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Neural aspects of anticipatory behavior

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Abstract

Anticipatory behavior reveals itself in the perceptual domain and in the motor domain. Expectant attention and motor preparation are characterized by selection, aimed at an amelioration of the signal-to-noise ratio in the information to be processed. The functional similarity of anticipatory attention and motor preparation is reflected in the underlying anatomical substrate. The prefrontal cortex, involved in a number of different networks, organizes anticipatory behavior in a top-down way by activating cortico-cortical loops and thalamo-cortical loops to sensory and motor areas. The sensory areas are set to receive the impinging stimulus presentation, the motor areas are set to implement and execute the different motor programs. Thalamic nuclei are also activated from the prefrontal cortex, especially the large association nuclei, the dorsomedial nucleus and the pulvinar. In different models of selective attention the reticular nucleus of the thalamus has a special role in the distribution of the inhibitory control upon the information processing in the “relay” nuclei. It is hypothesized that it has the same pivotal position in motor preparation. Although the anatomical relations do not allow a direct test of the proposed hypothesis, the available psychophysiological evidence does not contradict it. © 1999 Elsevier Science B.V. All rights reserved.

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Keywords: Anticipatory behavior; Anticipatory attention; Motor preparation; Thalamic reticular nucleus; Prefrontal cortex; Input modulation to the cortex; Slow brain potentials

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1. Introduction

Our life is lived on the ever moving border between Past and Future, in a *now* and *here*. Time and space are the fundamental categories in our cognitive system. Anticipatory behavior involves a temporary combination of Past and Future, for which the momentary situation is the point of departure. It implies plans for action, in which both time and space are essential: The future behavior will take place at a certain moment in time and at a certain place, not far from now, not far from here. Each action is aimed at a goal. Preparation of an action implies the foreseeing of the consequences of the crucial event that will trigger the action. In other words the preparation is based upon *a view from the future*. This future has not yet been changed in a now. We are able to imagine our future behavior as if it takes place now. The notion “Anticipation” has a teleological flavor, as if something in the future is determining our present behavior. In fact our view from the future is based upon our past experiences. These determine the possibility to imagine what will be going on in the nearby time to come. Actually it is the memory of these past experiences upon which our expectancies are based and which determines our future behavior. The imagination of future behavior initiates the temporo-spatially ordered activation of neural structures, which is a necessary condition for the realization of the action. The very existence of anticipatory behavior indicates that our behavior is organized in a top-down way instead of as a chain of reflexes. It is clear that such a top-down interpretation of behavior is in contrast to a *Stimulus–Response Psychology* which attributes to the stimulus the role of an exclusive determinant of a following response. In a critical review of “set” and related notions, Gibson (1941) concluded that behavior was determined by something else besides the immediately preceding stimulus. Hebb (1949, loc.cit., p. 5) added that this “does not deny the importance of the immediate stimulus, it does deny that sensory stimulation is everything in behavior.” In between, we are better informed about the central process “which seems to be relatively independent of afferent stimuli” (Hilgard & Marquis, 1940).

Consistency in our behavior becomes manifest in a well-balanced spatial and temporal relationship with our environment. It is based upon our ability to learn from experience. This helps us, where possible, to anticipate future events by which an optimal adaptation to our environment is realized. It involves an implicit time estimation, i.e. an estimation of the duration of the interval prior to the occurrence of an expected stimulus, or prior to the moment at which an action has to be generated. The aim of preparatory processes is to pre-activate certain brain structures during that interval in order to ameliorate the upcoming information processing. This is a selective process, in which – as far as possible – a choice is made between what is relevant and what is not. Selection can operate in two ways: by a local increase in excitation of the relevant structures, and/or by a local inhibition of the irrelevant structures. Each of these changes in excitability, or their combination, leads to a better signal-to-noise ratio. Anticipatory behavior implies an increase in alertness and a focused attention upon both the perceptual input and the motor output. In other words, it becomes manifest in the perceptual and the motor domain. In most circumstances “Attention” is indeed aimed at a better perception, but mostly *to do*

something with it, that is to integrate the perceived thing into an action. “Motor Preparation” is aimed at an appropriate action, but often this is a response upon some change in the stimulus environment. After all much of our behavior is triggered by changes in our environment, which have to be monitored in order to be discovered.

There are good reasons to suppose that the prefrontal cortex has a supervisory role in the planning of our behavior to come (Fuster, 1997), thus in the organization of the selective processes at different cerebral locations. Selection in *perception* may or may not concern just one modality, and it can but needs not to be directed upon one attribute within that modality. If some action is supposed to take place after the presentation of a green light, and another after that of a red light, green and red become relevant colors, while all other colors are irrelevant. Structures relevant for the perception of the green and the red light have to be selectively excited, and/or those for the perception of other colors have to be inhibited. The coupling of a color to a movement is the consequence of an instruction, or of a long-term learning process. The coupling has to be kept in *memory*, for the duration of an experimental session, or, in every day life, forever (e.g. the prohibitive meaning of a red light for all traffic participants). In other words for a concrete task a working memory network has to be formed that becomes activated either from the recent instruction or from a source in a long-term memory. In the latter case earlier experiences with comparable situations might become activated as well, and contribute to the actual working memory network. Since reaching the goal of an action is in general reinforcing, actions are also motivated. That implies that a contribution of relevant limbic structures is needed. Selection in motor preparation signifies that the crucial motor structures have to be activated, while others are inhibited. In the above mentioned example this means that perception of the color green or red will be coupled to the preparation and execution of a different movement or series of movements. Both stimuli signify a Go-command, but the response that is activated depends upon the color perceived. The Go-command following the color green results in action A, and that following the color red results in action B. In other words, once the relevant visual stimulus is presented, a timely ordered activation of a series of movements follows. How the series is composed depends upon the point of departure, that is the actual position the organism is in. Movements are executed by muscles, so the selection results in a concerted activation of agonistic and synergistic muscles, while antagonistic muscles are inhibited. The Go-command is probably issued by the prefrontal cortex, as is the decision not to act.

Although inhibitory and excitatory processes are ubiquitous in the CNS, I will restrict myself here to these processes in the thalamo-cortical pathways involved in perception and action. The neocortex of the human brain is beyond doubt the most important development in evolution. yet, the major statement of this paper is that thalamic input to the cortex is of vital importance for both perception and action.

2. Anticipatory attention: the perceptual domain

In most experiments the instruction to attend a certain (feature of a) stimulus is given before the experiment starts. This provokes an expectancy, a “waiting in

readiness”, during which subjects are primed by the instruction. Instructions can be simple, so that the subject knows beforehand what has to be done, once the imperative stimulus is presented. They can also be complex, asking for a certain response only if a target stimulus is presented in, e.g. a relevant place or a relevant color. In many experiments a kind of priming is used to provoke anticipatory behavior resulting in an ameliorated perception and hence in a faster response production. The precuing technique is also used in the research of motor behavior (Rosenbaum, 1985). In the first case we are used to speaking of anticipatory attention, in the second case of motor preparation. Both are based upon similar electro-physiological processes.

Paying attention results in a better performance. The benefits for an individual may concern the accuracy, the speed or the maintenance of mental processing (LaBerge, 1995). It is interesting that the first two goals of attentive behavior apply in the perceptual domain and the motor domain. Accuracy may be related to object properties like size, shape, color and orientation, the perception of which may be hindered by the presence of other objects that share one or more of the features of the target object. It also may be related to action, if similar solutions are available to reach the same goal, while only one can be executed at the same time. The increase in accuracy is realized by a selective process, directed either at the input side or at the output side. Something similar holds for speed. Expecting a traffic light to change green, facilitates the perception and by that the response of the driver. The response itself can also be prepared, resulting in a similar shortening of the reaction time.

On strictly biological grounds one can presume that perception is always coupled to action: we do something with which is in the center of our attended field. That does not necessarily hold for the processing of information in sustained attention (LaBerge, 1995). This possibility might well be a manifestation of a late development in evolution, characteristic for human beings. We may look at Canaletto’s paintings of Venice, or listen to the violin concert of Sibelius, while there is no need for these activities. They serve no extrinsic goal, we do it because we like it. An emotional experience may be the only result.

What we call attention, may manifest itself under three different forms: selection, preparation and maintenance (LaBerge, 1995). The selective operation of attention in perception is related to either the enhancement of activity in neural structures involved in the registering of what is relevant, or the inhibition of activity in neural structures involved in the registering of what is irrelevant. The selective operation of attention in action is in a similar way related to the enhancement of activity in neural structures involved in a series of relevant movements or the inhibition of irrelevant movements. In a certain sense the thesis could be defended that attention is nearly always preparatory. If on the basis of an instruction or a long lasting knowledge we pay attention to a stimulus feature, we do this because the stimulus is relevant for an action to follow. Trying to define the purpose of selectivity in attention Allport (1989) came up with the notion “selection for action”. Recent developments in the investigation of visual perception underline this concept, as we will see next.

It has been known for some decennia that there are two different pathways in the visual system. Fibers from the retina project to the superior colliculus in the

mesencephalon, or via the lateral geniculate body to the striate cortex. Schneider (1969) suggested that the former was involved in the localization of stimuli in visual space, and the latter in identification of the stimuli. Although this hypothesis has been abandoned in later years, it is important to note that subcortical structures were thought to be involved in the processing of spatial information. Another dichotomy was proposed by Ungerleider and Mishkin (1982), again related to the identification and localization of what is present in the visual world. The output of the striate cortex is either aimed at the inferotemporal cortex or at the posterior parietal cortex. The ventral system is related to object recognition, the dorsal system to where in the environment the object is situated. Hence these pathways have been termed the *What*- and the *Where*-system. Recently, the latter “perceptual” system has been reinterpreted as an action system (Milner & Goodale, 1995). On the basis of a large set of data the latter authors have made plausible that activity in the posterior parietal cortex should be understood in relation to a following action, rather than as reflecting an answer on the question, where the crucial stimulus is localized. Milner and Goodale (1995) suggested that there are different modules for different actions, like gaze directing, pointing and grasping. Enhanced activity of neurons in different parts of the posterior parietal cortex can be considered *preparatory* to one of those actions, rather than reflecting a pure perceptual process.

Years ago Weiskrantz (1986) was confronted with the problem to explain a phenomenon he has called *Blindsight*. His patient (D.B.) was unable to see what happened in the left visual hemifield because of a right-sided cortical lesion in the occipital areas. Yet he remained capable to point at a light stimulus, projected in his blind hemifield. Thus, a correct action could be executed without (conscious) perception. Weiskrantz, Warrington, Sanders and Marshall (1974) considered the unimpaired retino-collicular pathway accountable for the appropriate action. It is known that ascending fibers from the superior colliculus reach the posterior parietal cortex via the pulvinar. Thus, this important thalamic association nucleus (Fig. 1) is considered an intermediate for this perceptuo-motor task. Yet the pulvinar is also involved in tasks in which “pure” perception is investigated, which is supposed to be realized via the ventral system. Keeping the motor aspects of the task constant, LaBerge and Buchsbaum (1990) investigated whether the pulvinar is indeed involved in selective visual attention. The perception of a target stimulus was manipulated by changes in its direct environment. The target letter was an O, surrounded by eight comparable but not identical stimuli, making the perception of the O more difficult. Only if more attention is paid to the stimuli a correct answer can be given in due time. Subjects fixated on a central dot and pressed a button when the O appeared in the middle of eight flankers on the left side, and when the O appeared on the right side. Half of the time the O was replaced by a G or a Ø. LaBerge and Buchsbaum (1990) found a significant increase in glucose uptake in the pulvinar contralateral to the complex display as compared to what was found with the presentation of the O alone. In other words the pulvinar seems to be involved in attention related to both object recognition and visuo-motor activity. It has reciprocal connections to the posterior parietal cortex and to the temporal cortex via separate channels. Moreover it is not exclusively involved in the processing of visual information: somatosensory

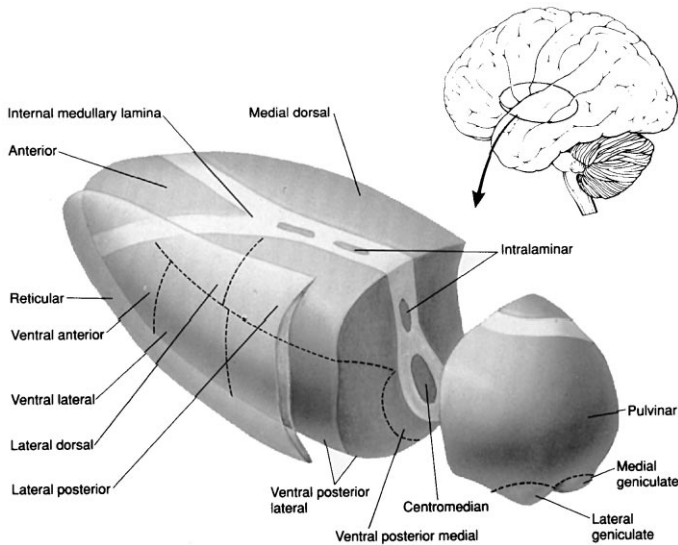


Fig. 1. The major nuclei of the left thalamus. The internal medullary lamina divides the thalamus into the anterior, lateral and medial nuclei. The lateral group is divided into dorsal and ventral tiers. Each nucleus in the ventral tier relays specific sensory or motor information. Visual information is transmitted via the lateral geniculate body to the occipital cortex and auditory information via the medial geniculate body to the temporal cortex. Somatosensory information reaches areas 3, 1 and 2 (see Fig. 2) via the ventral posterior nucleus. Pulvinar and dorsomedial nucleus are discussed in the text in relation to attention and motor preparation. The pulvinar is connected to the parietal cortex and the dorsomedial nucleus to the prefrontal cortex. The major motor nuclei project to different motor cortices, as can be seen in Figs. 3 and 5. The reticular nucleus (RN) caps the entire lateral aspect of the thalamus. It is the only nucleus with an inhibitory output and the only one that does not project to the cortex. Cells in the RN receive input from a particular relay nucleus and projects back to that nucleus. (Copied with permission of Elsevier from Kelly, 1991.)

and auditory information is also transmitted to this nucleus, again in mainly separated channels. Summarizing we conclude that it has become less simple to distinguish between perception and action, and that for both perception and visuomotor activity the thalamus seems to play an important role. In the next section we will see that the thalamus is crucial in all kinds of motoric activity.

3. Preparation to respond: the motor domain

Efficiency in behavior reaches an optimum when the person who is to act knows exactly what has to be done once the crucial situation has started. On the behavioral level it can be measured as a shortening of reaction time (RT) or a decrease in the number of errors. Event and time uncertainty deteriorate the final performance. Experiments in which motor preparation is investigated differ in the way subjects are informed about the future task. In a relative simple case an instruction at the onset of

the experiment can be sufficient for an appropriate response production. A warning signal which announces that after a certain period of time a movement has to be made, or a stimulus will be presented upon which a response has to be given, triggers a “waiting in readiness”. This has immediate consequences for the posture that will be used as the point of departure for the upcoming movement (Massion & Deat, 1991). The response itself can be a simple button press, but also a series of more complicated movements, a movement of the hand or of the foot, on the right side or on the left side. Response parameters may be different, in that force, speed or accuracy are emphasized. The distance that has to be bridged and the direction in which the movement has to be made, have to be defined. All requirements which have to be met and which are known in advance, can be prepared. Uncertainty about the final response can be (partially) neutralized by an informative prime stimulus, presented during the forepart. This precuing technique in the study of motor preparation (Rosenbaum, 1985) is of course similar to the technique used in the study of attention. In both cases precuing activates structures, involved in the function to be executed, in order to ameliorate the final performance. Playing a music instrument, typing a text or grasping a ball from the air imply a much more complicated pattern of movements than the button press, usually employed in psychophysiological research. Concerning the last example, Jeannerod (1997) has made clear that in grasping a ball, the fingers and the hand are shaped in advance in order to be able to catch and hold the ball in the closing hand. Thus while the hand is directed to a certain point in space, the next step is already prepared. Such anticipatory effects in the behavioral output are considered a strong argument in favor of the existence of motor programs (Rosenbaum, 1985). Motor programs are defined by Keele (1968) as a “set of muscle commands that are structured before a movement sequence begins”. These motor programs seem to be organized in a hierarchical way (Rosenbaum, Kenny & Derr, 1983). The hierarchy defines the identity and order of commands to the musculature, represented as terminal nodes in the hierarchy. Execution of a program is either based upon a linear readout of the terminal nodes, or it is based upon a readout of both terminal and non-terminal nodes in a tree-traversal process. The authors present evidence in favor of the latter hypothesis (see also Jordan & Rosenbaum, 1989). This implies that during programming apart from the terminal nodes also the nodes of different higher order have to be passed again and again, so that all members of the hierarchy are activated repeatedly. This seems very well in accordance with neurophysiological evidence for a continuous activity in subcortico-cortical loops involved in motor preparation, as we will see later on.

A motor program is a lower level form of preparation, in contrast to planning (Rosenbaum, 1985). Planning is a preparatory activity on a larger time scale. Presumably both kinds of preparatory activity are realized via different brain structures. Planning is considered a function of the prefrontal cortex (Fuster, 1997). It need not to be followed immediately by an action. Actualizing a plan signifies the implementation and the execution of one or more motor programs, for which the supplementary motor cortex (SMA), the premotor cortex (PMC) and the primary motor cortex (MI) have to be activated (Fig. 2). For a better understanding of their

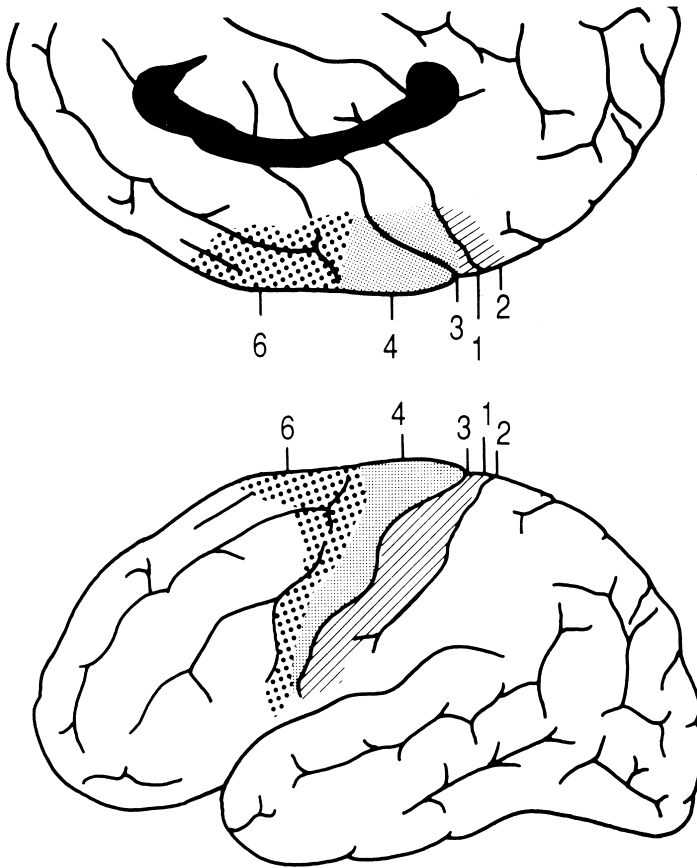


Fig. 2. Lateral (below) and medial view (above) upon the cortex cerebri. Area 4: Primary Motor Cortex, Precentral Gyrus or MI. Lateral Area 6: Premotor Cortex. Mesial Area 6: Supplementary Motor Area. Areas 3, 2 and 1: Somatosensory Cortex. Readiness Potentials (RPs) have been recorded in monkeys from each of the areas indicated. It is hypothesized that these RPs reflect different processes in the preparation for a movement. (Copied with permission of Elsevier from Brunia, 1988.)

function in anticipatory behavior, it is necessary to describe the relevant connections of these structures in some detail. This will be done in the next section, although far from exhaustively.

4. The neuroanatomy of anticipatory behavior

Anticipatory behavior is often triggered by a sensory stimulus. Therefore we will start with a description of how sensory information reaches the cortex. Fibers from each of the different sense organs ascend via different thalamic relay nuclei to their respective primary projection areas in the posterior cortex. Thalamic input is not

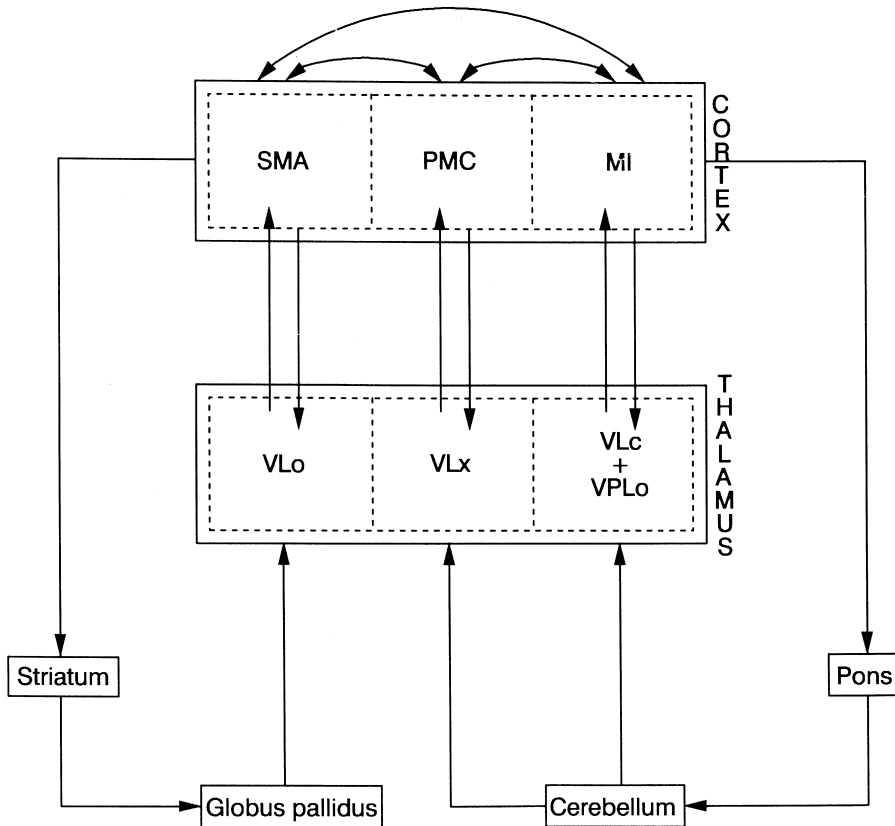


Fig. 3. Diagram of the major connections between cerebellum, basal ganglia, thalamus and motor cortical areas. MI is connected via nuclei in the pons and in the cerebellum to thalamic nuclei VLc, VLx and VPLo. The SMA is connected via striatum and pars interna of the globus pallidus to VLo. The different thalamic nuclei have reciprocal connections to the different cortical motor areas, which have themselves mutual reciprocal connections. For the abbreviations see text. (Adapted from Wise and Strick, 1985.)

restricted to sensory information. The different motor cortices also get an input from different thalamic nuclei, as is schematically depicted in Fig. 3.

4.1. Thalamic “relay” nuclei and the basal ganglia

Actually each cortical area gets its own input from a different thalamic nucleus (Creutzfeldt, 1995). About 30% of the afferent sensory and motor fibers to the cortex stem from one of the thalamic nuclei. All thalamo-cortical connections are reciprocal. Although there is a structural analogy between the way the sensory and motoric information is treated, the thalamo-cortical relations in the motor domain are more complicated. Fibers from the thalamic motor nuclei ascend to different parts of the frontal cortex. Their input stems from the cerebellum and the basal

ganglia. The ascending output from the cerebellum passes via the dentate nucleus to the thalamus and from there to the primary motor cortex, M1. The relation to the basal ganglia circuit is more complicated. Different parts of the cortex project to the neostriatum, consisting of the caudate nucleus and the putamen. The caudate nucleus gets its input from the association cortex, the putamen from the sensori-motor cortex (Fig. 4). The loop via the putamen is known as the motor loop, the one via the caudate nucleus as the complex loop. In between Alexander, DeLong and Strick (1986) have described five parallel functionally segregated circuits between basal ganglia and the cortex.

Since the basic properties of each of the different circuits are identical, we follow here the description of the motor loop, as suggested by Alexander and Crutcher (1990). Cortical areas send excitatory glutamatergic fibers to the caudate nucleus, the

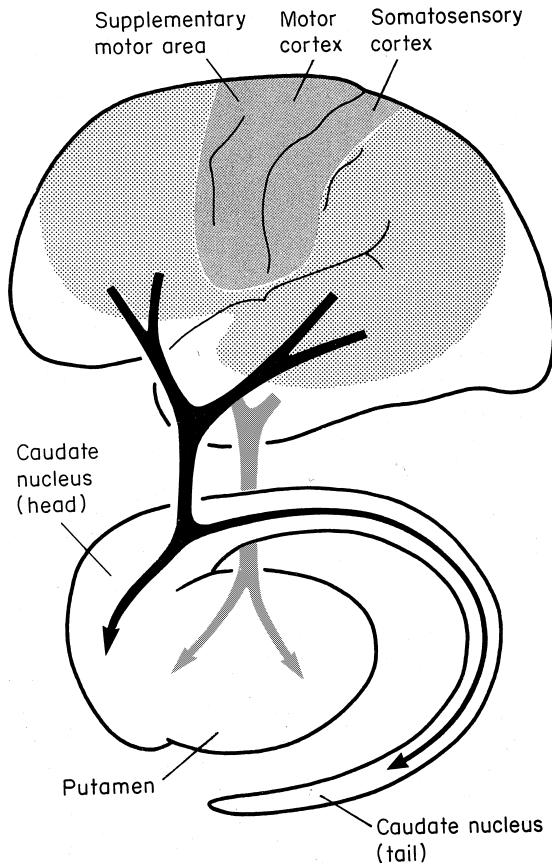


Fig. 4. Putamen and caudate nucleus get their input from different cortical areas. The putamen receives fibres from the somatosensory and motor cortex, the caudate nucleus from the association cortex. (Copied with permission of Tano Forlag from Brodal, 1992.)

putamen and the ventral striatum (Fig. 5). This input to the basal ganglia activates GABA-ergic cells in the globus pallidus externa and interna. The output channels from the basal ganglia, the globus pallidus interna and the substantia nigra pars reticulata, exert a tonic inhibitory control upon the different thalamic nuclei. This inhibitory outflow can be differentially modulated by opposing effects of a direct and an indirect pathway. Activation of the direct connection disinhibits the thalamus, activation of the indirect pathway inhibits the output to the thalamus. Disinhibition of the ventrolateral nucleus (VL) causes a gating of cortically initiated movements, while the indirect pathway might be involved in the braking or smoothing of the movements (Alexander & Crutcher, 1990). Another possibility is that a cortically initiated movement is supported by a reinforcement of the selected movement via the direct connection, while the indirect pathway is involved in the suppression of conflicting patterns. Focusing on the selected movement would be accompanied by a “surround inhibition”, comparable to what happens in the sensory systems. The

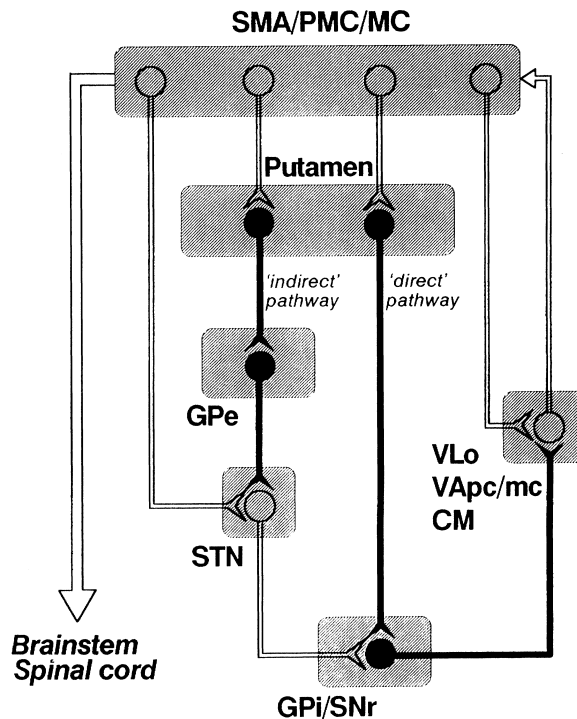


Fig. 5. Closed loop of the motor circuitry. Inhibitive neurons are depicted black and excitatory neurons grey. Besides the already mentioned cortical areas (see Fig. 2) the following nuclei are depicted: the globus pallidus externa (GPe), the subthalamic nucleus (STN), the globus pallidus interna (GPi), the substantia nigra pars reticularis (SNr) and the following thalamic nuclei: the nucleus ventralis lateralis pars oralis (VLo), the nucleus ventralis anterior (VA) and the centre median (CM). Both the indirect and the direct system have a double inhibitive connection to their targets. (Copied with permission of Elsevier from Alexander and Crutcher, 1990.)

motor circuit, which is the most relevant for the present discussion, projects to MI, the SMA and a part in the premotor cortex, called the arcuate premotor area (APA) in monkeys. There exists a somatotopical organization within the motor circuit, in which an extreme separation between the different participating fibers is maintained over the different nuclei involved in the circuit (Strick, Dum & Picard, 1995), although there are points of convergence and divergence of participating fibers (Graybiel & Kimura, 1995). The functional role of the extreme separation of the fibers within the motor circuit is not yet understood.

Alexander and Crutcher (1990) mention that at the different levels within the circuit neurons fire in relation to the direction of the movement, independent of the muscles activated. The *onset* of fast stimulus-triggered movements is accompanied by a change in the firing rate of cells, which occur at the cortical level somewhat earlier than in the basal ganglia, suggesting that: (1) these movements are initiated in the cortex and that, (2) there might be a serial processing of the information within the circuit. The *duration* of the burst of movement-related activity shows a complete overlap at the different levels, which is interpreted as an indication of parallel processing. Cells at each of the different levels within the motor circuit show also *preparatory* activity. The authors suggest that preparation and execution might be realized via different groups of neurons, and that target location, limb kinematics and muscle pattern might be mediated via separate subchannels (Alexander & Crutcher, 1990). In other words the available evidence is much more in favor of parallel than of serial processing. The fact that during motor preparation activity can be recorded from all levels of the circuitry is in agreement with the tree-traversing motor programming model of Rosenbaum et al. (1986), discussed in the foregoing section.

Next we will describe the thalamic reticular nucleus, which plays an exceptional role in circuits involved in anticipatory attention and motor preparation.

4.2. *The reticular nucleus of the thalamus and its possible function*

As can be seen in Fig. 1, each of the thalamic nuclei is covered by the reticular nucleus (RN). The RN is the only nucleus that sends no afferents to the cortex. It has a local inhibitory influence upon the underlying thalamic relay nuclei. Fig. 6 shows how three different parts of the RN do inhibit three different thalamic relay nuclei. The same holds for all other thalamic relay nuclei. This local inhibitory influence might play an important role in selective attention and motor preparation.

An important attempt to explain how selective attention might be brought about in the CNS, is the model of Skinner and Yingling (1977) which elucidates how a *between modality choice* might be realized. The model concerns the three major sensory modalities: vision, audition and touch. The different thalamic relay nuclei are inhibited by different parts of the RN. Neurons in the RN are under a dual control from the frontal cortex and the Ascending Reticular Activation System. The RN plays a role in both *arousal* and *selective attention*. The influence of the frontal cortex is excitatory, that of the ascending activation system inhibitory. Excitation of the RN

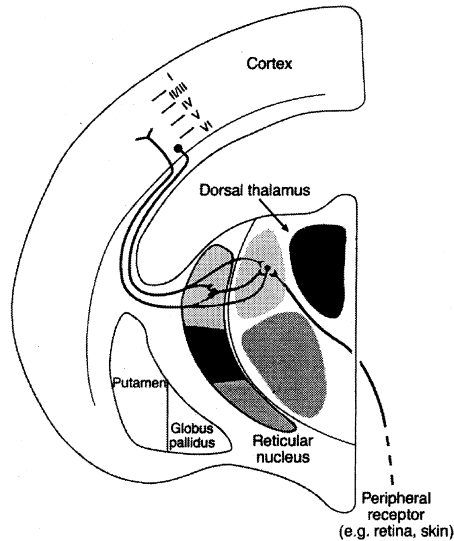


Fig. 6. Relay nuclei receive returning afferents from the cortical area to which it sends its fibres. All leaving and returning fibres send collaterals to a specific sector of the RN, allowing for a modulation of the local inhibitory influence the RN has on the relay nuclei. (Copied with permission of Elsevier from Mitrofanis and Guillery, 1993.)

stimulates its inhibitory function and causes a relative closing of a thalamo-cortical channel. Inhibition of the RN inhibits its inhibitory function. According to Skinner and Yingling this disinhibition takes place in all three channels simultaneously and its manifestation is known as *arousal*. *Selective attention* is supposed to take place via disfacilitation. Neurons in the RN inhibiting the irrelevant channels are excited. Those inhibiting the relevant channel are not, so in the relevant channel the information can pass to the cortex.

The model of Skinner and Yingling is based upon a large number of experiments, in which rhythmic brain activity, evoked potentials (EPs) and slow waves have been studied in both rat and cat. Stimulation of a certain part of the RN made amplitudes of EPs decrease or disappear in the relay nucleus underneath that part, while no effects were recorded in EPs transmitted via other relay nuclei. Stimulation of other parts of the RN had similar effects upon EPs from another modality. These results suggested to Yingling and Skinner (1977) a modality-specific organization in the RN, as has been confirmed recently by Mitrofanis and Guillery (1993).

4.3. Inhibition of irrelevant information

In essence the model of Skinner and Yingling (1977) claims that selective attention is brought about by an *inhibition of what is irrelevant*. In other words the signal-to-noise ratio is ameliorated by suppressing noise. Before Skinner and Yingling

proposed their model of selective attention it was known already that activation of certain sectors of the RN provokes postsynaptic inhibitory potentials (IPSPs) in the ventrolateral thalamic nucleus (Fig. 1), blocking the transmission of information from this nucleus to the cortex (Fig. 3). Purpura, Scarff and McMurtry (1965) noted for example that the cerebellar input to this nucleus during the IPSPs no longer elicited the regular monosynaptic cortical response to this stimulation. Purpura (1970) suggested that this effect can be described as a functional deafferentiation. The local inhibitory influence of the RN in the motor domain has also been described by Massion (1967), who considered the thalamic motor nuclei a gate that might be open or closed to a motor command.

Since the thalamic motor nuclei are equally well under the control of the RN, it seems plausible that the RN, comparable to what we have seen in perception, is also in a pivotal position to influence motoric processes (Fig. 7). In both cases, that is in anticipatory attention and motor preparation, its essential role is *input modulation to the cortex*. The diffuse disinhibition during arousal (Skinner & Yingling, 1977) is also manifest in overt motoric activity. Selection in motor preparation could imply a *blocking of irrelevant motor behavior* in order to ameliorate the signal-to-noise ratio in motor activity, which is aimed at the activation of just that action that is needed, and no other ones. Such a process could be a manifestation of the executive control, the prefrontal cortex has upon preparatory and ongoing behavior. It is interesting in this context that Fuster (1997) has hypothesized that one of the tasks of the prefrontal cortex is the suppression of irrelevant activity. This suppression of irrelevant activity could very well take place via the prefrontal connection with the RN: Excitation of cells in the RN controlling the irrelevant motor channels, would diminish activity in these channels. Yet more recent studies in attention have casted doubt upon suppression of irrelevant activity as the mechanism via which a better signal-to-noise ratio can be reached.

4.4. *Enhancement of relevant activity*

Contrary to Skinner and Yingling (1977), LaBerge (1995) has argued that *enhancement of relevant activity* is a more plausible mechanism via which selective processes in perception take place. Skinner and Yingling (1977) studied selective attention in a *between-modalities* design. Their stimuli were rather simple and the question is whether (presumed inhibitory) influences exerted by the RN upon the primary sensory thalamic nuclei are necessary and sufficient to explain higher order *within-modality* selective attention. Presumably they are only necessary: It is beyond doubt that the relay nuclei are a necessary station for the information passing to the cortex and that the RN exerts an inhibitory influence upon them. Yet there is sufficient evidence for the suggestion that information which is not immediately relevant for an upcoming perception can be perceived too (Posner, 1994). In other words there is reason to suppose that under circumstances irrelevant information can also reach the cortical level. This suggests at least that channels are not completely closed for irrelevant information. In the next paragraph we will see that details about the

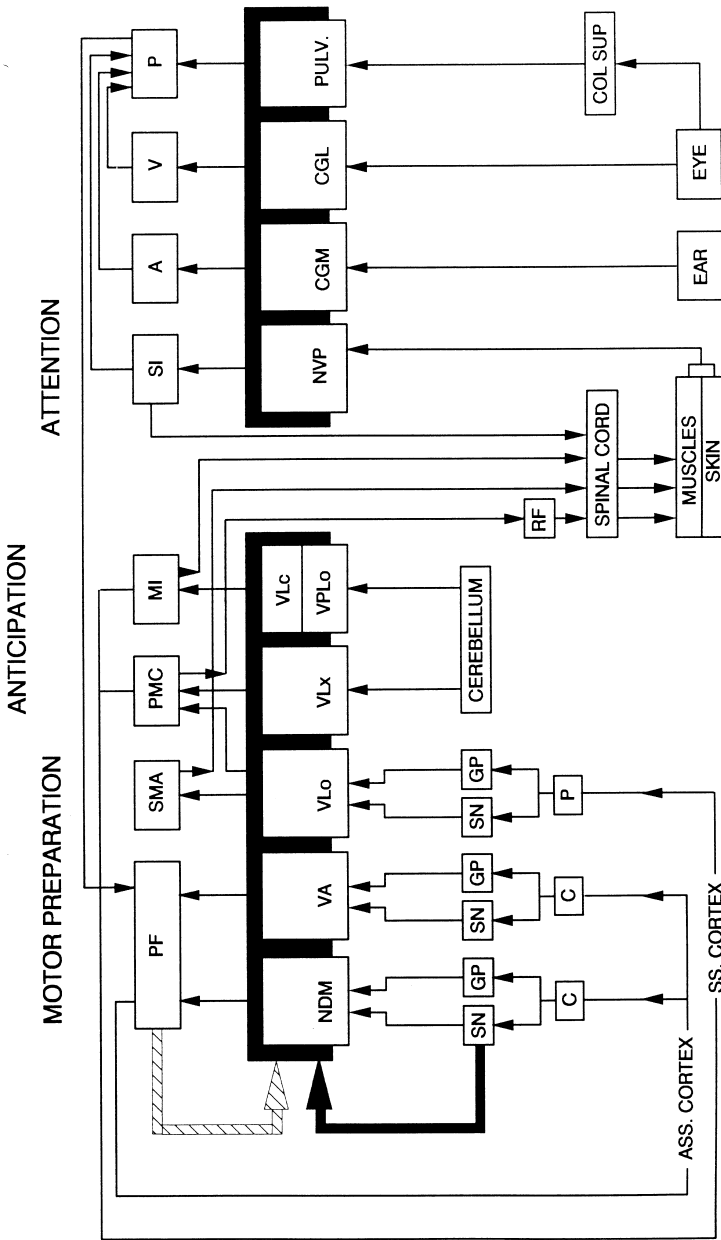


Fig. 7. The proposed neuroanatomy of anticipatory behavior. Diagram of the connections between cortex (upper row), thalamic nuclei (middle row) and subcortical nuclei and cerebellum (lower row), which are relevant for anticipatory behaviour. The motoric and sensoric thalamic nuclei are under the same inhibitory influence of the RN. The RN itself is under an excitatory influence from the prefrontal cortex and an inhibitory one via the neostriatum. The first give rise to an inhibition of the thalamo-cortical information transmission, the second causes a disinhibition thereof. It is suggested that selection at an elementary level takes place via suppression of irrelevant activity in both the sensory and the motoric domain. At a more complex level selection seems to be realized via enhancement of relevant activity. It is suggested that this is realized in a similar way for the sensory and the motor system. PF: prefrontal cortex, SMA: supplementary motor area, PMC: premotor cortex, MI: medial intraparietal cortex, VLo: n. ventrolateralis posterior, VLx: n. ventrolateralis posterior, VLc: n. ventrolateralis posterior, VPLo: n. ventroposterolateralis, VPLc: n. ventroposterolateralis, NVP: n. ventral posterior, CGM: medial geniculate body, CGL: lateral geniculate body, Pulv: pulvinar. SN: substantia nigra, GP: globus pallidus, C: N. caudatus, P: putamen, RF: reticular formation. ASS: association cortex, SS: somatosensory cortex.

connection of the RN and the underlying nuclei are still unknown. This leaves open the possibility that the inhibitory processes at the level of the “simple” relay nuclei are organized in a way which is different from that at the level of the association nuclei. Also the control mechanisms upon the simple and the association nuclei might be different. Another possibility is that *within-modality* attention is organized differently from *between-modality* attention.

Let us return for a moment to the thalamic circuitry. LaBerge argues on the basis of work of Steriade, Jones and Llinas (1990) that the standard thalamic circuit is similar across species. Depending upon the nucleus the input stems from the sensory afferents, the afferents from the superior colliculus and cortical afferents. These afferents terminate on principle relay neurons or interneurons. Under way from the relay neurons in the lateral geniculate body to the visual cortex, axons pierce the RN and send collaterals to the neurons herein. The axons themselves arrive in layers IV and III, project to layer II, from which layers V and VI are reached. Fibers from layer VI return partly to layer IV, thus closing this local excitatory minicircuit which is in principle able to keep some activity going within the cell column. Excitatory fibers from layer VI also return to the sensory nucleus of the thalamus. They arrive at the distal dendrites of the relay nuclei and cause a depolarizing shift in the membrane potential of the relay cells. Thus the following input to these cells can be modulated via this short-term potentiation (LaBerge, loc.cit., p. 175). Sensory impulses arriving via excitatory afferents near the soma meet a lower threshold than without that returning cortico-thalamic excitation. At the same time the RN cells are activated by descending excitatory collaterals, providing an inhibitory control of the relay cells. Realizing that the RN is covering the pulvinar, and that its role might be of importance for attentional processing, LaBerge (1995) pointed to the fact that there are still uncertainties concerning the exact wiring of the RN. Above we have seen that the fibers related to object perception and visuo-motor activity remain strictly separated in the pulvinar. Cells in the thalamic nuclei are arranged in columns, comparable to the cortical columns. At the moment it is not yet known whether the descending RN fibers are: (A) connected to the underlying relay cells and to the neighbouring relay nuclei, some columns apart, (B) to the latter only, or (C) exclusively to the relay cells that innervate the RN cells. The three possibilities, depicted in Fig. 8, left panel, were used in a neuronal network experiment in which LaBerge, Carter and Brown (1992) investigated selective attention.

The task was the same as the one discussed in the section “Anticipatory Attention” (LaBerge & Buchsbaum, 1990). The letter O had to be attended in the middle of distracting flankers. Target neurons were supposed to process the O and surrounding neurons to process the flankers. The basic problem was whether the perception of the signal, the O, is ameliorated by an attentional process, or whether a decrease in flanker perception took place. The results of this simulation experiment are depicted in Fig. 8, right panel. In all three cases, a better signal-to-noise ratio was found (LaBerge et al., 1992). Of course a demonstration of a process in a neuronal network is no proof for the existence of something like that in the reality of the nervous system. Interestingly, in all three cases a better result is reached after the circuit has been passed a number of times. The important message is that the loop

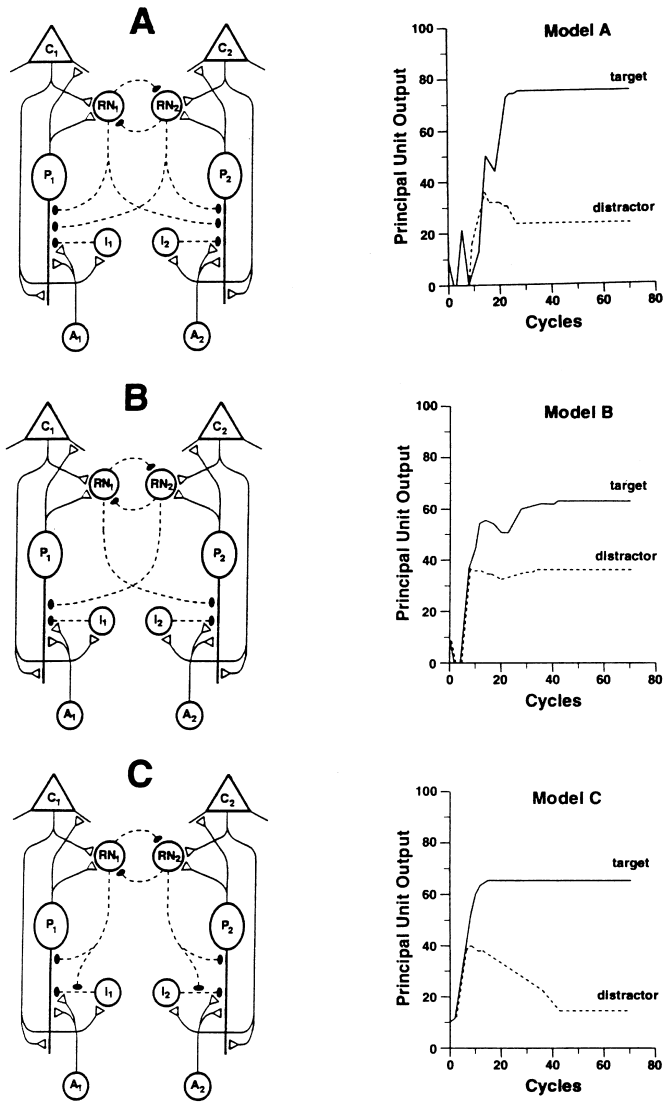


Fig. 8. Left panel: Three different ways in which inhibitory RN axons influence thalamic “relay” nuclei. (A): RN projects to neurons that innervate it and to neighboring neurons. (B) RN projects only to neurons in neighboring cell columns. (C) RN projects exclusively to neurons that innervate it. Solid lines: excitatory. Dashed lines: inhibitory. C₁, C₂: cortical cells in different columns. RN₁, RN₂: reticular nucleus cells. P₁, P₂: principal thalamic “relay” cells. A₁, A₂: afferent input from other cortical areas. I₁, I₂: interneurons. Right panel: Results of a simulation study of LaBerge et al. (1992) in which the corresponding circuitry of the left panel was implemented. Principal cells corresponding to the target site received a firing rate input of 38 units/s, those corresponding to the flanker received 37 units/s. Output of the principal cells involved in target perception started to diverge from those involved in distractor perception after a number of time cycles. (Copied with permission of Harvard University Press, from LaBerge, 1995.)

has to be passed a number of times before the amelioration of the signal-to-noise ratio becomes manifest. This illustrates the *dynamics* of the attentional process. At the same time it casts some doubt upon those opinions, which tell us that attentional processes are cortical, as if a stimulus, once it has arrived at the cortex, can only be influenced by cortical processes. The thalamo-cortical connection, that is here: the connection between pulvinar and parietal cortex, is a reverberating circuit, in which the information is processed over and over again, before – in this case – the O has been recognized between the distracting flankers. Returning to the two visual systems and the fact that the pulvinar is involved in visuo-motor performance it is plausible that the same mechanism might be at work when selecting a correct response in a visuo-motor task. It might also be involved in the processing of information via the dorsomedial nucleus, as LaBerge (1995) has suggested. Since the prefrontal cortex is defined as the projection area for this nucleus we might even suggest that selective processes in different cognitive domains pass in a similar way.

In the preceding text we have seen that there is serious evidence for a controlling function of the RN over the different thalamic nuclei in anticipatory attention and motor preparation. The anatomical relationships are not disposed to test the models discussed, *in vivo*. Even the precise implications of the activity going on in the basal ganglia circuits are not easy to test. Yet I will try to interpret data from psychophysiological experiments in the framework of the thalamo-cortical relations, discussed so far.

5. The psychophysiology of a anticipatory behavior.

In the present section three different anticipatory slow waves will be discussed: the Readiness Potential (RP), the Contingent Negative Variation (CNV) and the Stimulus Preceding Negativity (SPN). Another important phenomenon, the Event-Related Desynchronization has also its roots in thalamic nuclei, and might be helpful in the investigation of anticipatory attention and motor preparation.

5.1. *The readiness potential*

Voluntary movements are preceded by the Bereitschaftspotential (BP: Kornhuber & Deecke, 1965), also described as Readiness potential (RP). The distribution of this potential is rather widespread, especially over the anterior part of the skull. It starts about 1.5 s prior to the movement. Originally Kornhuber and Deecke distinguished a BP, a premotion positivity (PMP) and a motor potential (MP). The RP starts as a symmetrical slow wave, which over the last hundreds of ms becomes asymmetrical. The MP reflects the activity preceding the firing of the pyramidal tract neurons, which project to the agonist and synergist motoneurons in the spinal cord. It is not certain whether the PMP reflects physiological activity. It is also possible that it only marks the transition from RP to MP. Preceding finger movements RP amplitudes are larger over the hemisphere contralateral to the movement side, and preceding

foot movements over the hemisphere ipsilateral to the movement side (Brunia & Vingerhoets, 1981; Boschert, Hink & Deecke, 1983). This paradoxical lateralization suggests that the second part of the RP reflects the preparatory activation of a circumscribed area within the motor cortex. Arezzo and Vaughan (1980) recorded a transcranial reversal of the RP in the precentral gyrus of the monkey cortex. On the basis of this and the simultaneously recorded unit activity they concluded that the underlying electrophysiological source was localized in layer 5 of MI. Apart from confirming that, Hashimoto, Gemba and Sasaki (1979) also found a similar potential reversal in the PMC and the primary somatosensory cortex (SI). Later on the same reversal was also recorded in the SMA (Gemba & Sasaki, 1984). This is in line with the presence of preparatory unit activity in MI (Evarts & Tanji, 1976), the PMC (Mauritz & Wise, 1986; Riehle & Requin, 1989), the SMA (Tanji, Taniguchi & Saga, 1980) and SI (Nelson, 1988). Both the preparatory unit activity and the transcortical reversal of the RP in the different motor areas suggests that different electrophysiological sources, localized within these areas, contribute to the RP recorded over the skull. In other words the cortical origin of the RP is beyond reasonable doubt. Each of these different cortical areas has presumably a different function and the functional differences become probably manifest via the different networks they participate in. We will next see that the integrity of the subcortical input via different thalamic nuclei is a necessary condition for movement-preceding potentials to show up.

In the description of the anatomical structures involved in motor preparation we have seen that there are two major input channels to the motor nuclei of the thalamus: the cerebellum and the basal ganglia (Figs. 3 and 7). We will now analyze the role of these pathways in the emergence of the RP and start with the cerebellum. Sasaki, Gemba and Mizuno (1982) have demonstrated that a lesion in the dentate nucleus results in a disappearance of the RP in several cortical motor regions. Comparable results have been found in man by Shibasaki and his coworkers (Shibasaki, Shima & Kuroiwa, 1978; Shibasaki, Barrett, Neshige, Hirata & Tomoda, 1986; Ikeda et al., 1994). Thus lesions in the dentate nucleus hamper the electrophysiological manifestation of motor preparation. Cerebellar lesions, not involving the dentate nucleus, do not seem to hinder the emergence of the RP, suggesting that indeed the pathway via the dentate nucleus is essential. This fits with unit recordings in the cerebellum. Strick (1976) found an increase in the firing rate of cells in the VL preceding arm movements in the monkey. Thach (1987) reported preparatory activity in dentate nucleus *prior* to that in MI, while other cerebellar nuclei only fired *after* movement onset, suggesting that the dentate nucleus is involved in motor preparation and the other nuclei in the control of the movement execution. Although a dentate lesion caused the RP to disappear over the frontal cortex, it did so permanently only over MI, while it returned over the other frontal areas (Sasaki & Gemba, 1991). This suggests that the cerebello-VL-MI pathway is a *conditio sine qua non* for the emergence of the RP over the precentral cortex.

It cannot be the only pathway, though, since the RP seems to be less developed in Parkinsonian patients too, suggesting a contribution from circuitry via the basal ganglia (Deecke & Kornhuber, 1977; Dick et al., 1989; Jahanshahi et al., 1995;

Praamstra, Meyer, Cools, Horstink & Stegeman, 1996). Before presenting more details about that, another point of interest of the Ikeda et al., study should be mentioned. These authors also investigated the CNV in their cerebellar patient and recorded a CNV late wave in a 2 s foreperiod over the frontal electrode positions. This is in line with the monkey studies of Sasaki and Gemba, 1991, who after a cerebellar hemispherectomy, found apart from the above mentioned disappearance of the RP an intact movement related slow wave over the other frontal areas. Therefore the conclusion seems warranted that the cerebello-VL-MI pathway is not involved in the generation of stimulus-triggered movement preceding negativity.

We have seen that the RP preceding a self-paced movement is among others based upon the integrity of the cerebello-thalamo-MI circuitry. Deecke and Kornhuber (1977) were the first to argue that the midline RP is not a summation of the bilateral activity in MI, but a reflection of the contribution of the SMA. This brain area was supposed to be involved in self-paced movements, in contrast to the lateral PMC, which was thought to play a role in stimulus triggered movements (Goldberg, 1985). Similar arguments based upon unit recordings in monkeys, have been provided by (Passingham, 1987; Passingham, 1993). In between a number of studies have been published about RPs in Parkinsonian patients. In contrast to Barrett, Shibasaki and Neshige. (1986), who did not find abnormalities, other studies did (Dick et al., 1989; Jahanshahi et al., 1995). Since Shibasaki was also involved in studies in which abnormal RPs were found (Shibasaki et al., 1978), the conclusion seems warranted that most studies agree about the existence of abnormal RPs in Parkinson's disease. This implies that a malfunction of the substantia nigra at a certain moment becomes visible in the electrophysiological indications of self-paced movement preparation. In sum, the available evidence suggests that two different pathways are involved in the emergence of the RP: one via the dentate nucleus, the VL and MI, the other via putamen, PMC and SMA. Since it is improbable that both pathways have the same function, future research should be aimed at disentangling their role in the different processes hidden in the notion "motor preparation".

5.2. *The contingent negative variation*

The basal ganglia-thalamo-cortical circuitry seems to be involved in stimulus-triggered movements. The arguments are again based upon recordings of slow waves and unit activity. Recording slow waves between the warning stimulus and the imperative stimulus (the foreperiod) in a reaction time task in monkeys, Rebert (1977) found a Contingent Negative Variation (CNV) in the cortex and the mesencephalic reticular formation, and a contingent positive wave in the *caudate nucleus*. The subcortical slow waves were timelocked to the stimuli presented and had the same time course as the cortical slow wave, suggesting that subcortical cells were firing during the whole foreperiod. Originally the CNV was interpreted as an indication of sensori-motor association and expectancy (Walter, Cooper, Aldridge, McCallum & Winter, 1964), and not so much as an index of motor preparation. Since the use of longer foreperiods it became clear that the CNV consists of two different slow waves,

an early and a late one (Loveless & Sanford, 1974). The early wave has a frontal maximum and reflects the stimulus properties of the warning stimulus. The late wave is related to motor preparation, but the suggestion that it is identical to the RP (Rohrbaugh & Gaillard, 1983) is no longer tenable. It is certainly an example of movement preceding negativity, and as such an index of motor preparation, but stimulus-triggered movements and self-paced movements are presumably realized via different circuits (Goldberg, 1985; Passingham, 1987; Passingham, 1993). Moreover the very fact that stimulus-triggered movements are discussed means that the stimuli should be perceived, and that anticipatory attention can be given to the significance of the stimulus. Admittedly the anticipatory activity preceding an instruction stimulus might be small (Damen & Brunia, 1994), it is also the case that the more complicated the task, i.e. the more important the message the stimulus has for the future action, the more negative activity can be recorded. This is the reason why the amplitude of the CNV late wave is smaller when the response parameters are defined beforehand, than when at least one parameter is defined by the imperative stimulus itself (Van Boxtel & Brunia, 1994a). The use of cues is certainly clarifying in this respect. During a foreperiod of a reaction task Van Boxtel and Brunia (1994b) presented cues, instructing subjects to perform a squeeze on a force transducer with one of two velocities. There were two conditions. In one condition the cue was informative, in the other it was not. Trials were presented in blocks. The informative cue was preceded by a surface negativity that was larger than preceding the uninformative cue, while prior to the imperative stimuli the opposite picture was found: The CNV late wave was smaller if the subjects knew what to do next (Fig. 9). Thus in both cases the informative value of the stimulus is reflected in the size of the negativity preceding either the cue or the imperative stimulus. A similar result was reported by Chwilla and Brunia (1991a,b) with another slow wave we will discuss next.

5.3. *The stimulus preceding negativity*

Our CNV studies did convince us about a disadvantage of the paradigm: Attention to the imperative stimulus and the preparation of the movement are always confounded in time and so are the electrophysiological reflections of these processes. Therefore another paradigm was developed, in which subjects had to press a button after an estimated interval following a warning stimulus. Two seconds after the button press they were informed about the correctness of their response by a Knowledge of Results (KR) stimulus. This indicated whether the response was too early, correct or too late. The KR stimulus is preceded by a Stimulus Preceding Negativity (SPN: Damen & Brunia, 1987; Brunia & Damen, 1988; Chwilla & Brunia, 1991a), which has a rather widespread distribution and is larger over the right hemisphere than over the left hemisphere (Damen & Brunia, 1994). Over the frontal areas the SPN is manifest as a sustained negativity, while over the parietal cortex a steep increase in negativity is found. This suggests two different sources, one in the prefrontal cortex, another in the parietal area. In a source localization study Böcker, Brunia & van den Berg-Lenssen, 1994) found

Stimulus – Preceding Negativity

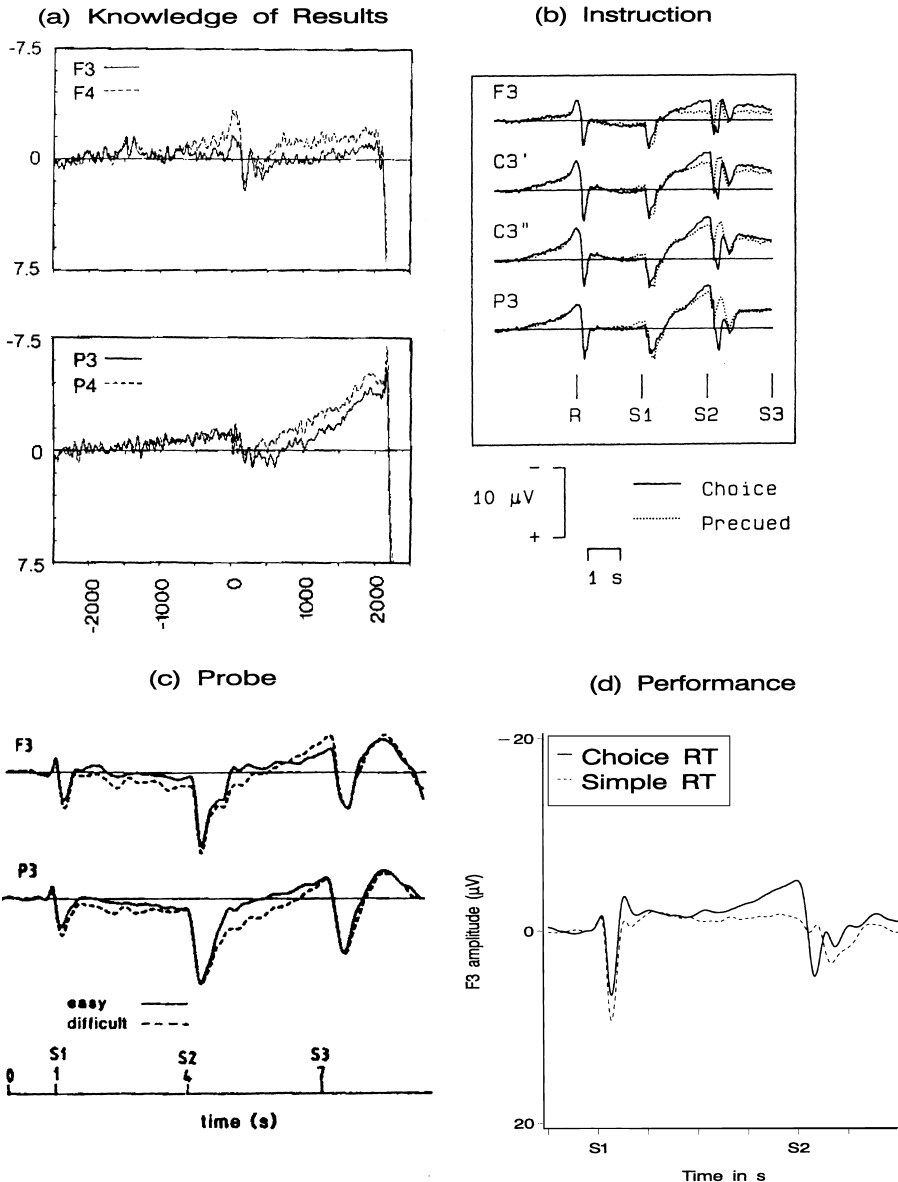


Fig. 9. Stimulus-Preceding Negativity recorded prior to different types of stimuli. (a) preceding a stimulus conveying Knowledge of Results about prior performance occurring at 2000 milliseconds after the response (adapted from Brunia and Damen, 1988), (b) preceding a stimulus providing an instruction about future performance (S1; adapted from Van Boxtel and Brunia, 1996b), (c) preceding a probe stimulus with which the outcome of a previous task has to be matched (S3; adapted from Chwilla and Brunia, 1991b). Panel (d) shows the frontal negative shift related to the control over task performance (adapted from Van Boxtel and Brunia, 1994a).

one equivalent dipole, possibly localized in the Insula Reili (temporal lobe). Therefore it seems plausible that waiting for a KR stimulus, which has consequences for the timing of a movement in a next trial goes along with activity in a network, in which the prefrontal cortex, the temporal cortex and the parietal cortex participate. Supporting evidence for this was found in a PET study (Brunia, De Jong, Paans & van den Berg-Lenssen, (1996).

An SPN is not exclusively recorded prior to KR stimuli (Böcker & van Boxtel, 1997). An instruction stimulus, presented at a known moment in time, is also preceded by a small negative wave (Damen & Brunia, 1994), while probe stimuli used to indicate a match with an earlier result, are preceded by an SPN too (Chwilla & Brunia, 1991b, 1992). Prior to probes, giving partial information about a future performance, van Boxtel and Brunia (1994b) found also an SPN (Fig. 9). In general, it seems a reasonable hypothesis, that in all circumstances in which subjects wait for some kind of informative stimuli, the brain areas involved in the future perception are activated. This excitatory activity contributes to a surface negativity, the distribution of which depends upon the upcoming function.

In this section we have seen first that movement preceding negativity can be recorded preceding both self-paced and stimulus-triggered movements. Next we have found that the presentation of imperative stimuli, cues and KR stimuli is also preceded by negative waves, the size of which reflects the information value of these stimuli. The distribution depends on the kind of task the stimuli play a role in. For both movement preceding negative waves, the RP and the CNV late wave we have seen that the basal ganglia play an essential role in their generation, although they reflect admittedly cortical activity. It is interesting that Schultz, Apicella, Romo and Scanati (1995) reported recently anticipatory firing of units in the basal ganglia *if* the subject knows that a stimulus will be presented and *if* the stimuli are relevant for the upcoming movement. The authors found anticipatory firing preceding three different events: the expectation of an instruction, a trigger or a reward stimulus. There is a striking similarity with anticipatory slow potential results in man, in which we found anticipatory negativity preceding an imperative stimulus (“trigger”), a cue (“instruction”) and a KR stimulus (“reward”). Obviously, the similarity in time course between the anticipatory cell activity in the monkey basal ganglia and the anticipatory cortical slow waves in man is *no proof* for the relation suggested, but it is at least compatible with it, and it can be regarded as supporting evidence. All the basal ganglia output has to pass the different thalamic nuclei – and thus the RN – before reaching the cortical target areas. Thus a final modulation via the RN is possible via these different pathways.

5.4. *Event-related desynchronization*

The more or less simultaneous firing of large numbers of pyramidal cells in the cortex results in rhythmic activity in the EEG. Schlag and Villablanca (1967) produced rhythmic activity in isolated cortex by electrical low frequency stimulation of the white matter. Next Schlag and Waszak (1970,71) demonstrated that

during spontaneous or electrically induced synchronization high frequency bursts of activity in RN cells are present, associated with IPSPs in the underlying thalamic nuclei. Yingling and Skinner (1977) considered the role of the RN essential for the production of spontaneous rhythmic activity. However, the coherence between alpha waves recorded in neighboring cortical areas is larger than the thalamo-cortical coherence (Lopes da Silva, van Lierop, Schrijer & Storm van Leeuwen, 1973). Yet the pulvinar plays an important role in the generation of alpha activity.

Rhythmic cortical activity can be recorded over different areas. Alpha rhythm is present over the occipital and parietal electrode positions in the human EEG. Over the somatosensory cortex a mu rhythm is recorded, with about the same frequency as the alpha rhythm. Recently a similar rhythmic activity from the auditory cortex has been recorded in the magnetoencephalogram (Tiihonen, Hari, Kajola, Ahlfors & Tissari, 1991). It has been termed “tau rhythm”. These cortical rhythms are partly the result of the input from the thalamus, showing a similar but not identical rhythmic activity (Lopes da Silva, 1996). Since blocking of spontaneous rhythmic activity might be based upon changes in the thalamo-cortical information transmission, the study of the so-called desynchronization with stimuli of different modalities might be helpful in the investigation of anticipatory behavior.

The alpha rhythm was discovered by Berger (1929), who was also the first to describe its blocking by the opening of the eyes. The rhythmic activity is considered an idling of the system, which can be terminated by the transmission of specific information. The presentation of this information results in a decrease in power, known as “event-related desynchronization” (ERD). Physiologically the ERD is caused by an inhibition of the locally inhibitory neurons. This can be the result of specific collaterals inhibiting the RN cells, or by non-specific fibers from the ARAS inhibiting them (Lopes da Silva, Van Rotterdam, Barts, Van Heusden & Burr, 1976). Thus event-related desynchronization (ERD) can be used as an index of a change in gating at the thalamic level. It indicates that a gate is open.

The visual ERD follows stimulus presentation and is restricted to the occipital and parietal cortex (Pfurtscheller, Steffan & Maresch, 1988). Responses may be different for different frequencies within the alpha band. ERD in the upper alpha band (10–12 Hz) is localized and restricted to the occipital areas, whereas ERD in the lower alpha frequencies seems to be more widespread over the visual association areas and other extra-striate cortical areas. The authors suggest that ERD in the higher frequencies reflect stimulus-related processes, and in the lower frequencies “attentional and motivational” processes. In the KR-paradigm mentioned in the former section, an anticipatory slow wave was found which had been termed SPN. Recently we investigated whether an *anticipatory* ERD might be present under these circumstances too. Indeed Bastiaansen, Böcker, Cluitmans & Brunia (in press) found an anticipatory ERD prior to a visual KR stimulus (but not preceding an auditory one).

The prevailing rhythm within the human sensorimotor cortex is the beta rhythm. Jasper and Penfield (1949) recorded this activity intracranially. They noted that the beta activity could be blocked by the initiation of voluntary movements. They fur-

ther found that *preparation of a movement* also blocks the beta activity and that the blocking sometimes was restricted to the local cortical area representing the part of the limb going to be moved (Penfield and Jasper, 1956, p. 191). In other words the preparatory processes in these cases were tuned very precisely. The subcortical input to the motor thalamus, e.g. from the cerebellum, is organized in a somatotopic way. This suggests that the RN could play a role in the precise tuning of the activity allowed to pass to the cortex.

The rolandic mu rhythm, recorded in the MEG over the somatosensory cortex, has two components, a 10 and a 20 Hz component. The first is somatosensory, the second somatomotor in origin (Hari, Salmelin, Mäkelä, Salenius & Helle, 1997). Pfurtscheller and Aranibar (1979) investigated the mu rhythm over the central electrode positions (C3, C4). They found an ERD following repetitive tactile stimuli, contralateral to stimulus presentation. Interestingly, they also recorded an ERD *preceding the stimulus presentation*. Expectancy in this case means a very localized activation of a part of the thalamo-cortical circuitry. Again, it has an obvious counterpart in the SPN.

A different ERD was found over the sensori-motor cortex *preceding the voluntary movement*. This happened about more than 1 sec prior to the movement, in other words in the same time window in which the RP emerges. In contrast to RP studies with finger movements however, the ERD starts over the contralateral hemisphere and is only present over the ipsilateral cortex during the last 700 ms prior to the movement (Pfurtscheller & Klimesch, 1991). This difference in laterality between the RP and the anticipatory motor ERD remains to be elucidated.

Although further research is needed to demonstrate the existence of an (anticipatory) ERD in the auditory modality, the available evidence suggests that the anticipatory ERD exists in the visual and somatosensory modality, and in the motor domain. Since we know that the rhythmic cortical activity stems from thalamic input to the cortex, this suggests that the ERD is a reflection of the modulation of thalamo-cortical input to the different sensory and motor cortices.

6. Conclusion

In the present paper we have argued that the control of anticipatory attention and motor preparation is organized in a similar way. We have presented evidence for the hypothesis that both functions are based upon the integrity of different thalamo-cortical networks. We have seen how both inhibition of irrelevant information and enhancement of relevant information can be brought about via a prefrontal influence upon the RN, which has an inhibitory influence upon thalamic relay nuclei. Modulation of thalamo-cortical input is an essential characteristic of anticipatory attention and motor preparation. Since the RN is a very thin sheet overlying the different thalamic relay nuclei, it is difficult to record activity directly from this structure, especially in behaving animals, let alone man. Therefore it is difficult to demonstrate that the proposed hypothesis is correct. The available results from psychophysiological experiments can only provide supportive evidence, which they do.

References

- Alexander, G. E., & Crutcher, M. D. (1990). Functional architecture of basal ganglia circuits: neural substrates of parallel processing. *Trends in the Neurosciences*, *13*, 266–271.
- Alexander, G. E., DeLong, M. R., & Strick P. L. (1986). Parallel organization of functionally segregated circuits linking basal ganglia and cortex. *Annual Review of Neuroscience*, *9*, 357–81.
- Allport, A. (1989). Visual attention. In M. I. Posner, *Foundations of cognitive science* (pp. 631–682). Cambridge, MA: The MIT Press.
- Arezzo, J., & Vaughan Jr. H. G. (1980). Cortical potentials associated with voluntary movements in the monkey. *Brain Research*, *88*, 99–104.
- Barrett, G., Shibasaki, H., & Neshige, R. (1986). Cortical potential shifts preceding voluntary movement are normal in parkinsonism. *Electroencephalography and Clinical Neurophysiology*, *60*, 276–281.
- Bastiaansen, M. C. M., Böcker, K. B. E., Cluitmans, P. J. M., & Brunia, C. H. M. (in press). Event-related desynchronization related to the anticipation of a stimulus providing knowledge of results. *Electroencephalography and Clinical Neurophysiology*.
- Berger, H. (1929). Über das Elektrenkephalogramm des Menschen. II. *Archiv für Psychiatrie und Nervenkrankheiten*, *87*, 527–570.
- Böcker, K. B. E., Brunia, C. H. M., & van den Berg-Lenssen, M. M. C. (1994). A spatio temporal dipole model of the Stimulus Preceding Negativity (SPN) prior to feedback stimuli. *Brain Topography*, *7*, 71–88.
- Böcker, K. B. E., & Van Boxtel, G. J. M. (1997). Stimulus-preceding negativity: a class of anticipatory slow potentials. In G. J. M. van Boxtel & K. B. E. Böcker. *Brain and Behavior: Past, Present, and Future* (pp. 105–116). Tilburg: Tilburg University Press.
- Boschert, J., Hink, R. F., & Deecke, L. (1983). Finger movement versus toe movement potentials: further evidence for supplementary motor area (SMA) participation prior to voluntary action. *Experimental Brain Research*, *52*, 73–80.
- Brodal, P. (1992). *The central nervous system*. New York: Oxford University Press.
- Brunia, C. H. M. (1988). Movement and stimulus preceding negativity. *Biological Psychology*, *26*, 165–178.
- Brunia, C. H. M., & Damen, E. J. P. (1988). Distribution of Slow Brain Potentials related to Motor Preparation and Stimulus Anticipation in a time estimation task. *Electroencephalography and Clinical Neurophysiology*, *69*, 234–243.
- Brunia, C. H. M., & Vingerhoets, A. J. J. M. (1981). Opposite hemisphere differences in movement related potentials preceding foot and finger flexions. *Biological Psychology*, *13*, 261–269.
- Brunia, C. H. M., de Jong, B. M., Paans, A. M. J., & van den Berg-Lenssen, M. M. C. (1996). Visual feedback about time estimation causes a right hemisphere rCBF increase as measured by PET. *European Journal of Neuroscience, Supplement*, *9*, 139 (Abstract).
- Chwilla, D. J., & Brunia, C. H. M. (1991a). Event-Related potentials to different feedback stimuli. *Psychophysiology*, *28*, 123–132.
- Chwilla, D. J., & Brunia, C. H. M. (1991b). Event-related potential correlates of non-motor anticipation. *Biological Psychology*, *32*, 125–141.
- Chwilla, D. J., & Brunia, C. H. M. (1992). Effects of emotion on event-related potentials in an arithmetic task. *Journal of Psychophysiology*, *6*, 321–332.
- Creutzfeldt, O. D. (1995). *Cortex Cerebri*. Oxford: Oxford University Press.
- Damen, E. J. P., & Brunia, C. H. M. (1987). Precentral potential shifts related to motor preparation and stimulus anticipation: a replication. In: R. Johnson Jr., J. W. Rohrbaugh & R. Parasuraman, *Current Trends in Event-Related Potential Research*, *40* (pp. 13–16).
- Damen, E. J. P., & Brunia, C. H. M. (1994). Is a stimulus conveying task relevant information a sufficient condition to elicit stimulus preceding negativity (SPN)? *Psychophysiology*, *31*, 129–139.
- Deecke, L., & Kornhuber, H. H. (1977). Cerebral potentials and the initiation of voluntary movement. In J. E. Desmedt, *Attention, Voluntary Contraction and Event-Related Cerebral Potentials* (pp. 132–150). Basel: Karger.

- Dick, J. P. R., Rothwell, J. C., Day, B. L., Cantello, R., Buruma, O., Gioux, M., Benecke, R., Berardelli, A., Thompson, P. D., & Marsden, C. D. (1989). The Bereitschaftspotential is abnormal in Parkinson's disease. *Brain*, *112*, 233–244.
- Evarts, E. V., & Tanji, J. (1976). Reflex and intended responses in motor cortex pyramidal tract neurons of monkey. *Journal of Neurophysiology*, *39*, 1069–1080.
- Fuster, J. M. (1997). *The Prefrontal Cortex. Anatomy, Physiology, and Neuropsychology of the frontal lobe.* (3rd ed.). Philadelphia: Lippincott Raven.
- Gemba, H., & Sasaki, K. (1984). Distribution of potentials preceding visually initiated and self paced movements in various cortical areas of the monkey. *Brain Research*, *306*, 207–214.
- Gibson, J. J. (1941). A critical review of the concept of set in contemporary experimental psychology. *Psychological Bulletin*, *38*, 781–817.
- Goldberg, G. (1985). Supplementary motor area structure and function: Review and hypotheses. *Behavioral and Brain Sciences*, *8*, 567–616.
- Graybiel, A. M., & Kimura, M. (1995). Adaptive neural networks in the basal ganglia. In J. C. Houk, J. L. Davis & D. G. Beiser, *Models of information processing in the basal ganglia* (pp. 103–116). Cambridge, MA: The MIT Press.
- Hari, R., Salmelin, R., Mäkelä, J. P., Salenius, S., & Helle, M. (1997). Magnetoencephalographic cortical rhythms. *International Journal of Psychophysiology*, *26*, 51–62.
- Hashimoto, S., Gemba, H., & Sasaki, K. (1979). Analysis of slow cortical potentials preceding self paced movements in the monkey. *Experimental Neurology*, *65*, 218–229.
- Hebb, D. O. (1949). *The organization of behavior: A neuropsychological theory.* New York: Wiley.
- Hilgard, E. R., & Marquis, D. G. (1940). *Conditioning and Learning.* New York: Appleton-Century.
- Ikeda, A., Shibasaki, H., Nagamine, T., Terada, K., Kaji, R., Fukuyama, H., & Kimura, J. (1994). Dissociation between contingent negative variation and Bereitschaftspotential in a patient with cerebellar efferent lesion. *Electroencephalography and Clinical Neurophysiology*, *90*, 359–364.
- Jahanshahi, M., Jenkins, I. H., Brown, R. G., Marsden, C. D., Passingham, R. E., & Brooks, D. J. (1995). Self-initiated versus externally triggered movements I. An investigation using measurement of regional blood flow with PET and movement-related potentials in normal and Parkinson's disease subjects. *Brain*, *118*, 913–933.
- Jasper, H. H., & Penfield, W. (1949). Electroencephalograms in man: Effect of the voluntary movement upon the electrical activity in the precentral gyrus. *Archiv für Psychiatrie*, *183*, 163–174.
- Jeannerod, M. (1997). *The cognitive neuroscience of action.* Oxford, Cambridge, MA: Blackwell.
- Jordan, M. I., & Rosenbaum, D. A. (1989). Action. In: M. I. Posner, *Foundations of cognitive science* (pp. 727–767). Cambridge, MA: The MIT Press.
- Keele, S. W. (1968). Movement control in skilled motor performance. *Psychological Bulletin*, *70*, 387–404.
- Kelly, J. P. (1991). The neural basis of perception and movement. In: E. R. Kandel, J. H. Schwartz & T. M. Jessell (Eds.), *Principles of neural science* (pp. 283–295). New York: Elsevier.
- Kornhuber, H. H., & Deecke, L. (1965). Hirnpotentialänderungen bei Willkürbewegungen und passiven Bewegungen des Menschen: Bereitschaftspotential und reafferente Potentiale. *Pflügers Archiv*, *284*, 1–17.
- LaBerge, D. (1995). *Attentional processing.* Cambridge, MA: Harvard University Press.
- LaBerge, D., & Buchsbaum, M. S. (1990). Positron emission tomographic measurement of pulvinar activity during an attention task. *Journal of Neuroscience*, *67*, 613–619.
- LaBerge, D., Carter, M., & Brown, V. (1992). A network simulation of thalamic circuit operations in selective attention. *Neural Computation*, *4*, 318–331.
- Lopes da Silva, F. H. (1996). The generation of electric and magnetic signals of the brain by local networks. In R. Greger & U. Windhorst, *Comprehensive Human Physiology*, (Vol. I, pp. 509–531). Heidelberg: Springer.
- Lopes da Silva, F. H., van Lierop, T. H. M. T., Schrijer, C. F. M., & Storm van Leeuwen, W. (1973). Essential differences between alpha rhythms and barbiturate spindles: spectra and thalamo-cortical coherence. *Electroencephalography and Clinical Neurophysiology*, *35*, 641–645.

- Lopes da Silva, F. H., Van Rotterdam, A., Barts, P., Van Heusden, E., & Burr, W. (1976). Models of neuronal populations : the basic mechanisms of rhythmicity. *Progress in Brain Research*, 45, 281–308.
- Loveless, N. E., & Sanford, A. J. (1974). Effects of age on the contingent negative variation and preparatory set in a reaction time task. *Journal of Gerontology*, 29, 52–63.
- Massion, J. (1967). The thalamus in the motor system. *Applied Neurophysiology*, 39, 222–238.
- Massion, J., & Deat, A. (1991). Two modes of coordination between movement and posture. In J. Requin & G. E. Stelmach, *Tutorials in motor neuroscience* (pp. 199–208). Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Mauritz, K. H., & Wise, S. P. (1986). Premotor cortex of the rhesus monkey: neuronal activity in anticipation of predictable environmental events. *Experimental Brain Research*, 61, 229–244.
- Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.
- Mitrofanis, J., & Guillery, R. (1993). New views of the thalamic reticular nucleus in the adult and developing brain. *Trends in the Neurosciences*, 16, 414–417.
- Nelson, R. N. (1988). Set related and premovement related activity of primate primary somatosensory cortical neurons depends upon stimulus modality and subsequent movement. *Brain Research Bulletin*, 21, 411–424.
- Passingham, R. E. (1987). Two cortical systems for directing movement. In: *Motor areas of the cerebral cortex. Ciba Foundation Symposium*, (Vol. 132, pp. 151–161). Chichester: Wiley.
- Passingham, R. E. (1993). *The frontal Lobes and Voluntary Action*. Oxford: Oxford University Press.
- Penfield, W., & Jasper, H. H. (1956). *Epilepsy and the Functional Anatomy of the Human Brain*. Boston: Little, Brown and Company.
- Pfurtscheller G., & Aranibar, A. (1979). Evaluation of event-related desynchronization (erd) preceding and following self-paced movement. *Electroencephalography and Clinical Neurophysiology*, 46, 138–146.
- Pfurtscheller, G., & Klimesch, W. (1991). Event-related desynchronisation during motor behavior and visual information processing. In C. H. M. Brunia, G. Mulder & M. N. Verbaten, *Event-related Brain Research (EEG Suppl. 42)* (pp. 58–65). Amsterdam: Elsevier.
- Pfurtscheller, G., Steffan, J., & Maresch, H. (1988). ERD mapping and functional topography: temporal and spatial aspects. In: G. Pfurtscheller & F. H. Lopes da Silva, *Functional Brain Imaging* (pp. 117–130). Bern: Hans Huber Publishers.
- Praamstra, P., Meyer, A. S., Cools, A. R., Horstink, M. W. I. M., & Stegeman, D. F. (1996). Movement preparation in Parkinson's disease—Time course and distribution of movement-related potentials in a movement precueing task. *Brain*, 119, 1689–1704.
- Posner, M. (1994). Attention in cognitive neuroscience. An overview. In M. Gazzaniga, *The Cognitive Neurosciences* (pp. 615–624). Cambridge, MA: The MIT Press.
- Purpura, D. P. (1970). Operations and processes in thalamic and synaptically related neural subsystems. In F. O. Schmitt, *The Neurosciences. Second Study Program* (pp. 458–470). New York: The Rockefeller University Press.
- Purpura, D.P., Scarff, T., & McMurtry, K. (1965). Intracellular study of internuclear inhibition in ventrolateral thalamic neurons. *Journal of Neurophysiology*, 28, 487–496.
- Rebert, C. S. (1977). Intracerebral slow potential changes in monkeys during the foreperiod of reaction time. In J. E. Desmedt (Ed.), *Attention, Voluntary Contraction and Slow Potential Shifts* (pp. 242–253). Basel: Karger.
- Riehle, A., & Requin, J. (1989). Monkey primary motor and premotor cortex: single cell activity related to prior information about direction and extent of an intended movement. *Journal of Neurophysiology*, 61, 534–549.
- Rohrbaugh, J., & Gaillard, A. W. K. (1983). Sensory and motor aspects of the contingent negative variation. In: A. W. K. Gaillard & W. Ritter, *Tutorials in event-related potentials research: endogenous components* (pp. 269–310). Amsterdam: North-Holland.
- Rosenbaum, D. A. (1985). Motor programming: A review and scheduling theory. In H. Heuer, U. Kleinbeck & K. -H. Schmidt, *Motor behavior. Programming, control and acquisition* (pp. 1–33). Berlin: Springer.

- Rosenbaum, D. A., Kenny, A. W., & Derr, M. A. (1983). Hierarchical control of rapid movement sequences. *Journal of Experimental Psychology: Human Perception and Performance*, 9, 86–102.
- Sasaki, K., Gemba, H., & Minzuno, N. (1982). Cortical field potentials preceding visually initiated hand movements and cerebellar actions in the monkey. *Experimental Brain Research*, 46, 29–36.
- Sasaki, K., & Gemba, H. (1991). Cortical potentials associated with voluntary movements in monkeys. In: C. H. M. Brunia, G. Mulder, & M. N. Verbaten (Eds.), *Event-related Brain Research (EEG Suppl. 42)* (pp. 80–96). Amsterdam: Elsevier.
- Schlag, J., & Villablanca, J. (1967). Cortical incremental responses to thalamic stimulation. *Brain Research*, 21, 286–288.
- Schlag, J., & Waszak, M. (1970). Characteristics of unit responses in nucleus reticularis thalami. *Brain Research*, 21, 286–288.
- Schlag, J., & Waszak, M. (1971). Electrophysiological properties of units of the thalamic reticular complex. *Experimental Neurology*, 32, 79–97.
- Schneider, G. E. (1969). Two visual systems: brain mechanisms for localization and discrimination are dissociated by tectal and cortical lesions. *Science*, 163, 895–902.
- Schultz, W., Apicella, P., Romo, R., & Scanati, E. (1995). Context-dependent activity in primate striatum reflecting past and future behavioral events. In: J. C. Houk, J. L. Davis & D. G. Beiser, *Models of information processing in the basal ganglia* (pp. 11–29). Cambridge, MA: The MIT Press.
- Shibasaki, H., Barrett, G., Neshige, R., Hirata, I., & Tomoda, H. (1986). Volitional movement is not preceded by cortical slow negativity in cerebellar dentate lesion in man. *Brain Research*, 368, 361–365.
- Shibasaki, H., Shima, F., & Kuroiwa, Y. (1978). Clinical studies of the movement-related cortical potential (MP) and the relationship between the dentatorubrothalamic pathway and the readiness potential. *Journal of Neurology*, 921, 15–25.
- Skinner, J. E., & Yingling, C. D. (1977). Central gating mechanisms that regulate event-related potentials and behavior. In J. E. Desmedt (Ed.), *Attention, Voluntary Contraction and Slow Potential Shifts* (pp. 30–69). Basel: Karger.
- Steriade, M., Jones, E. G., & Llinas, R. R. (1990). *Thalamic oscillations and signalling*. New York: Wiley.
- Strick, P. L. (1976). Activity of ventrolateral thalamic neurons during arm movements. *Journal of Neurophysiology*, 39, 1032–1044.
- Strick, P. L., Dum, R. P., & Picard, N. (1995). Macro-organization of the circuits connecting the basal ganglia with the cortical motor areas. In J. C. Houk, J. L. Davis & D. G. Beiser, *Models of information processing in the basal ganglia* (pp. 11–29). Cambridge, MA: The MIT Press.
- Tanji, J., Tanichuchi, K., & Saga, T. (1980). Supplementary motor area: neuronal response to motor instructions. *Journal of Neurophysiology*, 43, 60–68.
- Tiihonen, J., Hari, R., Kajola, M., Ahlfors, S., & Tissari, S. (1991). Magnetoencephalo-graphic 10-Hz rhythm from human auditory cortex. *Neuroscience Letters*, 129, 303–305.
- Thach, W. T. (1987). Cerebellar inputs to motor cortex. In: *Motor areas of the cerebral cortex. Ciba Foundation Symposium*, (Vol. 132, pp. 201–215). Chichester: Wiley.
- Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale & R. J. W. Mansfield, *Analysis of visual behavior*. Cambridge, MA: The MIT Press.
- Van Boxtel, G., & Brunia, C. H. M. (1994a). Motor and non-motor aspects of slow brain potentials. *Biological Psychology*, 38, 35–51.
- Van Boxtel, G. J. M., & Brunia, C. H. M. (1994b). Motor and non-motor components of the contingent negative variation. *International Journal of Psychophysiology*, 17, 269–279.
- Walter, W. G., Cooper, R., Aldridge, V. J., McCallum, W. C., & Winter, A. L. (1964). Contingent Negative Variation: an electric sign of sensori-motor association and expectancy in the human brain. *Nature*, 203, 380–384.
- Weiskrantz, L. (1986). *Blindsight: a case study and implications*. Oxford: Oxford University Press.
- Weiskrantz, L., Warrington, E. K., Sanders, M. D., & Marshall, J. (1974). Visual capacity in the hemianopic field following a restricted occipital ablation. *Brain*, 97, 709–728.
- Wise, S. P., & Strick, P. (1985). Anatomical and physiological organization of the non-primary motor cortex. In E. V. Evarts, S. P. Wise, & D. Bousfield, *The motor system in neurobiology* (pp. 315–324). Amsterdam: Elsevier biomedical Press.

- Yingling, C. D., & Skinner, J. E. (1977). Gating of thalamic input to the cerebral cortex by nucleus reticularis thalami. In J. E. Desmedt (Ed.), *Attention, Voluntary Contraction and Slow Potential Shifts* (pp. 70–96). Basel: Karger.