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Cognitive Integration in the Human Primary Sensory and Motor Areas: An Overview

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1. Introduction

Although many different definitions of cognition exist, there is a general acceptance that cognition can be defined as a higher function with respect to both the primary stages of sensory information processing and the final stage of motor output. This idea has been the basis of many well known psychological models where one can identify “input boxes” (i.e., visual, auditory, somatosensory information), and “output boxes” (i.e., motor commands), with, intermediate, high level (attention, language, memory, ...) and low-level (motor intention, preparation) cognitive functions (see, for instance, the information processing model of Smidt and Lee (2005), or the model for central representation of goal-directed movements of Jeannerod (1990)).

Although these models are, without doubt, well suited to the study of cognitive processes from a psychological standpoint, they are not very helpful from a neuroscientific point of view. Indeed, ever since the very first investigations into the functioning of the living brain, the main aim has been to localize cognitive functions into the cortical structures of the brain. There exist at least **two** problems related to this approach. Firstly, and this is not a recent objection (e.g., Posner and Raichle (1998) page 16), it is doubtful whether the cognitive functions as presently conceived have a meaning for the brain. Let us take for example the so-called “eye-hand coordination”. This “function” is much studied today and many publications report attempts to localize it in the brain. But, for a normally developed brain, this is not a specific function which is needed at specific moments and which is necessarily implemented in a specific brain structure. All input is continuously put in relation with each other as a function of the particular output. It seems more likely that eye-hand coordination is controlled in a continuous, implicit and distributed way. It is pertinent here to mention the ecological approach of perception (Gibson, 1986). This approach is based on the concept of “affordance” that characterizes the object of perception as a whole of many possible actions and interactions, and is in rupture with the cognitive approach. Indeed, according to the latter approach, the brain organizes the perception of the world, whereas in the ecological approach, the world organizes the perception: The role of the brain is to extract the information presented by the world. This theory suggests that the traditional approach of studying cerebral functioning is not very appropriate: the cognitive functions that we define do not have much sense for the brain and, what’s more, we generally put subjects in

environments which are too artificial in order to study brain functioning. However, since in their opinion perception is “direct”, Gibson and his successors have largely ignored the brain and have, therefore, not contributed to the understanding of brain functioning. Although there is much more to say on this subject, we will not develop this point any further in the present chapter.

The second drawback with the cognitive approach is the fact that cognition has mainly been sought outside the primary cortical areas. Indeed, since the above-mentioned cognitive models localize cognition between the input and the output, cognition is necessarily located in the secondary and associative cortical areas. For a long time, the primary motor area has been considered as a simple “execution area” of which the neuronal activity reflects the immediate output to the muscles. In the same way, the primary sensory areas are often presumed to simply transfer sensory information to higher order cognitive systems. For the same reason, studies concerned with the functioning of the secondary and associative areas do not really take into account the direct projections of the nervous system to peripheral structures.

In this chapter, we aim to show that the hierarchical and modular vision of brain functioning is no longer defensible. Cognition emerges from the interaction between regions that are distributed over the whole brain, including the primary cortical areas. After a brief review of the anatomy of the primary somatosensory (S1) and motor (M1) areas, we will develop arguments in favor of this hypothesis. We will mention the highly flexible functional organization of the primary sensorimotor cortical areas. We will show that the neuronal activity of S1 depends on the environmental and cognitive context, i.e., on the value of the stimulus at a given moment. Then, we will show that M1 is much more than a simple transmission area between the non-primary motor areas and the spinal cord. Indeed, M1 is active in tasks without any motor output and the M1 neuronal activity depends on the context in which a motor output is produced and can be adapted and modified in real time. We will end with an example of a clinical implication of this hypothesis, concerning phantom limb sensations in patients with upper limb amputations.

2. Primary cortical areas

2.1 Anatomical organization of the primary areas

What makes a primary cortical area “primary” is that it is, either, the first cortical structure receiving the sub-cortical projections transporting visual, auditory or somatosensory information, or the last cortical stage before the motor commands descend to sub-cortical structures. The cortex of each hemisphere contains one primary motor area (M1) and three primary sensory areas. M1 is localized on the pre-central wall at the depth of the central sulcus. The post-central gyrus contains the primary somatosensory area (S1), extending from the posterior wall of the central sulcus to the depth of the anterior wall of the post-central sulcus. The primary auditory area (A1) is situated in the superior temporal gyrus on the dorso-postero-medial part of the transverse gyri of Heschl (Liégeois-Chauvel et al., 1991). Finally, the primary visual area (V1) is located at the posterior poles of the occipital lobes in the calcarian sulcus.

Broadly speaking, the cortex contains at least 6 well defined neural layers that can often even be sub-divided into sub-layers. The cellular organization differs sufficiently between the different cortical regions that we can use it as a criterion to delimitate *functional* cortical areas. This was first done by Korbinian Brodmann at the beginning of the twentieth century

who established the well-known cerebral map based on the cytoarchitecture of the different regions of the cortex. Each region of the cortex containing the same cellular organization was attributed the same number, ranging from 1 to 52. Brodmann's assumption was that a given anatomical organization must correspond to a particular function. For instance, Brodmann's area 17, which receives information from a thalamic nucleus which in turn receives projections from the retina, is called the primary visual cortex; Brodmann's areas 41 and 42 form the primary auditory cortex; Brodmann's areas 1 to 3 form the primary somatosensory cortex; Brodmann's area 4 globally corresponds to the primary motor cortex. It is important to note that the Brodmann classification is based on adult brains and so were anatomically and neurophysiologically fully developed. It has been shown that the cytoarchitecture of the sensorimotor cortex is subject to considerable modifications from birth (or even before) until the age of 20 (Shumeiko, 1998). Today, it is not clear how the cytoarchitecture of the cortex depends on its *functional* development.

The primary sensory areas differ from other cortical areas mainly by the thickness of layer 4. Whatever the cortical structure, this layer receives sensory information. For instance, the axons from the optical radiation primarily project onto neurons of the fourth layer of V1. M1 has a fourth layer that is clearly thinner than S1, indicating that it receives less sensory information. However, M1 does receive some sensory input in layers 1 to 4, not only from cortical sensory areas but also directly from the thalamus. Also, several secondary motor areas, such as the premotor (PM), supplementary motor (SMA) and cingular motor areas, project directly onto M1 (Dum & Strick, 2002). Concerning the efferent fibers of M1, layer 5 contains the so-called "Cells of Betz" (large pyramidal neurons), visible with only little optical enlargement. Part of the corticospinal tract finds its origin in these pyramidal neurons. This tract consists of well myelinated axons which directly descend into the spinal cord. Some of these axons even project directly onto the motoneurons of the distal muscles without passing by interneurons (Maier et al., 2002). M1 also sends small efferent axons from layers 5 and 6 to other cortical areas.

2.2 Flexibility and plasticity of the primary cortical areas

The primary cortical areas represent the information coming from (or going to) the periphery according to a topological principle, i.e., retinotopic for V1, tonotopic for A1, and somatotopic for S1 and M1. These "maps" were long considered as stable and definitive once the neural functions are fully developed. We now know that this is not correct. Without elaborating on this huge research domain, we will give some examples involving M1 and S1 which show that these topologic maps are highly flexible and constantly re-actualized.

We begin with some basic details concerning the somatotopy of M1. In a normal subject, M1 shows a rather global somatotopic organization in a medial-lateral direction, representing the leg, back, arm, hand and face (Penfield & Boldrey, 1937). This rather fine somatotopic organization seems to reflect a "basic" organization that exists when the subject is passive. However, when engaged in a task, within each sub-area, we can identify a distributed representation adapted to the requirements of the task. This has been shown by Sanes and colleagues (1995) in an fMRI study. They asked subjects to make flexion/extension movements with different fingers (one at a time) or with the wrist. For each movement, they found multiple activation sites in the arm area of M1. Moreover, these sites showed an important overlap. These results, which have since been confirmed by other studies (see

Indovina et Sanes, 2001; for a review Sanes & Donoghue, 2000), strongly suggest that the neurons within the arm area of M1 form a distributed network controlling ensembles of arm muscles as a function of how they are implicated in the particular movement. Pascual-Leone and colleagues (1995), in a transcranial magnetic stimulation (TMS) study, confirmed this by showing a modification of the hand representation in M1 in subjects learning a 5-finger piano exercise. During a training period of 2 hours a day over 5 consecutive days, the cortical area targeting the muscles implicated in the task enlarged. Moreover, the activation threshold decreased. This modification was limited to the implicated hand. Similarly, again using TMS, it has been shown that the cortical area targeting an immobilized part of the body is diminished after immobilization, the reduction being correlated to the duration of the immobilization (Liepert et al., 1995).

Several animal studies have also shown a reorganization of S1 after tactile stimulation. For example, when monkeys are trained to get food out of holes of different diameters, the representation of the hand surface in area 3b of S1 shows less overlap of receptive fields for the trained fingers than for the control fingers (Xerri et al., 1999). Also, rats exposed to an environment rich in tactile stimulation, show an enlarged tactile representation of their paws with a higher spatial resolution in S1 (Xerri et al., 1996). It is interesting to note that this reorganization of S1 can be produced at all ages (Coq & Xerri, 2001).

In an extensive review, Xerri (1998) reported on the plasticity of the primary somatosensory and motor areas after either a peripheral or central lesion. A temporary anesthesia of the dorsal roots of the spinal cord related to the fingers gives rise very rapidly (i.e., within some minutes) to both an enlargement of the receptive fields close to the anesthetized fingers, and the appearance of new receptive fields. At the cortical level, this means that the cortical zone corresponding to the anesthetized fingers is invaded by the representation of the hand surface adjacent to the anesthetized fingers. This reorganization is reversible and disappears after dissipation of the anaesthesia. Contrary to the expanded zones seen immediately after denervation, those observed later on show a clear somatotopic organization. This means that there is an organized spatial redistribution of a large number of cortical input fibers. After amputation of the hand or forearm, the territories of the cortical representation of the lost body part are reoccupied by the afferent information from the adjacent body part and from the face (e.g., Florence & Kaas, 1995). This reorganization is known to be (at least partly) reversible. This has been confirmed in an fMRI study before and after a transplantation of both hands in an adult human subject (Giraux et al., 2001). This particular patient had had a traumatic amputation of both hands 4 years earlier. After the bilateral transplantation of the hands and an extensive rehabilitation, the centre of activity evoked by movements of the elbow and the hand was modified in such a manner that the cortical organization became similar to that before amputation of the hands. After six months, the transplanted hands were recognized and could be used quasi-normally. These examples show the important flexibility and plasticity at the level of the primary sensorimotor areas as a function of the afferent information and the task in which the subject is engaged.

2.3 Functional activity of the primary sensory areas

As mentioned before, the primary cortical areas have been long considered as a simple information transmission area between the outside world and the associative and cognitive areas. We now know that the activity of the primary areas is, on the one hand, not simply related to the input or output of information of the concerned modality, and, on the other

hand, a complex function of the sensory information and the cognitive context in which the activity is evoked. In this section, we will give several examples concerning the primary sensory areas to justify this hypothesis. We will then elaborate on the functioning of the primary motor area in section 2.4.

2.3.1 Multimodality

Several recent neurophysiologic studies have shown that the activity of the primary sensory areas can be influenced by the sensory information of another modality. This has long been established in blind or deaf subjects (e.g., Finney et al., 2001; Hunt et al., 2006; Théoret et al., 2004), but it has also been identified in normal subjects. Non-invasive neuroimaging studies in human subject have shown a cross-modal modulation of evoked activity in primary sensory areas. For example, when both the face and voice of a speaking person were presented, the BOLD level in A1 and V1 was increased compared to when only the face or only the voice was presented (Calvert et al., 1999; Clavagnier et al., 2004). Interestingly, lip reading (with no sound) evokes an increase of BOLD level in the auditory cortex (Calvert et al., 1997). Also, a vibrotactile stimulation of the fingers evokes a response in the auditory cortex (Caetano & Jousmäki, 2006), and tactile exploration without visual information increases the BOLD level in V1 (Merabet et al., 2007).

Unitary recording in monkeys has shown that the eye position in the head influences the activity of neurons in A1 (Fu et al., 2004). Not only is the sound-response of these neurons affected but also their spontaneous activity (Werner-Reiss et al., 2003). Broche and colleagues (2005) recently found neurons in A1 of the monkey whose activity was related to non-auditory but relevant-to-the-task events. The monkeys performed a difficult auditory categorization task: After the appearance of a light, the monkey had to initiate a sound sequence by pushing a lever, and subsequently release the lever only when the frequency envelop of the sound sequence was diminishing. The authors found neurons whose activity was synchronized either with the appearance of the light, or with the start or end of lever pushing. This activity in A1 did not exist when the same monkeys performed a visual discrimination task.

All these results suggest the existence of corticocortical projections binding cortical areas of different modalities. Indeed, direct projections from the auditory cortex on V1 have been identified (Falchier et al., 2002), as well as bidirectional projections between S1 and A1 (Budinger et al., 2006) and between the visual cortex and S1 (Cappe & Barone, 2005). This shows that part of the activity of the primary sensory areas can be due to information coming from other modalities. In other words, the primary sensory areas cannot be considered as isolated centres for unimodal information processing.

2.3.2 Influence of the cognitive context

First of all, S1 can be active before the arrival of the sensory information. For example, when one is anticipating being tickled, S1 is already active before the real tickling starts in a similar way to when the tickling is actually happening (Carlsson et al., 2000). Moreover, the level of S1 activity during the anticipation of a painful stimulus seems to be correlated to the level of temporal predictability of the stimulus, i.e., the activity is higher when one knows exactly the moment of arrival of the stimulus (Carlsson et al., 2006). In a similar way, we recently showed an increase in BOLD level in S1 during the anticipation of a motor perturbation to which the subject had to react, i.e., well before the arrival of the

proprioceptive information evoked by the perturbation (De Graaf et al., 2009). These examples clearly show that the activity of S1 is not only found following a somatosensory stimulus but that it can precede it. Maybe even more surprising, the simple observation of another person being touched evokes an activity in S1 of the observer which has a somatotopy corresponding to the part of the body of the person who is being touched (among others, Blakemore et al., 2005). In this case, there is no corresponding somatosensory stimulus of the observer's own body at all.

Secondly, the activity in the primary sensory areas appears to depend in an important way on the cognitive context in which the activity is evoked. This is already clear from the above-mentioned study from Broche and colleagues (2005) showing that as a function of the task the activity can be multimodal, but there are other examples. For instance, Molchan and colleagues (1994) presented pairs of sounds and air puffs in the right eye (evoking an eye blink) and measured the metabolic cerebral response by PET. After the initial learning process, they found not only that the sound alone evoked an eye blink, but also that the same sound evoked a higher activity in A1 compared to the activity level before learning. This implies that the activity of A1 depends on the "associative value" of the sound. Another example is the long established fact that electrophysiological responses depend on the level of the attention we give to a signal (Hillyard et al., 1973). More recently, it has been shown that this attention level dependent activity can be localized in the primary areas. Indeed, Woldorff and colleagues (1993), in an auditory dichotic listening task, found increased short-latency neuromagnetic responses (20-50 ms) for the sound presented in the attended ear. Localization techniques placed the neural generator of these short-latency responses in A1. This suggests that auditory attention can selectively modulate early sensory processes, i.e., before or at the onset of the cortical processing. Another example is the observation that the somatotopic organization of S1 is modulated as a function of the cognitive context of the task in which the subject is engaged. Schaefer and colleagues (2005) analysed the functional organization of S1 of subjects performing a "Tower of Hanoi" task, and compared this to the organization of S1 in the same subjects performing the same movements but without the cognitive demands of the puzzle. The results clearly showed that the representation of the fingers implied a larger neural population in S1 during the Tower of Hanoi task than during the control task, although the executed movements (and thus the somatosensory information) were the same. This does not only confirm the flexibility in real time of S1, but also, and more importantly, shows that the functional organisation of S1 depends on the cognitive context.

In two reviews concerning unitary recording in A1, Weinberger (2007a, b) has shown how neuronal activity in A1 of animals depends on the behavioural context. The optimal frequency of the receptive field of different cells was determined in several Guinea pigs. The animals were then presented with 30-45 sound/shock pairs, the sound having a frequency different from the optimal frequency. After the experimental session, the optimal frequency of the cells was found to be modified, approaching the frequency of the sound used in the experimental session, whereas the response to the prior optimal frequency was reduced. This modification of the response in A1 develops very fast (detectable after only 5 trials, like cardiac and behavioural responses). It was also found to be stable in time after 8 weeks, even without further training (Weinberger 2004). It is worth noting that these characteristics are one of the most important features of the associative memory. This implies that not only the frequency response in A1 depends on the environmental context of the animal, but also a neurophysiologic trace of memory might exist in a primary sensory area.

The neuronal activity of V1 also depends on the context. It has been shown that the spatial and temporal contexts of the visual stimulus can influence cellular responses to the stimulus. For instance, when a stimulus with an optimal orientation for a given cell is presented at the same time as other stimuli with orthogonal orientations, the cell response increases, whereas when the same optimal stimulus is presented at the same time as other stimuli with the *same* orientation, the cell response decreases (Gilbert and Wiesel, 1990). Also, when monkeys are trained in visual discrimination tasks with the same stimuli at the same position in the visual field, the neuronal response characteristics depend on the task (Li et al., 2004). Another example is the fact that the evoked activity of neurons in V1 significantly depends on the location to which the spatial attention is directed without changing the gaze direction: When the attention is directed to the location of the receptive field, the cellular response increases (Motter, 1993).

All these examples strongly suggest that the primary sensory cortical areas do more than simply transmit peripheral sensory information. The neuronal activity depends strongly on the environmental context (i.e., other sensory information) as well as the cognitive context (i.e., the task in which the subject is engaged), in other words, on the value that we give to a stimulus at a given moment. A too restricted vision of the functioning of the primary sensory areas would lead to a loss of important information and would impede a full understanding of the functioning of these areas.

2.4 Functional activity of the primary motor area

At the cortical level, voluntary motor control is well-known to involve several areas: M1, and three non-primary motor areas (the pre-motor cortex, the supplementary motor area and the cingulate motor cortex) (e.g., Rouiller, 1996). Concerning the functional role of area M1 within this network, the most classical view suggests that the primary motor cortex is the final output of a complex network in which the most cognitive aspects of movement control (e.g. action preparation and/or planning) are processed upstream within the non-primary motor areas. This model supports a hierarchical organization of the cortical control of movement. Alternatively, some recent physiological findings suggest that area M1 is itself involved in important movement-related cognitive functions (see Requin et al., 1991; Georgopoulos, 2000; Bonnard et al., 2004 for reviews), arguing in favor of a more distributed model.

2.4.1 M1 activity without motor production

M1 can be active during the preparation of an action, i.e., well before the motor production. Indeed, in several human EEG and fMRI studies it has been shown that M1 is active during the preparation phase of a voluntary movement, either just before the execution (Ball et al., 1999; Cunnington et al., 2003; Toro et al., 1993; Wildgruber et al., 1997), or from the very beginning of the preparation phase in the case of sequential movements (see Zang et al., 2003). In a different context, we recently reported an important activity in M1 during the whole duration of the preparation of a reaction to a motor perturbation (De Graaf et al., 2009). Similarly, unitary recordings in monkeys have also shown active neurons in M1 during the preparation without any accompanying muscular activity (see Riehle (2005) for a review). Moreover, Lu and Ashe (2005) found neurons in M1 with an anticipatory activity that was exclusively related to a specific movement sequence. These neurons showed an interaction between the temporal order of the movement and the associated direction, i.e.,

their sensitivity to movement direction depended on the movement sequence to prepare. This suggests that M1 activity is not limited to “simply” coding the next movement direction (Bremner, 2005).

In these examples, although the activity of M1 is observed *before* the movement, it still involved preparation of a real movement. Recently, it has been shown that M1 is also active during motor imagery which is not followed by an action. Indeed, when imagining performing a movement, the blood flow in M1 increases, even without any muscular activity (Porro et al., 1996; Roth et al., 1996; see Grèzes and Decety, 2000, for a review). Moreover, through TMS, it has been shown that the corticospinal excitability (reflected by the amplitude of the motor evoked potentials recorded for the muscles that would be implicated in overt movement execution), depends on the content of the motor image (Yahagi and Kasai, 1998). The temporal dynamics of the corticospinal excitability during imagery is similar to that found during overt movement execution (Hashimoto and Rothwell, 1999). Another example is the implication of M1 during the observation of another person’s movements (e.g., Fadiga et al., 1995; 2005; Raos et al., 2004). A Bereitschafts potential has even been found while observing predictable movements (Kilner et al., 2004). Also, a movement illusion, evoked by muscular vibration (without any associated movement), evokes an activity in M1 (Casini et al., 2006). Moreover, the increase of the BOLD level in M1 during the illusion is correlated with the force of the illusion (Romaiguère et al., 2003). Longcamp and colleagues (2006) found M1 to be implicated in passive reading of hand written texts. Very interestingly, Hauk and colleagues (2004) published a study concerning the passive reading of words that represented actions of the tongue, the arm or the leg (for example “lick”, “pick”, “kick”). Although no muscular activity could be found, the BOLD level in M1 was increased following the somatotopic organization of this area. In other words, they found an activity in the arm area of M1 for words concerning actions of the arm, in the tongue area for tongue words, etc. All of these examples clearly show that M1 is active in circumstances where, although there is some sort of “motricity”, it is not necessary to have an actual motor output: The simple reading of verbs representing an action can evoke an activity in that area that is classically accepted as the area of motor production.

2.4.2 Influence of the context on M1 activity

Several results in the literature show that, for a given motor output, the activity of M1 can strongly depend on the context. One example is the result of our fMRI study on the awareness of muscular force (De Graaf et al., 2004). In a reference condition, subjects made rhythmical hand movements and they were informed that, in a subsequent condition in which the resistance to the movement would be increased, they had to either reproduce their initial muscular forces or reproduce the movement kinematics (Fig. 1B). To vary the external force, the subject had a manipulandum attached to the right forearm and hand over the wrist joint (Fig. 1A). This manipulandum was an fMRI-compatible mechanically jointed arm, only allowing flexion and extension movements at the wrist. A laterally attached lever allowed the internal friction of the manipulandum to be varied. The lever had two possible positions: High and low internal friction. During the experiment, the subjects easily changed the lever position themselves in response to an instruction given on a screen. A potentiometer was fixed on the rotation axis of the manipulandum to record the subjects’ wrist movements.

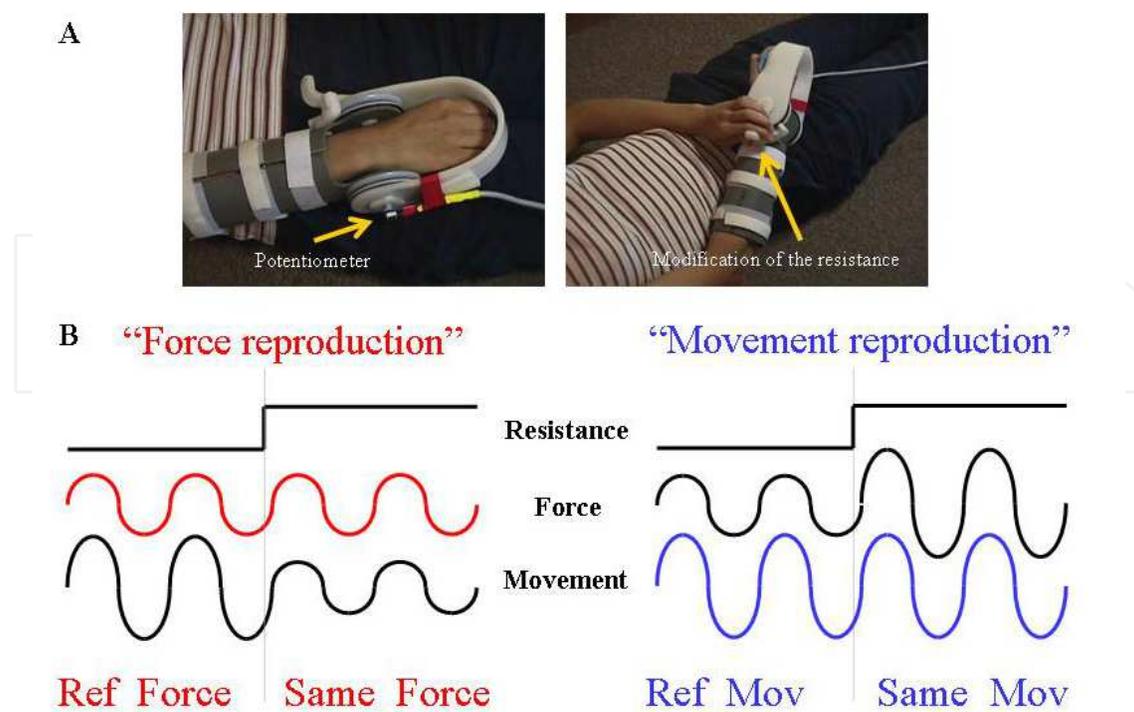


Fig. 1. Manipulandum used to measure the rhythmical wrist extension/flexion, as well as to vary the resistance to the movement (A). Schematic representation of the protocol (B). Note that during the reference conditions (Ref_Force and Ref_Mov), the actual motor output was the same.

The contrast in M1 activity between the condition during which the subjects had to pay attention to their muscular forces (Ref_Force) and the condition during which they had to pay attention to their kinematics (Ref_Mov) (conditions in which the actual motor output was equivalent!) suggests that obtaining awareness of muscular forces exerted during movement execution makes much higher demands on many brain structures, in particular the primary sensorimotor areas (Fig. 2). Interestingly, for the contrast between Same_Force and Same_Mov, conditions for which the actual muscle forces were very different, we did not find any difference in BOLD level. This clearly suggests, on the one hand, that for a similar motor output the BOLD level of M1 can vary with the specific attention the subject gives to the task, and, on the other hand, that different levels of force production do not necessarily imply different levels of BOLD activity in the primary sensorimotor areas. In a subsequent study (Bonnard et al., 2007), we showed an increase in BOLD level as well as corticospinal excitability of M1 when subjects were required to produce forces with higher precision, although the actual force level was the same. So, as a function of the attention the subject gives to certain aspects of the task, the global level of activity of M1 can vary for the same motor output.

At a unitary neuronal level, Hepp-Reymond and colleagues (1999) gave a very powerful demonstration of the dependence of the coding of the force production on the context. Several monkeys were trained to finely control their force production with a precision grip in a visuomotor force pursuit task: The monkeys had to follow a rectangle presented on a screen with a cursor by exerting pressure on a force transducer held between their thumb and index. They were presented with either two or three different force levels in a trial.

Importantly, the monkeys knew in advance which trial type was going to be presented by means of a colour coding of the rectangle. The discharge frequency of M1 neurones for a given force level appeared to vary with the *total* force the monkeys had to produce during the trial, i.e., the discharge frequency was lower for the second force level when the monkeys also had to produce the third force level during the trial than when the second force level was the maximum force level of the trial. This clearly shows that the coding of force in M1 neuronal population depends on the context of the task, in this case the total force range. Moreover, this adaptation to context is achieved in real time (here, trial per trial), suggesting an important flexibility at the level of functioning of the neuronal network within M1.

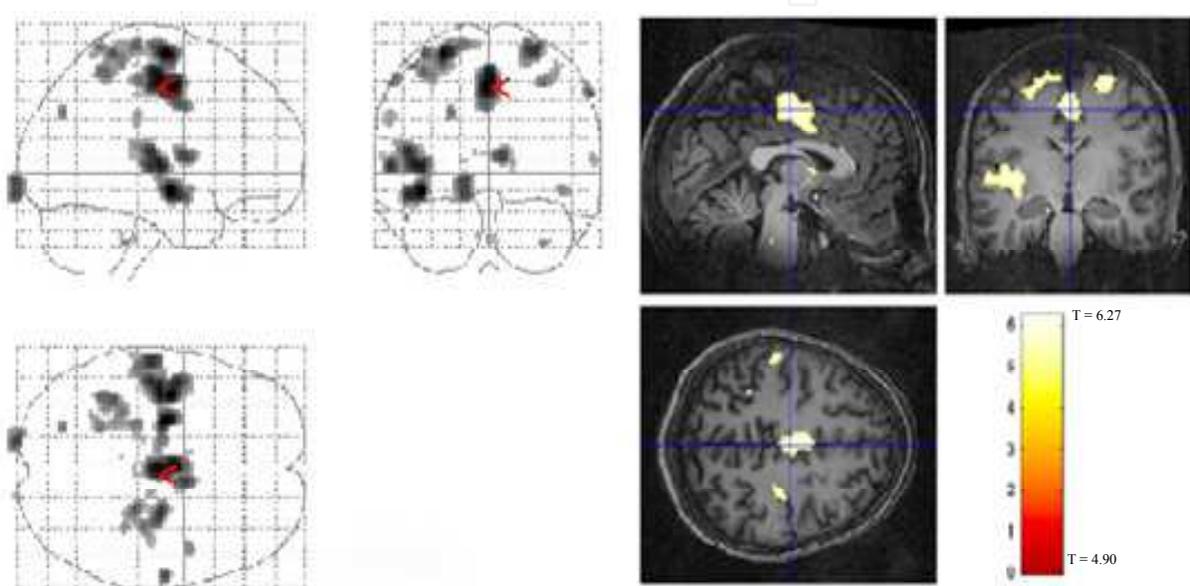


Fig. 2. Result of the t-contrast Ref_Force- Ref_Mov. Height threshold of significance: corrected $P < 0.01$ ($T = 4.90$). Voxel extent threshold: 20 voxels. The voxels, all seen in the glass brain representation, are superimposed on the spm single subject canonical brain on the anatomical slices passing through Talairach coordinates $[-2 -13 47]$.

All of the above-mentioned results concerning the neuronal activity of M1 clearly show that M1 is not a simple transmission relay between the non-primary motor areas (that anticipate, prepare) and the spinal cord, but rather a real crossroad playing an important role in cognitive motor integration. Indeed, M1 is implicated in tasks without any motor output. Moreover, the functioning of M1 depends on the cognitive context in which a motor output will be or is produced: Its functioning is modulated in real time.

3. Secondary cortical areas

It is important to remember that M1 is not the only origin of the corticospinal tract. In monkeys, the topographical distribution of these projections has been studied by isolating the corticospinal neurons projecting on the spinal cord between the cervical and thoracic level (C5-T1), using an injection of a retrograde marker in the region of the motoneurons in the spinal cord (Dum and Strick, 1991; Maier et al., 2002). It has been shown that half of the

fibers of the pyramidal tract find their origin in M1, the other half comes from non primary motor areas, i.e., SMA proper (12-19%), premotor area (21%), and cingular motor area (17-21%). Also, a large number of unitary recording studies in cortical neurons in awake monkeys have shown that neurons presenting particular parametric relations with different phases of movement execution can be found in all structures of the cortical motor network, i.e., in M1, premotor cortex and the supplementary motor cortex (for reviews see Porter and Lemon, 1993; Requin et al., 1991; Georgopoulos, 2000). This strongly suggests that these non primary cortical regions can also send motor commands directly to motoneurons. We have already seen that M1 is not uniquely a “motor execution area”, and now we can add that premotor areas, classically regarded as “preparation centres”, can also have executive functions.

In a similar way, direct projections from the thalamus to non-primary visual areas have been found. For example, there exists a direct projection from the lateral geniculate nucleus onto MT (V5) without passing by V1. These projections represent about 10% of those coming from V1 (Sincich et al., 2004). Also, direct thalamo-cortical projections on secondary auditory areas (Barth et al., 1995; Di and Barth, 1992) and on secondary somatosensory areas (Hiraga et al., 2005; Stevens et al., 1993) have been identified.

Since the topic of this chapter is the primary cortical areas, we will not elaborate on the possible function of these direct projections onto and from secondary cortical areas. However, it was important to mention this since the existence of these direct projections confirms that the segmental and hierarchic vision of brain functioning is no longer defensible. Indeed, the primary cortical areas are an integral part of a cortical network underlying cognitive integration, and, whatsmore, the secondary motor areas have executive functions.

4. A clinical implication

An important implication of this conception of cerebral functioning is that the whole cortex should be considered when studying, for instance, the consequences of cortical plasticity following central or peripheral lesions. In this last section of the chapter, we will use as example the amputation of the hand and/or forearm.

As already mentioned in section 2.2, after amputation of the hand or forearm, the territories of the representation of the lost body part in S1 seem rapidly occupied by afferent information from adjacent body parts (e.g., Florence & Kaas, 1995; Gagné et al., 2011; Vandermeeren et al., 2003). The same reorganization is known to hold for M1, i.e., neurons originally sending motor commands to hand muscles pre-amputation send them to stump muscles post-amputation. Indeed, TMS on this reorganized part of M1 evoked MEPs in the stump muscles (Mercier et al., 2006).

This reorganization, however, is very complex and appears to be incomplete. Indeed, after amputation, patients very often report a vivid perception of presence of their lost limb. This “phantom limb” can be the object of mechanical, thermal and even painful sensations (Kooijman et al., 2000). Even more surprisingly is that the phantom limb can often be “moved” at will (Kooijman et al., 2000; Reilly et al., 2006). Although these voluntary phantom movements are slow and more effortful than movements of the intact limb, the patients feel these movements to be “executed” corresponding to their will (e.g., Reilly et al., 2006), and they are able to imitate with their intact arm the movements they execute with

their phantom limb. Some results in the literature suggest that the sending of motor commands is necessary in order to “perform” voluntary phantom limb movements. These motor commands, as they cannot arrive on the muscles of the lost limb, arrive on the muscles of the stump instead. Indeed, during voluntary phantom limb movements, the EMG pattern found on the stump muscles correspond to neither the EMG patterns for real movements of the stump, nor to the EMG patterns found on the corresponding muscles of the intact arm during imitation of the phantom limb movements (Reilly et al., 2006; Gagné et al., 2009). This strongly suggests that specific motor commands are sent from M1 when “executing” a specific phantom limb movement. Moreover, when the hand area of M1 in an amputated patient is stimulated with TMS, a phantom limb movement is evoked (Mercier et al., 2006). So, there exists a reorganization of the primary somatosensory and motor areas, leading to new relations between body parts and neuronal populations, where motor commands to the missing limb can still be sent.

There seems to exist a relation between the degree of cortical reorganization and the degree of phantom limb pain. Lotze and colleagues (2001), in a fMRI study, reported that patients without phantom limb pain showed significantly less reorganization of the primary sensorimotor areas than patients with phantom limb pain. This raises the question whether cortical reorganization should be avoided, and, if so, how.

Currently, it is not known what exactly underlies the appearance of phantom limb sensations such as movements or pain, but it seems likely that it is, at least partly, related to the complex cortical reorganization following amputation. The search for answers to questions such as “What causes phantom limb pain and how can we avoid it?”, “Why are phantom limb movements slow and effortful?”, and “Can we use phantom limb movements to increase control of prostheses?”, must take into account that the primary cortical areas are an integral part of a cortical network underlying cognitive (motor) functioning, and the secondary motor areas can have an executive function. With respect to this latter point, a possible reorganization of the secondary motor areas following amputation has not yet been investigated.

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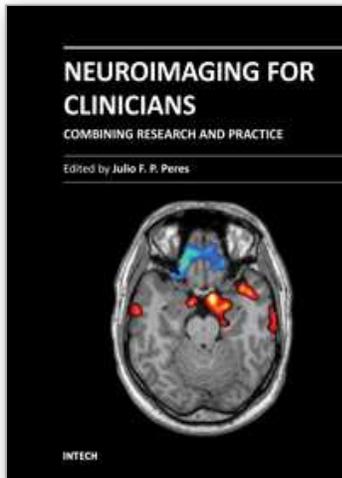
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