition relative to the sequential components.

RP_{sym} that starts slightly earlier than when preceding simple motor acts (Lang et al. 1989), and the same is true for foot as opposed to finger movements (Brunia & Van den Bosch 1984). The onset of the RP_{sym} is very consistent within subjects when measured in different recording sessions (Deecke 1987). There are, however, marked differences in onset time between electrode positions. At the vertex electrode (Cz), the RP_{sym} starts as much as 400–500 msec earlier than at precentral or parietal electrode sites (Deecke 1987). The amplitude of the RP_{sym} has a straightforward relation to its onset: it is greater the earlier it starts (Deecke, Grözinger, & Kornhuber 1976). Therefore, the amplitude of the RP_{sym} is also related to the factors influencing its onset, such as response rate, movement complexity, and extremity. In addition, the RP_{sym} has its maximum at the vertex electrode at which the earliest onset was observed.

The early onset and maximum amplitude of the RP_{sym} over the vertex electrode, which is located approximately over the supplementary motor area (SMA), have been used as evidence for the claims that the RP_{sym} is an index of SMA functioning and that SMA activity precedes activity in the primary motor cortex (Deecke 1987). In line with this suggestion, Goldberg (1985) hypothesized that the RP_{sym} is produced by activity in the basal ganglia-dependent loop (see section on basal ganglia), in which input from wide regions of the cortex is gathered and then focused back to restricted premotor regions, especially the SMA. This so-called medial system, as Goldberg referred to it, is schematically represented in Figure 5. Input modulation of this loop is possible at the level of the reticular thalamic nucleus, which overlies the lateral ventral thalamic nucleus and exerts an inhibitory influence on it (Brunia 1993; Skinner & Yingling 1977). It is hypothesized that this loop selects task-relevant features from the environmental context and associates these features with the actions to be executed. Hence, a strategy for future ac-

tions is thought to be specified through the activity of this predictive feedforward loop, a process that may be called motor programming.

If it is true that the RP_{sym} is indeed a measure of the functioning of the medial system, then it should be abolished or attenuated in patients with deficiencies in this loop. Indeed, patients with Parkinson's disease seem to have an abnormally small RP_{sym} (Dick et al. 1989). However, generation of the RP_{sym} may not depend only on the medial loop, since Ikeda and co-workers (1994) described a patient with a cerebellar lesion in which the RP_{sym} was completely abolished. Recent attempts to determine the neural generators of the RP_{sym} in healthy subjects using spatiotemporal dipole modeling failed to establish a significant SMA contribution (Böcker, Brunia, & Cluitmans 1994a; Börzel et al. 1993). However, Praamstra and colleagues (1996b) suggested that this negative finding might be explained by a failure of the previous models to discriminate between SMA and motor cortex contributions to the RP_{sym}; they presented an improved model that included a generator in the SMA. These findings are consistent with intracranial measurements of Ikeda et al. (1992), who recorded an RP_{sym} bilaterally in the SMA. Taken together, the available evidence suggests that the SMA provides a major contribution to the RP_{sym}.

The second component that precedes the motor act is the lateralized portion of the RP, which we termed RP_{lat}. This component, which Shibasaki et al. (1980) referred to as the negative shift (NS'), starts about 500 msec before the motor act, again depending on factors such as the rate with which the actions are issued. Not all researchers recognize the RP_{lat} to be a separate component (see Table 1), but it can be shown to have underlying neural generators that differ from those of the RP_{sym}. We are therefore justified in treating RP_{lat} as a different component. The asymmetry in the RP_{lat} is restricted to central electrode locations,

MOTOR PREPARATION

where greater amplitudes can be recorded over the hemisphere contralateral to the hand or finger with which the motor act is performed. Foot movements result in an ipsilaterally greater amplitude of the RP_{lar} ; this paradoxical finding was hypothesized by Brunia (1980) to be due to the anatomical organization of the motor cortex. The orientation of the cell columns is such that their activity can be most easily picked up by an electrode over the contralateral hemisphere in the case of hand movements, because the hand area is located in the crown of the gyrus. For foot movements, however, their activity is most easily picked up by an electrode over the ipsilateral hemisphere, since the foot area is located in the mesial wall of the gyrus. This interpretation has been confirmed by spatiotemporal dipole modeling of ERPs (Böcker, Brunia, & Cluitmans 1994b) and magnetoencephalographic (MEG) recordings (Hari et al. 1983).

The foregoing explanation of the paradoxical lateralization for foot movements already suggested that the neuronal sources underlying the RP_{lar} are situated in the primary motor cortex. Indeed, in favor of that view is much evidence based on a variety of different techniques: slow intracortical potential studies in nonhuman primates (Arezzo & Vaughan 1975; Gemba, Sasaki, & Hashimoto 1980; Sasaki et al. 1979); unit studies in nonhuman primates (Requin 1985); MEG measurements in humans (review in Lang et al. 1991); regional cerebral bloodflow studies in humans (Roland et al. 1980), and spatiotemporal dipole modeling of scalp-recorded potentials in humans (Böcker et al. 1994a; Bötzel et al. 1993; Praamstra et al. 1996b). Gemba et al. (1980) recorded a transcranial inversion of the RP not only in the primary motor cortex but also in the premotor and primary somatosensory cortex (of monkeys). Therefore, it is plausible that there are several generators of the RP_{lar} . Although these sources are cortical, it does not mean that the subcortical input is of minor importance. In fact, it seems to be essential since cerebellar hemispherectomy abolished the potentials in all three areas; after a few weeks, recovery in the premotor and somatosensory areas was observed but not in the primary motor cortex (Sasaki et al. 1979). Later on it was demonstrated that the dentate nucleus is essential. Cerebellar outflow runs from the dentate nucleus (via the thalamus) to the motor cortex. In humans, the RP_{lar} depends also on the functioning of this nucleus (Ikeda et al. 1994; Shihasaki et al. 1986).

The finding that the RP_{lar} disappears upon ablation of the dentate nucleus contralateral to the motor cortex in-

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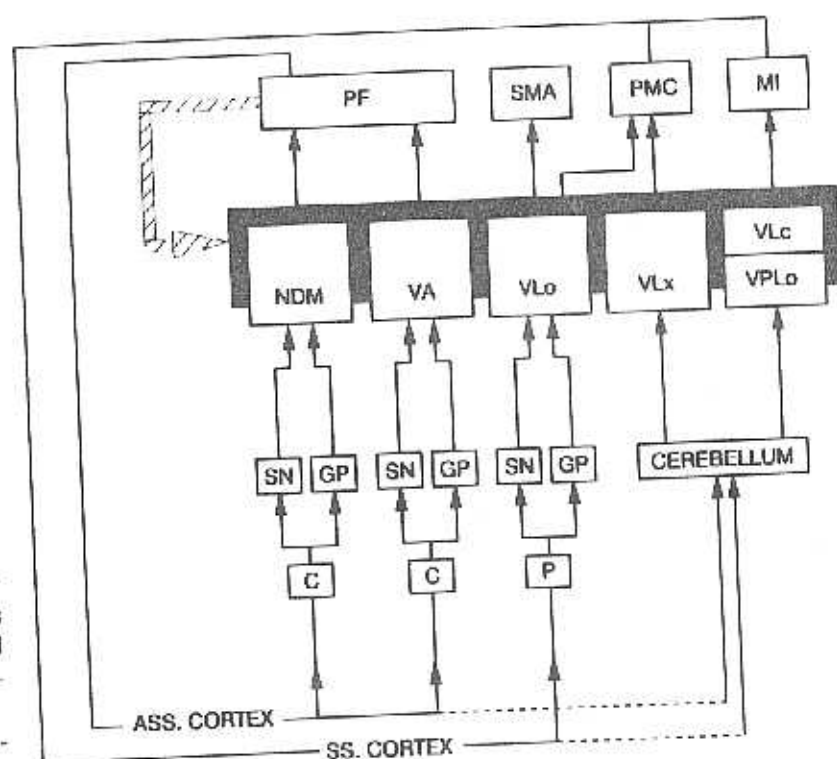


Figure 5. Simplified representation of the different cortical areas connected to caudate nucleus (C), putamen (P), and cerebellum. (Key: MI, primary motor cortex; NDM, dorsomedial nucleus; PF, prefrontal cortex; PMC, premotor cortex; SMA, supplementary motor area; VA, nucleus ventralis anterior; VLc, nucleus ventralis lateralis pars caudalis; VLo, nucleus ventralis lateralis pars oralis; VLx, pars X of the nucleus ventralis lateralis; VPLo, nucleus ventralis posterolateralis; black shell, nucleus reticularis thalami, which inhibits locally the underlying relay nuclei.) The major input to the caudate nucleus stems from the association cortex, to the putamen from the somatomotor cortex, and to the cerebellum from the somatomotor cortex but also from the association cortex. The neostriatum outflow runs via the putamen in a motor loop or via the caudate nucleus in different complex loops. Substantia nigra and globus pallidus (externa) are the output channels, which are connected via different thalamic nuclei to different cortical areas. What Goldberg has called the medial and lateral systems are the motor loop via the putamen and the route via the cerebellum, respectively.

involved in the response (hence ipsilateral to the response itself) indicates that the cerebello-thalamo-cortical loop is necessary for the generation of the RP_{lar} . The ipsilateral dentate nucleus of the cerebellum projects to the contralateral thalamus (caudal part of the lateral ventral nucleus) and thence to the contralateral primary motor cortex, while input to the cerebellum is provided by motor and sensory association cortices (Allen & Tsukahara 1974). In the model presented by Goldberg (1985), this loop is called the lateral system (see Figure 5), which is thought to provide context-dependent adjustments of the parameters of

the movement strategy selected by the medial system; this loop is therefore a feedback system, in contrast to the medial system (which was thought to operate in a feedforward mode). In patients with Parkinson's disease, the RP_{lat} is greater than in normal age-matched controls (Dick et al. 1989). This finding has been explained by assuming that these patients rely more on the lateral system because their medial system is defective, as indicated by the attenuated RP_{sym} . This explanation is consistent with the clinical observation that patients with Parkinson's disease depend on visual information for the successful initiation and performance of various motor acts (Brooks 1986).

The next component preceding the motor act is the premotion positivity (PMP). The PMP is a widespread bilaterally symmetrical positive wave with a maximum at the midline parietal electrode (Pz). It starts about 50–90 msec before the onset of muscle activity as determined by the EMG. Over central areas, it is more positive over the hemisphere ipsilateral to the response side, probably owing to the overlap with the negative motor potential (which immediately follows the PMP). Deecke and Kornhuber (1977) hypothesized that the PMP corresponds to the actual command for the movement. There are no animal data available related to the possible neuronal generator of the PMP, and spatiotemporal dipole modeling of human scalp potentials have not yielded reliable models of the PMP either (see e.g. Böcker et al. 1994a). It is also possible – as suggested by Neshige, Lüders, and Shibasaki (1988) – that the PMP is merely an epiphenomenon reflecting the transition between two negative waves, the RP_{lat} and the MP, and does not have a real neurophysiological generator. This possibility is supported by the failure to identify the PMP in subdural recordings (Ikeda & Shibasaki 1992).

The motor potential (MP) is the last premovement potential, starting about 10–50 msec prior to the onset of muscle activity. There has been some confusion regarding whether the MP precedes or follows the motor act. Gerbrandt, Goff, and Smith (1973) recorded a negativity after the onset of muscle activity, making its role in initiation of the motor act unlikely. Yet it turned out that the negativity measured by Gerbrandt et al. (1973) was actually part of the reafferent potentials and that the MP indeed occurs preceding the motor act (Gerbrandt 1977; see also Deecke & Kornhuber 1977). The MP is a unilateral negative wave with a maximum over precentral electrode positions contralateral to the responding hand (ipsilateral for foot movements). Combined recording of slow intracortical potentials and unit activity in nonhuman primates (Arezzo & Vaughan 1980) showed that the neuronal source of the MP is located in layer V of the hand area of the primary motor cortex, where a high density of pyramidal tract neurons are known to originate. This location is confirmed by human spatiotemporal dipole models (Böcker et al. 1994a; Bötzel et al. 1993; Praamstra et al. 1996b) and

magnetoencephalographic recordings (Lang et al. 1991). These findings confirm the original interpretation of the MP by Kornhuber and Deecke (1965; see also Deecke & Kornhuber 1977 and Deecke 1987) that the MP reflects the corticospinal outflow innervating the motor act.

In sum, these findings suggest that three processes are involved in the initiation of voluntary, self-paced, motor acts:

1. selecting a motor strategy, presumably an activity of the medial system involving the basal ganglia and the SMA and reflected in the RP_{sym} ;
2. setting the appropriate parameters for the movement depending on the external context – a function of the lateral system, involving the cerebellum and the primary motor cortex and reflected in the RP_{lat} ; and
3. the command to move – involving discharge of pyramidal tract neurons in the primary motor cortex and reflected in the MP.

The independence of the actual motor command from the preparatory processes agrees also with behavioral models of motor preparation and performance, such as Büllock and Grossberg's (1988) vector integration model, in which prepared movements are energized by a separate Go command.

The Contingent Negative Variation

The early work of Walter and his colleagues was aimed not at motor preparation but at the concept of expectancy. Walter et al. (1964) showed that the CNV (a) developed in the 1-sec interval between a click and a series of flashes and (b) was terminated by a button press. The simple pairing of the click and the flashes, without a motor response, did not result in an appreciable potential shift. When S2 (and hence the response) was omitted, the CNV gradually declined; it was restored if the target stimulus was reintroduced. Yet the CNV did not merely depend on the response, because a CNV was found if the subjects had to estimate a time interval *without* producing a response. Walter and co-workers associated the CNV to the probability that a response to S2 was required. Because the attitude of the subjects and the instructions given to them also seemed of importance, the concept of "expectancy" was used, and for some time the CNV was known as the expectancy (E) wave. In subsequent research the CNV was associated with such other constructs as conation (defined as intention to act; Low et al. 1966), motivation (Irwin et al. 1966), and attention (Tecce 1972).

The use of longer intervals between the two successive stimuli showed that the original 1-sec CNV was actually a summation of two separate waves (Loveless & Sanford 1974). The early or O-wave (for orientation) had a frontal maximum and was thought to be a response to the first stimulus because it was shown to be related to such stimulus characteristics as modality, intensity, and duration. The late or E-wave (for expectancy) – sometimes referred

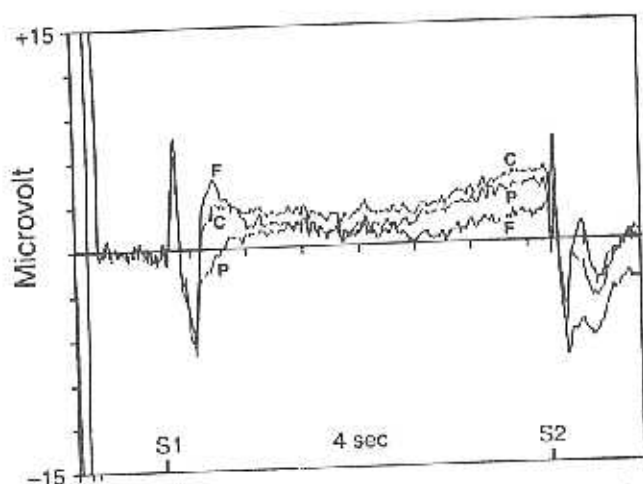


Figure 6. Contingent negative variation recorded during a foreperiod of 4 sec. The early wave after the first stimulus has a frontal maximum decreasing toward more posterior sites. The late wave increases up to the second stimulus and exhibits a central maximum. (Adapted from Brunia & Haagh 1986.)

to as the "terminal" CNV - had a central maximum; it was initially believed to be a sign of the expected occurrence of the second stimulus but was later related to motor programming (see Figure 6). The existence of early and late components with (respectively) frontal and central dominance was demonstrated by McCarthy and Donchin (1978) - using principal components analysis - to constitute the CNV recorded in a short (1-sec) foreperiod. Rohrbaugh, Sydulko, and Lindsley (1976) recorded CNVs in a 4-sec interval between paired stimuli (a tone and a flash, followed by a manual response). They compared the morphology and scalp distribution of the CNV with the potentials elicited by unpaired tones and uncued responses. The early wave of the CNV showed the same morphology and scalp distribution as the potential recorded after the unpaired tone, namely, a frontal maximum and parietal minimum within one second after the tone. The late wave of the CNV had a shape that was similar to the potential elicited by the uncued response and exhibited a central maximum with slightly larger amplitudes over the hemisphere contralateral to the responding hand. Rohrbaugh et al. (1976) concluded that the late CNV is essentially a readiness potential.

In an influential review, Rohrbaugh and Gaillard (1983) reiterated their view that the CNV consisted of an independent early and late wave, of which the late wave was identical to the RP and hence related to motor processes. Their arguments in favor of the motor programming interpretation of the late wave can be summarized as follows.

1. During short foreperiods, the CNV is attenuated when no motor response is required. During longer foreperiods, the late CNV is attenuated (or even absent) when no response to S2 is required or when a delayed instead of an immediate response is required.

2. The amplitude of the late CNV varies as a function of task variables assumed to be related to motor preparation, such as foreperiod duration and foreperiod variability. In addition, it is increased (a) under speed as opposed to accuracy instructions and (b) preceding fast as compared to slow responses within the same series. The late CNV does not vary as a function of sensory manipulations such as stimulus degradation.
3. The late CNV is similar in morphology and scalp distribution to the RP, with a maximum over cortical motor areas. Preceding manual responses, both are dominant over the hemisphere contralateral to the movement side, whereas an ipsilateral dominance is found preceding pedal movements. In addition, the CNV is greater when larger amounts of muscular effort are required for the response to S2, which has also been found for the RP.

Rohrbaugh and Gaillard (1983) also described a number of methodological issues that could bias the interpretation of late CNV findings, such as the length of the foreperiod and the resulting contribution of the early wave as well as the influence of movements (both instructed and non-instructed). In this way, they reinterpreted findings which suggested that the RP and the late CNV were to some extent different phenomena. As a result, the contribution of motor variables to the late CNV is now beyond doubt.

However, there also remain some issues which suggest that the late CNV is more than just an RP. First, the CNV is usually greater than the RP (Brunia & Vingerhoets 1981; van Boxtel & Brunia 1994b), suggesting that additional negativity underlies the CNV. This finding agrees with the clinical observation of Ikeda et al. (1994) that frontal negativity can be measured during the foreperiod of a reaction time task in a patient with a cerebellar lesion that abolished the RP. The additional negativity may be an instance of the stimulus-preceding negativity, which will be briefly discussed in the next section. Second, contralaterally greater amplitudes have been more frequently found for the RP than for the CNV. In part, this may be due to the fact that, in a reaction time task, the lateralized portion of the CNV may be contained in the interval between the second stimulus and the response, and not before S2. However, the more general problem is that the components distinguished in the context of voluntary motor acts, as discussed in the previous section, can not be demonstrated in a CNV paradigm - for instance, by spatiotemporal dipole analysis of scalp-recorded potentials (Böcker 1994). Third, although the late CNV is attenuated when no motor response is given, it can still be recorded when no motor response is required, even when taking into account the methodological pitfalls pointed out by Rohrbaugh and Gaillard (1983; see also Ruchkin et al. 1986).

The RP and the late wave of the CNV are measured in different paradigms in more than one respect. The

increased timing constraints induced by the speed instructions in the CNV paradigm may be of special importance. From this perspective, it should come as no surprise that additional waves may be present in the CNV paradigm, contributing to the late wave. For instance, van Boxtel (1994) concluded from a series of precueing studies that at least two nonmotor components contributed to the late wave of the CNV. The first was related to the anticipation of task-relevant stimuli (SPN of second category in next section) and exhibited a bilaterally symmetrical parietal maximum. This component probably reflects the presetting of cortical networks to speed up the imminent processing of stimulus information in these networks. The second nonmotor component was tentatively related to the effortful control over task performance; it showed a bilaterally symmetrical maximum over the frontal cortex. The presence or absence of the various components, motor and nonmotor, depends on the exact task circumstances, instructions to the subjects, their subjective interpretation, and so on. As a consequence, the amplitude and scalp distribution of the CNV late wave is often found to differ from experiment to experiment.

In the more simple CNV tasks, the late wave of the CNV is mainly determined by the level of motor preparation and is therefore at least functionally similar to the RP. The hypothesis that the late wave is mainly determined by activity in the medial (basal ganglia-dependent) system depicted in Figure 5 is supported by two lines of evidence. First, the late wave is attenuated in patients with Parkinson's disease who are thought to have a defective medial system (Praagstra et al. 1996a). Second, CNVs can be recorded in the caudate nucleus of monkeys, although with reversed polarity (Rebert 1977). The presence or absence of the activity in the lateral (cerebellum dependent) system, which produces the contralaterally greater amplitudes, depends on experimental variables that are not yet completely understood. When the side of responding is an important task variable indicated by the second stimulus, then the lateralization can be shown to be present in the reaction time interval (Kutas & Donchin 1974).

The Stimulus-Preceding Negativity

Brunia (1988) hypothesized that the additional negativity distinguishing the CNV from the RP was related to anticipation of the upcoming S2. Motor preparation and stimulus anticipation are necessarily confounded in the foreperiod of a reaction time task. Damen and Brunia (1987) showed that stimulus anticipation without simultaneous motor preparation resulted in a negative wave with a parietal maximum and a right hemisphere preponderance. They termed the negativity stimulus-preceding negativity (SPN); although thought to be exclusively related to nonmotor factors, it frequently contaminates movement-related negativity and it is therefore briefly discussed here. In particular, tasks involving continuous motor output that can

be visually monitored (e.g., tracking tasks) may be susceptible to this contamination. When such tasks are executed with the right hand, the left-hemisphere preponderance of the movement-related potentials is likely to be canceled by the right-hemisphere dominance of the SPN, resulting in a bilaterally symmetrical wave. Whether this is actually the case can be demonstrated by studying responses with the left hand, since right-hemisphere dominance of the SPN is greater for responses with the left than with the right hand (Damen & Brunia 1987).

Van Boxtel (1994) reviewed research into the SPN and concluded that the SPN (a) can be recorded preceding three types of stimuli and (b) probably also has different neural generators in those cases (Figure 7; see also Böcker & van Boxtel 1997).

1. *Stimuli providing knowledge of results about prior performance.* In this case, the SPN has a parietal maximum and a right hemisphere preponderance, especially over anterior electrode positions (Damen & Brunia 1987). This instance of the SPN is probably generated by bilateral parietal sources and a unilateral source in the right fronto-temporal cortex (Böcker 1994).
2. *Stimuli transmitting information about a future task.* In this case the SPN also has a parietal maximum, but it is bilaterally symmetrical and much smaller than the SPN prior to stimuli providing knowledge of results. This instance of the SPN can be recorded preceding all task-relevant stimuli; it contributes to the late wave of the CNV (van Boxtel & Brunia 1994a), although the contribution is small. It probably is generated by a pair of bilateral parietal cortical sources.
3. *Probe stimuli with which the outcome of a previous task must be matched.* Again, a parietal maximum is found in this case, but a left-hemisphere advantage is observed (Chwilla & Brunia 1991). The sources of this instance of the SPN are unknown.

Another negative shift of frontal cortical origin, possibly related to the effortful control over task performance in the forewarned reaction time task, is thought to contribute to the late wave of the CNV (van Boxtel 1994; see also Figure 7). This negativity corresponds to the difference between the RP and the CNV in the cerebellar patient described by Ikeda et al. (1994).

The Lateralized Readiness Potential

The most important development of the last decade in the psychophysiology of motor control is the use of the lateralized readiness potential (LRP). As already indicated, Kutas and Donchin (1974) showed that the lateralized part of the readiness potential (RP_L) can be measured after an imperative stimulus that calls for a response with either the left or the right hand. They suggested that the difference can be used as an on-line index of the degree of motor preparation in reaction time tasks. This idea was

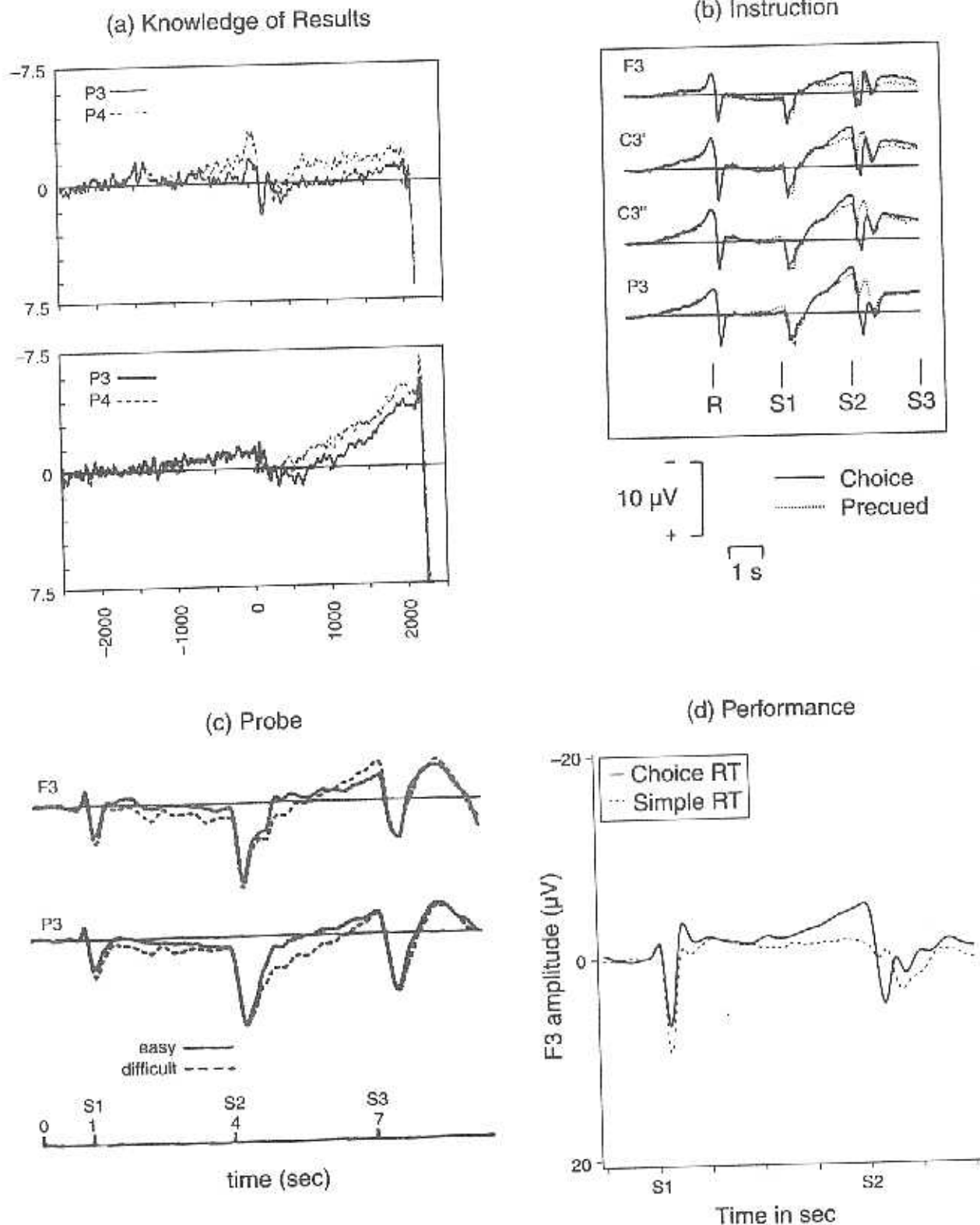


Figure 7. Stimulus preceding negativity recorded prior to different types of stimuli: (a) preceding a stimulus conveying knowledge of results about prior performance occurring at 2,000 msec after the response (adapted from Damen & Brunia 1987); (b) preceding a stimulus providing an instruction about future performance (S1; adapted from van Boxtel & Brunia 1994b); and (c) preceding a probe stimulus with which the outcome of a previous task has to be matched (S3; adapted from Chwilla & Brunia 1991). Panel (d) shows the frontal negative shift related to the control over task performance (adapted from van Boxtel 1994).

elaborated in the studies of De Jong et al. (1988) and Gratton et al. (1988) and has been frequently used since then to monitor the amount of direction-specific motor preparation (see also Coles 1989). De Jong et al. (1988) termed this measure the "corrected motor asymmetry" in order to avoid any confusion concerning this measure's being obtained in a reaction time task – unlike the RP, which is obtained when movements are self-paced. Nevertheless, the term lateralized readiness potential is used most frequently nowadays, justified by the fact that it is calculated from RP_{lat} even though obtained in a CNV-like paradigm.

Calculation of the LRP is a two-step process. First, the lateralized portion of the signal is isolated by subtracting the ipsilateral potentials from the contralateral potentials, measured over the motor cortex. The next step is to average or subtract the lateralization for left- and right-hand conditions. As a result, asymmetries in the brain that are irrelevant to the direction of the correct response disappear from the signal. Further details about procedures and uses of the LRP in psychological research are outside the scope of this chapter but are discussed elsewhere in this volume (see Chapter 3). We want to emphasize one interesting property of the LRP: around the start of muscle activation, the LRP amplitude is almost constant across conditions (Gratton et al. 1988). Based on this finding, Gratton and colleagues proposed that a fixed level of response activation must be exceeded in order to trigger a response. Cognitive models of response preparation, known as "accumulator" models, similarly assume a gradual accumulation of response-related activity toward a certain threshold. These models account for the observed variability in reaction times by assuming a variable accumulation rate, a variable response threshold, or both. Hanes and Schall (1996) provided support for the fixed-threshold hypothesis with single-cell recordings in the motor areas of monkeys performing specific eye movements. The constancy of the LRP amplitude at muscle activity onset is consistent with that view (Coles 1997).

Whether the amplitude of the LRP at muscle onset provides a reliable index of the response threshold in the motor cortex remains an open question. It can be argued that the threshold is always overestimated in that case, since the neural transmission from the motor cortex to the muscle takes time (estimates range from about 25 msec to 50 msec). De Jong, Coles, and Logan (1995) used the LRP amplitude at 50 msec before response (not muscle) onset as the response threshold. However, it is unknown if the use of that value leads to an underestimation of the response threshold in the motor cortex. This might be the case because, on trials in which no response was issued, the maximum LRP amplitude exceeded the virtual threshold (as determined at 50 msec before response onset) but remained below the amplitude at response onset. Other criteria for the response threshold have been suggested, but to date there does not seem to be a consen-

sus about this matter (Band & van Boxtel 1999). This area will undoubtedly prove to be a fruitful one for future investigations, which will also have to be concerned with the relation of the threshold in the motor cortex and the MP of Kornhuber and Deecke (1965).

REFLEXES

The cortical manifestations of motor preparation discussed so far are a reflection of excitatory postsynaptic changes in the membrane potential of cells in the different motor areas. Firing of these cells excites in turn the cells in brainstem and spinal cord, causing similar changes in their membrane potential. If such changes in membrane potential take place in motoneurons of the spinal cord, they cause a change in that potential toward the firing threshold (but not necessarily so far that the cells discharge). Thus, spinal changes in excitability of motoneurons need not be manifest in the surface EMG. In their survey of a number of monkey studies, Evarts, Shimoda, and Wise (1984) explicitly denied that peripheral anticipatory EMG activity was present; they suggested that a subthreshold activation of motoneurons or interneurons might have taken place. In contrast to Evarts et al. (1984), a small EMG activity was reported in monkeys by Riehle and Requin (1989) – in accord with some EMG studies in humans (Brunia & Vingerhoets 1980; Haagh & Brunia 1984). In the latter study, subjects had to prepare a plantar flexion of the right foot. Apart from a systematic increase in EMG activity in the agonist (the calf muscles), a similar increase was recorded in the antagonist (the anterior tibial muscle) and in several other muscles in the same leg. No such increase in activity was found in the other leg, while a decrease was recorded in the EOG (electro-oculogram) and the mylohyoidius muscle (mouth bottom). So, preparation of a simple foot movement results in a complicated picture. The decrease in facial muscle activity is in line with Obrist's idea that motor preparation goes along with a quieting of irrelevant muscle activity (Obrist 1976), but the rest of the findings do not (Brunia 1984a). The small increase in EMG activity found in a number of leg muscles showed a significant negative correlation with reaction time. However, there was no indication of a stronger correlation for the agonist than for the other muscles. It is therefore doubtful that the slight increase in EMG activity is selectively related to response preparation.

Subthreshold changes in excitability of a motoneuron pool can be investigated with reflexes (Paillard 1955). All other things being equal, an increase in excitability would cause an increase in reflex amplitude and a decrease in excitability would result in a decrease in amplitude. Thus, the size of the reflex amplitude can be considered an estimate of the changes in spinal excitability. Achilles tendon and Hoffmann reflexes have been used to study motor preparation during the foreperiod of a warned reaction time task

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(Bonnet et al. 1981; Brunia & Boelhouwer 1988; Requin, Bonnet, & Semjen 1977). These reflexes can be evoked bilaterally in the calf muscles at unpredictable points in time by using a (mechanical or electrical) stimulus while subjects prepare for a unilateral response with the foot or a finger. If a unilateral finger movement is prepared then the calf muscles are not involved in the response, so eventual changes in reflex amplitude cannot be considered to be specifically or selectively related to the preparatory process. If a unilateral plantar flexion is prepared, contralateral calf muscles are likewise not involved in the response. Only changes in amplitude of homolateral reflexes can be considered to be selectively related to the preparatory process. The following picture emerges from our different studies (Brunia, Scheers, & Haagh 1982; see also Figure 8).

1. The warning stimulus is followed by an increase in reflex amplitude, which is independent from the involvement in the response.
2. In case of unilateral plantar flexion, there is a differential effect present in the second half of the foreperiod. If the calf muscles are uninvolved in the response, the reflex amplitude is larger during the foreperiod than during the intertrial interval. If the calf muscles are involved in the response then the reflex amplitude is slightly larger (or not different) from baseline.
3. Immediately following the imperative stimulus, the differential effect reverses: reflex amplitudes in the involved muscles become larger than in the uninvolved muscles. Both are above baseline.
4. In case of a unilateral finger flexion, both calf muscles are uninvolved. Reflex amplitudes remain larger than baseline.
5. Immediately following the imperative stimulus, a further increase takes place that is comparable to what happens in the contralateral leg with a unilateral plantar flexion.

The changes in reflex amplitude are independent of the length of the foreperiod (Brunia 1983; Brunia et al. 1982). Preceding a unilateral dorsiflexion of the foot, in which the calf muscles are considered uninvolved, reflex amplitudes on both sides remain above baseline (Brunia 1984b).

It is counterintuitive that in none of our experiments was there any sign of increased reflex activity in the agonist, even though indications of an increase in excitability seem to be present when the calf muscles are uninvolved. Although these results might seem puzzling at first, it has been hypothesized (Requin & Paillard 1971) that a presynaptic inhibition of Ia afferents to the agonist motoneuron pool might be the cause of this phenomenon (see also Bonnet et al. 1981; Brunia et al. 1982). We have already discussed the slight increase in surface EMG activity found in the agonist but not in the contralateral calf muscle (Brunia & Vingerhoets 1980; Haagh & Brunia 1985). This points to an increased excitability in the agonist motoneuron pool,

which is stronger than on the uninvolved side. Yet on the uninvolved side there was an increase in reflex amplitudes compared to the control condition, pointing to an increase in excitability on that side, too. The presynaptic inhibition of the Ia afferents from the agonist might be part of the preparatory process, its function being the defense of the motoneuron pool against possibly disturbing influences from the periphery, which might cause a premature response. Thus, the absence of a facilitation of the reflexes evoked via the agonist motoneuron pool might be the result of a balance between an increase in excitability of the cells in the agonist motoneuron pool and the presumed presynaptic inhibition of the Ia afferents from the agonist to that same pool. We therefore consider the reflex findings in the agonist as a lack of facilitation rather than as a sign of inhibition (Brunia 1984b).

This interpretation is at variance with several publications of the Marseille group claiming that reflexes evoked not only in the agonist but also (sometimes) in the uninvolved muscles show a decrease in amplitude (Bonnet et al. 1981; Requin, Lécas, & Bonnet 1984; Requin et al. 1991). Yet in a large series of experiments we have never found a decrease in amplitude below baseline (Brunia 1983, 1984b; Brunia & Vuister 1979; Brunia et al. 1982; Scheers & Brunia 1982, 1985) – except in one study (Scheers & Brunia 1986) where the agonist was deliberately contracted. In the latter study a decrease was indeed present. This made us conclude that reflexes are reliable estimators of spinal excitability only when there is no background EMG activity in the agonist. The divergent results between the Marseille group and ours might very well be related to this. Moreover, the decrease in H-reflex amplitude reported by Requin et al. (1977, 1991) is at variance with some of the other studies of the same lab and of others. For example, no such decrement was found during a 1-sec foreperiod (Hayes & Clarke 1978; Sullivan 1980), a 2-sec foreperiod (Semjen & Bonnet 1982), or a 4-sec foreperiod (Brunia & Vuister 1979). Bonnet (1981) did not find a decrease in T-reflex amplitudes below baseline in a 1-sec foreperiod preceding a ballistic movement, and Bonnet and Requin (1982) reported that the M1 response, which is comparable to the T-reflex, remained above baseline as well. Thus, although the results of a large number of experiments do not necessarily point to a rather generalized inhibition, the very existence of the differential effect – that is, the difference in reflex amplitude between muscles involved and uninvolved in the response – is beyond doubt. Still, its predictive value for performance is questioned (Requin et al. 1991) because the size of the effect is not correlated with reaction time. On the contrary, in a Go-No-Go experiment with response probabilities at 80%, 50%, and 20% in blocks, we found only a differential effect in the first condition; in the last condition, reflex amplitudes behaved as uninvolved: they remained above baseline on both sides (Brunia & Boelhouwer 1988).

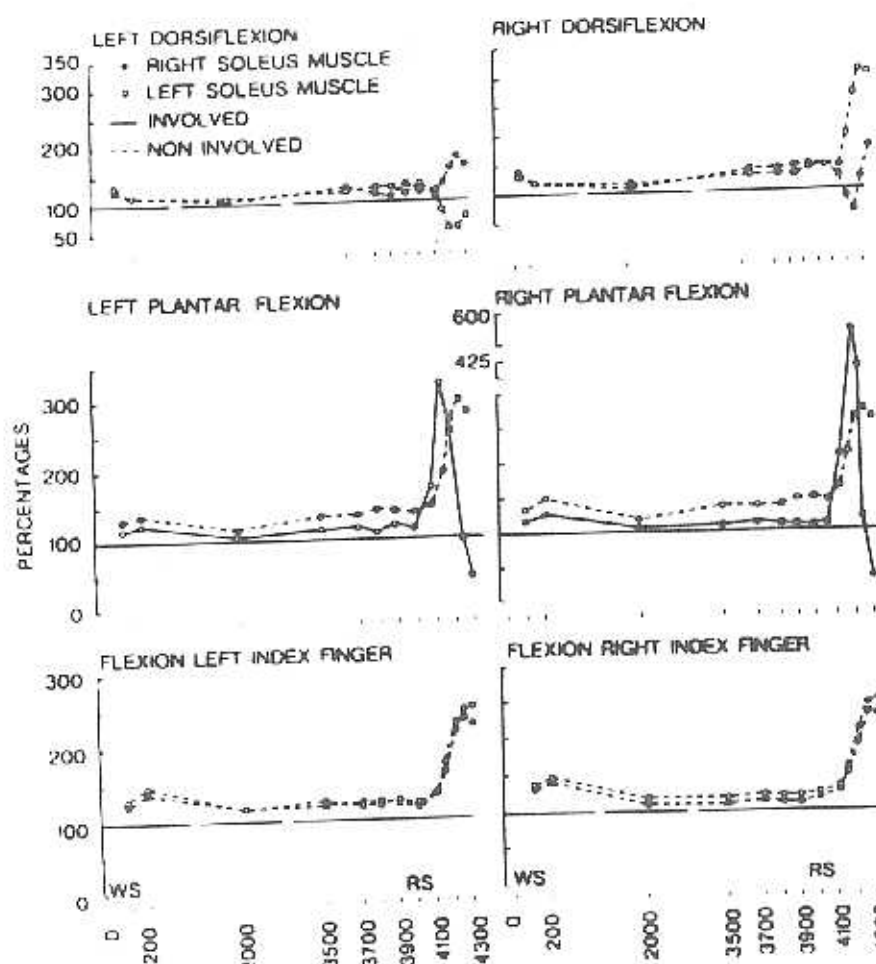


Figure 8. Summary of the results of a number of experiments in which Achilles tendon reflexes were evoked bilaterally in the calf muscles of healthy subjects during the 4-sec foreperiod of a reaction time task. Reflexes evoked during the intertrial interval served as baseline. The responses were: (1) a left or right dorsiflexion of the foot (top); (2) a left or right plantar flexion of the foot (middle); and (3) a button press with the left or right index finger (bottom). Calf muscles are agonist in a plantar flexion. After a phasic increase in amplitude following the warning stimulus, reflex amplitudes in all cases remain above baseline when the muscle is uninvolved in the response (bilateral in 1 and 3 and unilateral in 2). Reflexes evoked in the agonist are not different from baseline. In involved muscles, the differential effect reverses within 100 msec after the imperative stimulus. There is a sharp increase in amplitude in the involved muscles and also (though to a lesser extent) in the uninvolved muscles.

The results of Haagh and Brunia (1984) pointed to an activation of a number of muscles in one and the same leg, rather than to an activation of the agonist alone. This might be related to a stabilizing of the knee and the ankle joint. We have no experimental data to suggest that the afferents from these muscles are also under a presynaptic inhibitory control, although that seems plausible. Taken together, outcomes of the reflex experiments suggest that motor preparation is accompanied by an increase in excitability of agonist motoneurons and of

synergist motoneurons, while a presynaptic inhibitory control protects the agonist motoneurons and presumably the synergist motoneurons against a premature firing. There seems to be no reason to think that the preparatory process in the periphery does more than organizing this general response pattern. In other words, most of the preparation is organized at a higher (presumably, cortical) level.

For the analysis of human information processing, investigators mainly studied responses with the upper limb. There is an obvious reason for that, since our hands are pre-eminently the instruments we use to manipulate the world around us. In the studies mentioned before, reflexes were investigated in legs. Although these results may have a degree of ecological validity with respect to automobile driving, it is unclear whether they apply to movements of the upper extremities. The soleus muscle plays a role in the maintenance of posture, while arm and hand are involved in reaching and grasping. Our efforts to start a series of reflex studies in arm muscles failed because it is not possible

to evoke sufficiently stable reflexes over the necessary number of trials to permit averaging. However, Bonner and Requin (1982) were successful in evoking long loop reflexes in arm muscles. If a sudden stretch in a lightly tensed involved muscle is evoked then two responses show up, M1 and M2; M1 is comparable to the monosynaptic reflexes discussed before and M2 is the long loop reflex. The first showed an increase followed by a decrease, while M2 was increased during the whole foreperiod. The authors interpreted the decrease in M1 as due to presynaptic inhibition; the second response was considered a sign of increased excitability of the agonist motoneurons. Up to now, only a few similar studies have been carried out.

Hasbroucq and associates (1997) used transcranial magnetic stimulation to study changes in spinal excitability. This stimulation induces the firing of cortical interneurons that project to the corticofugal pyramidal tract cells. The response obtained in the muscle is the motor-evoked potential (MEP), which has two drawbacks: it is highly variable and it renders impossible any distinction between cortical and spinal contributions. During a short foreperiod, the authors found indications of a decrease in excitability in the agonist motoneurons prior to arrival of the imperative stimulus. How this relates to results obtained with leg

reflexes is not clear. It would be interesting to replicate – using this new technique in arm muscles – the series of reflex studies discussed previously.

Epilogue

While a subject is waiting to respond, the arrival of an imperative stimulus is anticipated and the response is prepared. It has been argued here that both processes are based upon a thalamo-cortical stream of information via different thalamic nuclei. Each thalamo-cortical pathway functions as a channel that transmits specific sensory or motor information to the relevant cortical structures. These channels are neither completely open nor completely closed; they can be gated via a control mechanism in which the RN plays a crucial role. This nucleus overlaps the different sensory and motor thalamic relay nuclei and exerts a local, topographically organized, inhibitory influence upon them. The RN itself is open for a generalized inhibition from the reticular formation via the ARAS, as Skinner and Yingling (1977) demonstrated for the sensory nuclei. We claim that the same holds for the motor thalamic nuclei. The generalized inhibition of the locally inhibitory RN cells results in a generalized disinhibition of the thalamic relay nuclei. This process is at the basis of an increase in the state of arousal: all gates are open, both sensory and motor. The RN is also open for an excitatory frontal control mechanism. In contrast to the influence from the reticular formation, this is topographically organized and so allows for a localized activation of the locally active inhibition. The consequence of activity in this system is the closing of a gate. This mechanism is responsible for selection in both the sensory and the motor domain. A gate is open only if the excitation from the frontal cortex does not show up. Neither perception nor movement is possible unless the relevant gates are open. An adequate response to a No-Go or a Stop command could be realized via the immediate closing of the motor gates by frontal excitation of the local inhibitory RN activity.

We have discussed results of ERPs and reflexes. Slow potentials are a manifestation of activity in one or more cortical areas, which are from moment to moment under the influence of subcortical loops (via basal ganglia or cerebellum) and different thalamic nuclei. This subcortical input is a necessary condition for the slow waves to show up.

The results of reflex experiments suggest that, during the fixed foreperiod of reaction time experiments, a general increase in excitability is present that is more pronounced in agonist and synergists but is also present when muscles are not involved in the response. The lack of increase in amplitude in the agonist is thought to be the result of a balance between an increase in excitability of the motoneurons and a simultaneous presynaptic inhibition of the Ia afferents from the muscles. Whether there is really an inhibition during the foreperiod with amplitudes be-

low baseline remains an unsolved problem. We expect that transcranial magnetic stimulation will provide important information in the near future about changes in excitability of motoneurons in arm and hand muscles.

NOTES

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 1. Consistent with the conventional plotting – with negativity upward – of these kinds of slow potentials, we will use the terms “maximum” and “greater than” to denote “most negative” and “more negative than” (respectively) and the terms “minimum” and “smaller than” to denote “least negative” and “less negative than” (respectively).

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