

The specific function of scientific explanation is ...to turn the unexpected, as far as possible, into the expected.

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1.1 Brain Economics

Any everyday activity is composed of a succession of different tasks. For instance, for many of us the typing of a sentence in an electronic document requires pressing keys on a keyboard and checking the screen to see whether the pressed keys correspond with the sentence that must be typed. No matter how simple, any task requires that sensory input received from the outside be elaborated (i.e., understood, compared, etc.) before executing an action (or response). When composing a sentence, the words retrieved from the writer's memory form the input for the task, and the representation of the words must be held in working memory before the letters composing the words are matched with the letters keys on the keyboard. When the position on the keyboard of the key corresponding to the input letter has been found, the finger which will execute the response must be selected. When the response finger has been selected the action to push the key will be initiated, and, finally the correspondence between the input text and the typed one must be visually checked.

Information processing is generally assumed to require processing resources, which may be defined in terms of general-purpose processing units (Hockey, 1997), or a commodity of limited availability which enables or energizes performance on a task, such as the various form of memory capacity, or communication channels (Norman & Bobrow, 1975). Availability of processing resources affects the speed and accuracy with which a task can be executed. Support for the existence of processing resources comes from demonstrations of poor performance when resources normally available for a task are pulled away by another task. For example, driving a car and simultaneously conversing with the passenger is possible under normal traffic conditions.

However, performance on one or both tasks may degrade depending on the demands of the concurrent task, resulting in a disrupted conversation when driving in a busy city center or in poor driving performance when the conversation gets more intriguing (see, e.g., Wickens, 1984).

Driving while conversing is an example of multitasking behavior. Multitasking is commonly used to study the allocation of processing resources, or how attention is divided between two or more tasks (Kahneman, 1973). One of the assumptions supporting the energetic concept of resources is that if the resources demands do not exceed the available supply, several tasks can be performed simultaneously (Kinsbourne & Hicks, 1978). The ability to execute several tasks simultaneously does not depend solely on the availability of processing resources, but also on the allocation policy with which the available supply is distributed across the tasks. The ability to allocate resources at appropriate times is defined as efficient timesharing (Salthouse & Miles, 2002), and it implies that the processing resources needed to execute one of the tasks are allocated to the specific task at the appropriate time, thereby effectively preventing the different tasks from drawing from the same resource pool concurrently (Salthouse & Miles, 2002). Timesharing can be inefficient when the resources necessary to perform both tasks are drawn from the same resource pool simultaneously and the available limit is reached, thereby impeding or delaying task execution (Wickens, 1984).

Another type of dual-task interference is structural interference (see, e.g., Broadbent, 1958). Interference is structural when the same process (e.g., response selection) is recruited simultaneously by two different tasks. This type of interference has been studied extensively with the psychological refractory period (PRP, e.g., Smith, 1967) paradigm in which two tasks, each requiring a speeded response, are to be executed (for reviews see Pashler, 1994; Jolicoeur, 1999). The temporal separation between the stimuli for the two tasks is systematically varied between long (e.g., 1500 ms) and short (e.g., 150 ms). The typical outcome is an increment in the response time to the second stimulus when it follows the first within a short interval. The delay in the reaction time has been interpreted as the result of a structural bottleneck (Broadbent, 1956) which lies at the stage of response selection. A bottleneck is a stage in the sequence of information processing which obstructs the flow of information processing for one task when it is already being used by another task.

The PRP effect is robust, and is still present when tasks requiring different stimulus or response modalities are combined (e.g., Creamer, 1963; Borger, 1963; Pashler

1994; Jolicoeur 1999; but see Greenwald 1972, 2003). Moreover, the effect does not disappear upon extended practice (Dutta & Proctor, 1992; Proctor & Dutta, 1993).

An alternative account for the PRP effect attributes it to executive control (Meyer & Kieras, 1997). Meyer and Kieras suggested that the fixed sequential order in the execution of the two tasks imposed by the task instructions explains the PRP effect more effectively than the response-selection bottleneck theory. The account proposed by Meyer and Kieras, named executive-process interactive control (EPIC), diverges from the response-selection bottleneck approach by arguing that the PRP effect reflects a strategic bottleneck adopted by participants to defer the execution of the second task until the first has been accomplished, rather than a fundamental structural bottleneck.

That multiple-task performance can be constrained by sharable energetic resources (or general capacity, see e.g., Kahneman, 1973), in addition to non-sharable structural bottleneck stages or processes, is supported by a large number of studies showing that the cognitive load associated with a secondary task can have a graded effect on the performance on the primary task. In a classic study, Allport, Antonis, and Reynolds (1972) reasoned that it is not necessary that two different tasks share the same structure or function to interfere with each other, but the scarce availability of general processing resource should be sufficient to induce performance costs. Allport et al. tested this assumption, showing first that the simultaneous execution of two task decreased performance levels, and, second, that dual-task performance was even more impaired if the two tasks shared a common structure than if they did not. Allport et al. asked their participants to divide their attention between a shadowing task and a task of remembering words. The shadowing task consisted of repeating spoken messages as they were presented, and it was performed only to pose a general load on cognitive processing, which should have a 'general' detrimental effect on performance. The memory task consisted of reporting if a word presented visually or auditorily (the presentation was dichotic) belonged to a set of already presented words. Allport and colleagues predicted that the shadowing task would interfere less with the visual memory task than with the auditory memory task because the simultaneous presentation of two auditory stimuli added a structural interference in the processing of sensorial input to the already present capacity load posed by the concurrent shadowing task.

Memory performance was better in the absence of the shadowing task, suggesting that the shadowing task per se drew resources away from the memory task, independently of the modality of the stimulus presentation. When the shadowing had to be performed simultaneously with the memory task, performance was poorer for words

presented auditorily than visually. This suggests structural interference at the level of the phonological loop. In fact, when the words to be compared were presented in the visual modality, Allport et al.'s (1972) participants executed the comparison using visual characteristics of the words displayed (e.g., the number of letters, the presence of repeated letters, or small marks on the slides used to display the words) and ignoring the verbal characteristics (e.g., semantic or phonological properties), therefore bypassing the phonological loop. In conclusion, these results sustained the claim that resources had a general 'energetic' connotation because performance costs were present when the tasks had to be performed simultaneously, and it showed that these performance drops were not exclusively related to structural interference because performance was worsened when the tasks combination also shared a structure.

The study of Allport et al. (1972) was one of the first to indicate that multitasking interference can result from more complex interactions involving specific structures, processes, or resources (Navon & Gopher, 1979). In his *multiple resources theory*, Wickens (1984) proposed that processing resources are represented by three dichotomous dimensions: processing stages (perceptual-cognitive and response processes), processing codes (verbal and spatial), and input-output modalities (visual/auditory and manual/vocal, respectively). While this proposal was not meant to provide a complete picture of resource-dependent processing in the brain, it has served to provide a reasonable coherent and simple explanation, and indeed prediction, of patterns of interference, or lack thereof, between many different task combinations (Sanders, 1997). Despite such successes, the resource framework has been criticized and several additions, next to structural bottlenecks, or alternative theoretical accounts have been proposed. Navon (1984) argued that the graded trade-offs in multiple-task performance might be due to demand characteristics rather than real limits to available resources. Others have pointed to the critical role of strategic resource allocation that must be managed by another coordinating process (e.g., Baddeley's, 1986, executive control or Gopher's, 1992, attentional control) that might be tightly associated with the executive processes subserved by prefrontal cortex (Duncan & Owen, 2000).

Within the framework of cross-talk models, dual-task interference is explained in terms of different forms of outcome conflict, in which one task may produce outputs, throughputs, or side effects that are harmful to the processing of the other task (Navon & Miller, 1987, 2002). An appealing feature, for present purposes, of the latter two proposals is that they lend themselves more easily than the more abstract resource concept to an interpretation of dual-task performance interference in terms of neuronal

crosstalk or interference or in terms of dynamic competition for neuronal workspace.

1.1.1 Individual differences and resources

The concept of resources, considering its multiple aspects and various links with higher level functions, is considered by some to be analogous to Spearman's g-factor (see, e.g., Sanders, 1997). The study of processing resources through the observation of individual differences in task performance can thus be considered a way to study resource management. Task performance depends on the resources available to an individual but also on how these resources are allocated to the different operations necessary to fulfill the task. For example, it has been hypothesized that individuals with higher IQ are capable of more efficient timesharing than individuals of lower IQ, because they employ a more efficient overall task structure (see e.g., Damos & Wickens, 1980; Kramer, Larish, & Strayer, 1995; Kramer, Larish, Weber, & Bardell, 1999).

Another source of individual differences which affects task performance is the level of familiarity with the task at hand. With sufficient practice, the operations necessary to execute the task will be performed more quickly and accurately, reducing interference and temporal overlap with other tasks. As a consequence of this automation processes, the execution of these operations becomes less subject to voluntary control, which can be interpreted as if fewer resources are required to execute the tasks (Schneider & Shiffrin, 1977).

Spelke, Hirst, and Neisser (1976) reported an example in which task automation following extensive practice (i.e., 17 weeks) on a task can be interpreted in terms of a reduction in the resources required to perform the task. Spelke et al. showed a reduction of interference in the task of automatic writing (for a review see Koutstaal, 1992) in which participants read short stories while writing down spoken words. Participants' performance at the beginning of the experiment was very poor, however after practicing automatic writing for an hour a day for seventeen weeks, participants were able to execute the task approximately as quickly as when performing only one of the two tasks. Broadbent (1982, see also Welford, 1980) proposed that, rather than automaticity of task execution, the results of Spelke et al. (1976) could be better accounted for by switching of attention between the two tasks. Nonetheless switching from one task to another is time consuming, it could facilitate dual task execution if participants developed a strategy of efficient response-buffering by which the response to one of the tasks is hold until it cannot be executed without compromising

the performance on the other task, in other words this approach could be thought of as sophisticated timesharing. Rather than attempting to disentangle if the best account for performance improvements as a consequence of task practice results from efficient timesharing (e.g., Broadbent, 1982) or economization of resources (e.g., Spelke et al., 1976) it is important to note that task performance improves as a function of practice, and it is therefore connected with resource management or resources per se.

Practice effects are even stronger when familiarity with a task has been acquired outside the experimental laboratory. For example a highly skilled typist can perform several tasks simultaneously (e.g., shadowing or reciting nursery rhymes) while typing words, whereas the performance in the same tasks of less skilled typists is likely to be more error prone, if possible at all (Shaffer, 1975). Individuals who are more familiar with a certain task or who have practiced for longer periods are likely to perform better than persons who encounter the problem for the first time. For example, experienced taxi drivers have a very detailed mental map of the city they drive in; thus it is likely they will be more capable than a naive person, such as a tourist, of finding alternatives routes when traffic is heavy (e.g., Grabner, Stern, & Neubauer, 2003; Woollett, Glensman, & Maguire, 2008). Yet, the acquisition of a specific ability is not a 'direct' source of individual differences as, for example, IQ would be, because extensive practice on a task is independent from the amount of resources that a person has available to resolve it.

If learned skills are not directly linked to the concept of resources, there is a temporal aspect to the ability of learning a new task or transferring acquired knowledge to new situations which can be related to efficient resources management and individual differences. In fact, if one person is faster than another in learning a skill or in transferring consolidated knowledge to a new skill, it can be assumed that one has more resources available or is more flexible in allocating resources. Evidence showing individual differences in transferring knowledge to a new situation was provided in a study by Grabner et al. (2003), who showed that for individuals who are equally familiar with a certain task (e.g., driving a taxi), individuals with lower cognitive abilities are less able to transfer acquired skill into a new task than are individuals with higher cognitive abilities. Grabner et al. studied the abilities of relatively high IQ and low IQ experienced taxi drivers with respect to learning new maps. After a period of familiarization with the map the two groups of taxi drivers were questioned about routes in the familiar environment (their city) and in the novel one (routes in an artificial map). The two groups of experienced taxi drivers did not differ on the familiar

task, but did differ in the novel task of memorizing routes in the artificial map (for evidence of individual differences in transferring time-sharing skill, see Ackerman, Scheider, & Wickens, 1984; Somberg & Salthouse, 1982).

1.1.2 Will the last be first?

One of the reasons that resource demands are studied is to determine possible sources of interference between tasks or task components so that training techniques can be developed to resolve or avoid the interference and therefore improve task performance (Polson & Friedman, 1988). Mathews, Hunt, and MacLeod (1980) presented evidence suggesting that appropriate instructions on the execution of the sentence verification task (Clark & Chase, 1972) can abate IQ differences. Mathews et al. (1980) tested the persistence of IQ-related differences when the strategies to solve the task were controlled for. The authors, in two separate sessions, explicitly instructed participants on the use of the two different strategies, the imagery one which was found in a study by (MacLeod, Hunt, & Mathews, 1978) to be used by high IQ individuals and consisted in visualizing an image of the sentence before proceeding to the comparison, and the linguistic one which was used by the group with low IQ and consisted in reiterating the sentence when the figure was displayed. The results showed no differences in accuracy between the two groups nor between the two strategies, which sustain the claim that individual differences in performance can be reduced, or even eliminated, with appropriate training.

Another example of how appropriate training may benefit human performance is a study by Kramer et al. (1995) in which it was tested whether training elderly persons to divide their attention more effectively could help them overcome the age-related deficit in rapidly re-deploying attention across different tasks. Elderly persons are not as efficient in dividing their attention as younger individuals, therefore it may be advantageous to devise a training method which could help elderly persons to divide their attention between tasks in a more effective way. Kramer et al. provided on-line feedback about performance on a monitoring task performed simultaneously with an alphabet arithmetic task to help their participants to re-distribute their attention better across the two tasks. In the monitoring task six different gauges had to be monitored and participants had to push a button when one of the gauges reached the digit 9 or a higher number. The state of the gauges could be checked by pushing a button and would remain displayed on an indicator for 1.5 s. Simultaneously participants had to perform “alphabet arithmetic” in which equations such as “H - 3 = E” must

be verified (where letters correspond to their ordinal position in the alphabet, e.g., A = 1, B = 2, ..., Z = 26). Two groups of elderly individuals participated in the study, one group received feedback to divide their attention equally between the two tasks, whereas the other was trained to divide their attention with a variable-priority strategy (i.e., participants were to dedicate 20% of their attention to one task and 80% to the other). Training with the variable-priority strategy led to better performance and better transfer of timesharing skill to a new situation.

The previous examples support the idea that differences in human performance may be reduced if accurate management of processing resources or optimization of timesharing are achieved through appropriate training. However, performance improvement does not consist solely of reducing differences between persons of different abilities, but can also aim to exploit the abilities or capabilities of information processing of any person, as, for example, by studying a task that is already performed and investigating if it is possible to develop new strategic solutions which are more efficient than the ones currently used.

Research by Seagull and Gopher's (1997) illustrates how individuals can be instructed to integrate different sources of information to better perform the complex task of piloting a helicopter. Seagull and Gopher (1997) studied the effect of instructing helicopter pilots to strategically restructure two tasks to increase task performance thus improving timesharing efficiency. They devised a training program which instructed helicopter pilots to use more effectively their helmet-mounted displays, displays which pilots avoided using because to collect peripheral information through these displays head movements are necessary and head movements may cause a loss of orientation. However, collecting peripheral information improves pilots' abilities to focus on a specific point, which may be useful, for instance, to avoid a collision or to spread the field of view in order to gain a broader perspective of the surroundings. Pilots who followed the training devised by Seagull and Gopher eventually outperformed the performance of the pilots who had not received the specific training.

Formulating schemas or guidelines to configure tasks optimally in terms of workload as well as in terms of interference or integration with other tasks will increase human performance (Polson & Friedman, 1988; Seagull & Gopher, 1997). However Polson and Friedman warned that such improvements will be possible only if the factors which affect human performance are determined. This includes, for example, the rigorous definition of which resources are involved in the execution of a particular task, how resources are recruited across multiple tasks, if a particular environment

may influence which resources are required or recruited, which variables interact in resource management, and how different task components interact in task execution. Also, it should not be forgotten that, as suggested by (Salthouse & Miles, 2002), the different abilities of each participant (e.g., individual differences in resource availability but also in task proficiency) must be taken into account when analyzing resource allocation policies. This type of research could lead to the development of specific training programs to acquire specialized skills as the ones devised by Gopher and collaborators (see e.g., Seagull & Gopher, 1997; Erev & Gopher, 1999; Kramer et al., 1995; Gopher, 1992; Gopher, Weil, & Bareket, 1989), which may help economizing resources in information processing, and perhaps boost the limited potential of lower IQ individuals.

1.1.3 A physical/neural counterpart for resources

Kinsbourne and Hicks (1978) proposed that resources are a generalized commodity reflected by functional cerebral space. Functional cerebral space is any cerebral area used to accomplish a mental operation and it depends on the specifics of localization of functions in the brain. What cerebral areas (or space) is used is determined by the processing requirements of the task at hand. For example, language areas are used when language production is involved (Ojemann, Ojemann, Lettich, & Berger, 1989; Ojemann, Fried, & Lettich, 1989) and areas specific for the elaboration of spatial information when the task requires mental rotation (Cohen et al., 1996). In Kinsbourne and Hicks's view, the functional topographic map (or arrangement) of the cerebral cortex can be used as a basis to explain dual task interference. The topographical organization of the cerebral cortex (Penfield & Rasmussen, 1950) refers to the spatial correspondence between the origin of the sensorial stimulation and the cerebral areas receiving it (e.g. in the cerebral cortex the sensory information from the hand is represented next to sensory information coming from the arm, i.e., somatotopically). According to this view, the simultaneous execution of two tasks would be hampered if the tasks involve partially overlapping or topographically nearby cerebral circuits (note that this view bears a distinct resemblance to crosstalk models of dual-task interference, Navon & Miller, 1987, 2002).

Polson and Friedman (1988) revisited multiple resource theory (Wickens, 1984) and the theory of functional cerebral space (Kinsbourne & Hicks, 1978) with their hypothesis that there are two primary resources pools, represented by the two cerebral hemispheres. This hypothesis was substantiated by results from studies on cere-

bral specialization that showed that the simultaneous execution of two tasks requiring complementary hemispheres interfered less than two tasks that involved the same hemisphere.

Other proposals for possible neural correlates of mental resources are found in studies investigating neural differences in information processing. These studies have focused on correlates of brain activity which could help interpreting individual differences in tests measuring cognitive abilities (e.g., IQ tests). Brain activity has been operationalized as cerebral glucose metabolism (or consumption of energy) as measured through positron emission tomography (PET, see e.g., Haier et al., 1992), level of brain activation as revealed by functional magnetic resonance imaging (fMRI, see e.g., Jaeggi et al., 2007), or amplitude of specific brain rhythms as quantified using electroencephalography (EEG, see e.g., Neubauer, Freudenthaler, & Pfurtscheller, 1995). The assumption behind these studies is that brain use requires brain activation, and that lower activation reflects more efficient brain use, a concept that is referred to as neural efficiency (Vernon, 1993).

The neural efficiency theory was proposed by Vernon (1993) based on a large body of literature which consistently showed that individuals with high cognitive abilities used their brain more efficiently as reflected by, for example, lower brain activations, when performing a task at a comparable level than individuals with low cognitive abilities. Vernon substantiated this idea with evidence showing more restricted patterns of brain activity in high than in low cognitive abilities individuals (measured by PET (see e.g., Haier & Bembow, 1995), EEG (see e.g., Neubauer et al., 1995), or fMRI (see e.g., Gray et al., 2005)) and that transmission of information was faster in individuals with high than low cognitive abilities (as revealed by nerve conduction velocity studies, see e.g., Vernon & Mori, 1992). In the context of neural efficiency, the notion of resources can be associated with neuronal activity, and the efficient use of resources is reflected by the reduced neural activity in individuals with higher cognitive abilities as compared to those with lower cognitive abilities.

Although the neural efficiency perspective has been supported by a number of studies, many of these studies reported a difference in brain activity between two groups of individuals without addressing the cause of the difference (see e.g., Jausovec & Jausovec, 2004a, 2005a). It must be noticed that differences in brain activity between individuals with high or low cognitive abilities do not unequivocally substantiate the conclusion that these differences reflect differences in neural efficiency. An alternative interpretation could be a higher level of automaticity of performance of one group

compared to that of the other. Petersen, Mier, Fiez, and Raichle (1998) showed that practice not only significantly reduced the amount of activation in a cerebral area, but also shifted the cerebral areas involved in task execution toward task-dependent areas. It can therefore be hypothesized that practice could account for the reduction in brain activity between individuals of different cognitive abilities if individuals with higher abilities are faster in devising and automating strategies to solve the task (for evidence substantiating this claim see e.g., Gevins & Smith, 2000; Grabner et al., 2003).

Shifts in brain activation as reported by Petersen et al. (1998) could also reflect that participants used a different strategy to solve the task. For example, Reichle, Carpenter, and Just (2000) showed that brain activation patterns of individuals executing a sentence verification task (Clark & Chase, 1972) reflected the strategy employed by the participants. The sentence verification task can be performed with two strategies (see MacLeod et al., 1978), one requiring verbal-linguistic abilities (i.e., predominantly located in the left hemisphere) the other spatial-imagery abilities (i.e., predominantly located in the right hemisphere). Reichle and collaborators instructed their participants to execute the task with one or the other strategy to observe if the patterns of their participants' brain activations were located mostly on the right hemisphere when the imagery strategy was used and in the left hemisphere when the linguistic strategy was used. Their results showed a strategy-dependent hemispheric activation, which supports the claim that the use of different strategies can induce different brain activity. These results also points to the possibility that individual differences in brain activation patterns between individuals of different IQs may reflect the adoption of different strategies to solve the same task.

Duncan et al. (2000) proposed a somewhat different perspective on the relation between brain activity and cognitive abilities. Using PET, they showed that prefrontal recruitment was an increasing function of the amount of g required by the task, and was not specifically related to the precise nature of the task. This evidence is consistent with the notion that prefrontal cortex implements a general capacity for top-down or executive control, and may account for the fact that substantial dual-task costs are generally observed for combinations of relatively difficult tasks that both require executive control.

Evidence for lower-level neural correlates of mental resources can be found in a study by Diamond, Scheibel, Murphy, and Harvey (1985) which showed that neurons and glial cells in the cerebral cortex of an outstanding scientist (i.e., Albert Einstein) had a smaller ratio in comparison with control individuals. Neurons and glial cells are

the two main types of cells which constitute the nervous system (for an introduction see Bear, Connors, & Paradiso, 2008). Neurons are the functional unit of the nervous system which through electrochemical impulses receive and transmit information to other cells. Glial cells sustain the neurons and constitute the sheath (i.e. myelin) which increases the speed and power of pulse propagation within a neuron (Bullock, Moore, & Fields, 1984). Einstein's neurons were supported by a higher number of glial cells than those of the control individuals. This could account for the outstanding cognitive ability of Einstein because a higher number of glial cells per neuron may reflect more sophisticated or efficient neural circuits (Colombo, Reisin, Miguel-Hidalgo, & Rajkowska, 2006; Fields, 2008a, 2008b; Kreutzberg, Klatzo, & Kleihues, 1992).

The ratio of neuron:glial cells may represent a plausible low-level neural correlate of mental capacity or efficiency. Myelination, the process by which myelin improves the connections between neurons, is a dynamic process by which white matter structure is modified by impulse activity or, in other words, use of a brain area modifies its connectivity similarly to the effect of physical exercise on muscles. Acquisition of skill modifies the structure of white matter, as has been shown for professional musicians (e.g., Bengtsson et al., 2005), working memory tasks (e.g., Nestor et al., 2007), cognitive development (e.g., Liston et al., 2006), reading skills (e.g., Gold, Powell, Xuan, Jiang, & Hardy, 2007), and IQ (e.g., E. M. Miller, 1994). For example, a recent study by Schmithorst, Wilke, Dardzinski, and Holland (2005) using diffusion tensor imaging (DTI; a relatively new MRI technique which reproduces the brain's neural tracts and connections, see Filler et al., 1991), showed higher brain connectivity, as reflected by the volumes of regional white matter, in children of higher as compared to lower cognitive abilities (see also, Posthuma et al., 2002, for similar evidence in an fMRI study with adult individuals).

1.2 A brief overview of EEG-based reflections of mental resources

EEG is a method for the visualization of temporal changes in brain activity, in optimal recording conditions temporal resolutions of 1 ms can be reached, which permits to observe the online processing of information (Luck, 2005b). On the other hand EEG spatial resolution is poor because the signal measured by an electrode reflects the summed contribution of many different electrical sources; as a consequence it is difficult to define univocally the internal generator for a given EEG pattern, therefore impeding the identification of the neurocognitive process eliciting it (Regan, 1989).

The EEG is composed of three types of cerebral activities which depends on the occurrence or absence of an experimental condition or event (Tallon-Baudry & Bertrand, 1999; Herrmann, Grigutsch, & Bush, 2005). Spontaneous background activity is by definition uncorrelated with the experimental condition. Induced activity is correlated with the experimental condition, but it is not precisely phase-locked to the onset of the condition or an event, in contrast to evoked activity that is by definition phase-locked. Evoked activity is generally quantified by means of event-related potentials (ERPs). Each type of activity has been linked to mental resources in the literature, and these linkages will be selectively reviewed for each type of activity.

1.2.1 Event-related potentials

As several recent reviews of the relationships between specific ERP components and mental resources are already available (e.g., Kok, 1997), the present discussion will be limited to those components that are directly relevant to the research reported in this thesis.

N2pc. If a participant is instructed to search for a target item (e.g., a red bar) among several distractor items (e.g., green bars) a negative-going deflection 200-300 ms post-stimulus that is located primarily at posterior scalp sites contralateral to the horizontal position of the target item can be observed (i.e., N2pc, N2-posterior-contralateral, Luck & Hillyard, 1994a). Luck and Hillyard (1994a) showed that the N2pc reflects the focusing of attention onto a potential target item, in the attempt to select the relevant item, whereas Eimer (1996) suggested that the N2pc may reflect the suppression of the irrelevant items. The N2pc is also elicited by non-targets that resemble targets, but not by nontargets that differ from the relevant target in a perceptually salient manner (Luck & Hillyard, 1994a). It is generally accepted that the N2pc reflects attentional capture by a target event (see e.g., Kiss, Velzen, & Eimer, 2008; Lien, Ruthruff, Goodin, & Remington, 2008). Whether the N2pc may also, or perhaps primarily, reflect a spatial shift of attention to the position of the target is more controversial (Woodman & Luck, 1999, 2003; Kiss, Velzen, & Eimer, 2008). More specific evidence linking N2pc to resource-limited information processing comes from several studies that have found the N2pc to be largely absent when the second target in an attentional-blink paradigm remained undetected (Dell'Acqua, Sessa, Jolicoeur, & Robitaille, 2006; Jolicoeur, Sessa, Dell'Acqua, & Robitaille, 2006a; Robitaille, Jolicoeur, Dell'Acqua, & Sessa, 2007).

P3. The P3 (or P300) component is a positive-going deflection that is located primarily at parieto-central scalp sites and is elicited by relevant target events (Donchin, 1981). Its amplitude is highly dependent on the probability and general informativeness of the eliciting event, suggesting that it may reflect the amount of information provided by and extracted from the event (R. Johnson, 1986). A substantial body of evidence from both single-task and dual-task studies is consistent with the related notion that P3 amplitude reflects primarily limited perceptual-central resources that are mobilised by target categorization (for review, see Kok, 1997).

1.2.2 Frequency-domain EEG components and mental resources

Human EEG activity is composed of rhythmical activity which is associated with general mental states. The most dominant oscillation, which was also the first one to be discovered (Berger, 1929), is characterized by a periodicity of approximately 10 Hz and is called alpha-band activity. The term alpha refers to the fact that it was the first rhythm to be discovered; Berger (1929) used the first letter of the Greek alphabet for the first rhythm he discovered and the second (beta, 12-30 Hz) for the second. Subsequently gamma was used for the rhythm in the 30-80 Hz, delta was attributed to the oscillations below 4 Hz, and theta for the rhythm in the 4-8 Hz.

A very general way to link specific EEG frequency bands with specific cognitive demands is based on the observation of intervals of synchronization (enhanced presence) and desynchronization (diminished presence) of a certain rhythm. Synchronization indexes a state of cortical rhythmicity, whereas desynchronization refers to the interruption of rhythmicity. For example, (Nunez, Wingeier, & Silberstein, 2001) showed that alpha desynchronization correlated with mental effort, such that the alpha rhythm (8-12 Hz) decreased with increased mental effort – in contrast the theta rhythm (4-8 Hz) increased with increased mental effort. Thus, alpha-band and theta-band activity may show an opposite, but not necessarily unrelated, dependency on momentary mental effort.

The alpha rhythm. The EEG oscillations measured from a participants sitting quietly in a dimly illuminated room roughly resemble a 10 Hz sinusoidal activity. This rhythmicity increases in amplitude approximately one or two seconds after that the participant is asked to close his eyes and it will be temporarily suppressed immediately after he opens his eyes again. This 10 Hz rhythm with highest amplitude in the posterior part of the brain is known as alpha rhythm (Berger, 1929). The alpha rhythm

has been associated with an idling state of the nervous system (Adrian & Matthews, 1934) because decrease of alpha rhythm is generally observed when a participant gets involved in any kind of task (for a review see Pfurtscheller, Stancak, & Neuper, 1996). Only recently N. R. Cooper, Croft, Dominey, Burgess, and Gruzelier (2003) reinterpreted the functional significance of the alpha rhythm not as an idling state but as an inhibitory process of task-irrelevant cerebral areas. The claim of Cooper and collaborators was based on previous evidence showing that the alpha rhythm increases when performing an imagery task (Ray & Cole, 1985) or when it is necessary to suppress processes which may conflict with the execution of the task at hand (Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999).

Many studies have provided evidence consistent with the view that a reduction in the amplitude of the alpha rhythm reflects increase mental effort (e.g., A. P. Anokhin, Lutzenberger, & Birbaumer, 1999; A. Anokhin et al., 1992; Hanslmayr, Sauseng, Doppelmayr, Schabus, & Klimesch, 2005; Jausovec & Jausovec, 2004a, 2005b; Jausovec, Jausovec, & Gerlic, 2001; Jausovec & Jausovec, 2000; Klimesch, 1997; Neubauer et al., 1995; Nunez et al., 2001). Some studies, however, have found alpha amplitude to be increased with focusing of attention (Kelly, Lalor, Reilly, & Foxe, 2006), inhibition of irrelevant information (Toffanin, Johnson, Jong, & Martens, 2007), and top-down control (Klimesch, Sauseng, & Hanslmayr, 2007). The hypothesis that increments in alpha rhythm reflect inhibition of irrelevant task areas has been further exploited in two studies where increments of alpha rhythm were artificially induced using repetitive transcranial magnetic stimulation (rTMS, Klimesch, Sauseng, & Gerloff, 2003) or neurofeedback (Hanslmayr et al., 2005) in order to reduce the input from task-irrelevant areas – such induced increments in alpha rhythm were associated with improved performance in a mental rotation task. Taken together, the evidence may indicate that the relation between mental effort and alpha-band activity is a complex one, with the results depending on the ratio of activation of relevant versus inhibition of irrelevant cortical areas and the site of registration. This strongly suggests that more attention to the cortical distribution of alpha-band activity in relation to the processing requirements of the task is warranted.

The beta rhythm. EEG oscillations within 13-30 Hz are defined beta rhythm, which is distributed primarily in the central brain regions. The beta rhythm has been related to motor action (e.g., movement, the intention to move, or sensorial stimulation, Pfurtscheller & Berghold, 1989; Neuper & Pfurtscheller, 1996), which results in a

desynchronization of the rhythm in motor cortex contralateral to the limb to move and, possibly, synchronization, reflecting motor idling, in ipsilateral motor cortex (Pfurtscheller et al., 1996). Tallon-Baudry, Bertrand, and Fischer (2001) have found the beta rhythm to be also related to memory retrieval.

The gamma rhythm. EEG oscillations within 30-80 Hz are defined gamma rhythm. Engel, Fries, and Singer (2001) have reported that the gamma rhythm is associated with higher cognitive functions such as the perceptual binding (C. M. Gray, König, Engel, & Singer, 1989), the maintenance of working memory (Pesaran, Pezaris, Sahani, Mitra, & Andersen, 2002), and selective attention (Fries, Reynolds, Rorie, & Desimone, 2001). Tallon-Baudry and Bertrand (1999) have linked induced gamma activity to the generation of an object representation from the different features represented in different parts of the brain. Melloni et al. (2007) proposed that long-range synchronization of gamma rhythm is the neural process mediating conscious perception.

An alternative interpretation of the gamma rhythm has been proposed by Chen and Herrmann (2001) after noticing the special interrelation between alpha (8-12 Hz), beta (13-30 Hz), and gamma (30-80 Hz) rhythms, which may suggest that these rhythms are harmonics or subharmonics of one another. Already Haenschel, Baldeweg, Croft, Whittington, and Gruzeliier (2000) suggested that the beta rhythm may be a subharmonic of the faster gamma rhythm. Chen and Herrmann (2001) suggested that both alpha and beta rhythms may represent subharmonics of gamma oscillation after observing the coexistence of beta, gamma, and alpha rhythm after sensorial stimulation. However, it remains unclear how that hypothesis can account for the fact that many studies have found these rhythms to show qualitatively different dependencies on such factors as task, condition and mental effort (see e.g. Jausovec & Jausovec, 2005a).

The delta and theta rhythms. EEG oscillations within 0-4 Hz or 4-8 Hz are defined delta and theta rhythm, respectively. The delta rhythm has usually been related to deep sleep (Steriade, Nunez, & Amzica, 1993). The theta rhythm has been related to cognitive effort (Nunez et al., 2001) and to working memory functions (Jensen & Tesche, 2002), such that an increase in theta synchronization is functionally related to high cognitive effort or to the maintenance of more objects in working memory. (Bastiaansen, Berkum, & Hagoort, 2002b, 2002a) showed a linear and positive relationship between amplitude of theta and working memory load. Jausovec and Jausovec (2004b)

showed a relationship between theta amplitude and cognitive abilities. Their participants performed a figural n-back (Gevins & Smith, 2000) in which a colored (i.e., black, blue, brown, yellow, green, gray, purple, and red) form (i.e., a square or circle) had to be compared to the one that had appeared previously while counting the number of squares displayed. The theta rhythm was synchronized for a longer time (i.e., 1000-2000 ms) in individuals of lower than higher cognitive abilities (100-500 ms), suggesting that lower-ability individuals put more effort into executing the task.

1.2.3 Steady state evoked potentials and frequency tagging

Steady-state evoked potentials (SSEP) are evoked potentials (EP) to rapid repetitive stimulation (Regan, 1989). Regan (1989, p. 35) distinguished EP from SSEP because of the transient nature of the first ones: “The averaged transient EP can be regarded as a true transient response to the extent that the relevant brain mechanisms are in their resting states before each successive stimulus, and return to their resting state before the next stimulus. This requirement implies that the EP to any given trials does not depend on any previous trial.” On the other hand, when SSEP are considered they should not be idealized as a perfect repetition of the same EP waveform in time, but as a series of EP constituted by discrete frequencies with constant amplitude and phase.

After its introduction the SSEP method had been amply used in fundamental physiological research (see e.g., Derrington & Lennie, 1984), with questions ranging from the generators of the synchronous response characteristic of the SSEP response (see e.g., Stephen, Ranken, & Aine, 2006), its dependency on frequency of the eliciting stimulus (see e.g., Herrmann, 2001), to what methodology is best suited to localize the source of the resonance phenomenon (see e.g., Srinivasan, Bibi, & Nunez, 2006). However, such questions never were very interesting for cognitive scientists who were focused on aspects of information processing and attention rather than on the physiological properties of the response of rods and cones to flickering patterns (see e.g., Levitt, Schumer, Sherman, Spear, & Movshon, 2001). For this reason, the SSEP method was for a long time ignored by the cognitive scientist, until the first report of a meaningful functional relationship between SSEP amplitude and allocation of attention by Morgan, Hansen, and Hillyard (1996).

The motivation behind Morgan et al. (1996) study was to devise a technique which could unravel the brain mechanisms involved in visual selective attention and simultaneously overcome the limitations imposed from the recording of EP. One constraint in EP research is that, due to their transient nature, EP are evoked by stimuli which have

an abrupt onset, and which must follow one another with a fairly long interstimulus interval to avoid temporal overlap of successive EPs. Typically, visuo-spatial attention experiments require to selectively attend a stimulus or location. However, abrupt onsets of irrelevant items may cause attentional capture (Yantis & Jonides, 1990), making it difficult to ignore that stimulus.

Morgan et al. (1996) reasoned that a possible way to overcome the effect of attentional capture by an onset stimulus (stimulus transient) was to display stimuli on a background that was flashing constantly. The presentation of repeatedly flashed stimuli was also the main characteristic of the SSEP method devised by Regan (1966a, 1966b), which lead the authors to try to adapt Regan's method to study the brain mechanism underlying selective attention. Morgan et al. devised an experiment in which participants were presented with two streams of alphanumeric characters (the randomized presentation of the letters A through K and the digit 5) each superimposed on a background square that rapidly alternated between white and black (each square had a specific frequency, i.e., 8.6 or 12 Hz). Participants' task was to detect the digit 5 embedded in the stream of letters any time it appeared in the stream to be attended. Participants were informed that the two streams were displayed against a flickering background and were told that the flickering was irrelevant for the execution of the task. The two streams were displayed at the left and right of a fixation mark; the characters followed one another at a rate of six per second.

Morgan et al. (1996) showed that the amplitude of the SSEP was modulated by visuo-spatial attention; it increased when attention was directed toward the location and decreased when attention was drawn away from it. Additionally, the obtained high signal-to-noise ratio of the SSEP, due to its precise definition in frequency domain suggested two other advantages of the SSEP over the EP method. The first advantage concerns the relative "immunity" of the SSEP method from artifacts such as muscles (EMG) and eye movements which frequently force the exclusion of participants from the data set because their EEG trace is destructively contaminated by artifacts (for an introduction to artifacts-related problems in psychophysiological research see Luck, 2005b). The second advantage concerned the ability to perfectly discriminate between the SSEPs associated with the attended and unattended locations, as these were tagged by different frequencies.

These initial results established the SSEP method as a useful and powerful psychophysiological tool to investigate mechanisms of perception and attention, and has given rise to a number of subsequent studies (see, e.g.: Belmonte, 1998; Cosmelli et

al., 2004; Russo & Spinelli, 1999a, 1999b; Hillyard et al., 1997; Kelly et al., 2006; Kim, Grabowecky, Paller, Muthu, & Suzuki, 2007; Malinowski, Fuchs, & Muller, 2007; Morgan et al., 1996; M. M. Muller, Picton, et al., 1998; M. M. Muller, Malinowski, Gruber, & Hillyard, 2003; M. M. Muller & Hillyard, 2000; Pei, Pettet, & Norcia, 2002; Srinivasan, Russell, Edelman, & Tononi, 1999; Srinivasan et al., 2006; Wang, Clementz, & Keil, 2007, and others). The method seems especially suitable in studies where competition between simultaneously displayed stimuli is addressed such as, for example, conscious perception in binocular rivalry (Tononi, Srinivasan, Russell, & Edelman, 1998). Binocular rivalry consists of experiencing alternating perceptions of two simultaneously displayed incongruent visual stimuli, each presented to one eye. Tononi and collaborators (1998) used SSEP (measured using magnetoencephalography, or MEG) to show that the conscious percept of a stimulus was associated with a broadly distributed and coherent pattern of neural activity. Given the power of the SSEP to trace neural activity associated with each of the rivaling stimuli throughout the brain, they referred to the method “frequency tagging”. In the present thesis, we sought to employ these compelling advantages offered by the SSEP method to investigate mechanisms of focused and divided attention, both within modalities and across modalities.

1.3 Linking dynamics of resources management to brain rhythms: How does the human brain deal with difficult situations?

Dual-task paradigms permit the study of how resources are allocated to one or another task because the execution of multiple tasks results in interference when they compete for limited resources (Kahneman, 1973). Important questions are: what information has priority, how is priority attributed, and how can multiple tasks be simultaneously accomplished?

In this thesis questions were approached in a threefold manner. The first approach involved observing individuals with different levels of cognitive abilities to investigate whether correlations exist between higher cognitive abilities and brain activity as measured by EEG. In the second approach an innovative methodology (frequency tagging) was used to visualize the dynamics of the brain resource allocation policy when multiple tasks are performed simultaneously and attention is divided between them. In the third approach the neurological correlates of attentional disengagement (see Posner & Petersen, 1990) was investigated. Attentional disengagement is the

process through which attention is released from a previous objective to focus on the next one. The identified neurological correlate constitutes a significant development in the study of the time course, dynamics, and interplay of the processes involved in attentional control, especially with regard to top-down influences.

The management of resources and the dynamics of resource allocation occur on the fly. Therefore, to capture the time course of these changes at a neurophysiological level, a technique which permits the observation of changes in brain activity millisecond by millisecond must be employed. Electroencephalography (EEG) is a neuroimaging technique which allows to observe the very rapid changes in brain states which may correlate dynamic resource management in the brain.

In Chapter 2 EEG was used to investigate individual differences in resource management. EEG was measured in two groups with different levels of cognitive abilities (i.e. high vs. low IQ). While participants performed a sentence verification task using the same strategies, possible IQ-related and strategy related differences in brain rhythms were studied.

Chapter 3 and 4 focused on EEG changes, in a specific frequency range as determined by a frequency tag, between single- and dual-task performance and between attending one versus multiple sources of information to establish a more direct link between allocation of resources and EEG. Chapter 3 addressed the competition for resources within the visual modality, where two locations had to be monitored simultaneously, or one attended and the other ignored. Chapter 4 addressed the same questions and the same methodology using a cross-modal paradigm (i.e., stimuli were presented auditorily and visually).

Chapter 5 puts to a direct test the possible existence of a distinct disengagement-related waveform following the N2pc, which is an event-related potential linked to the automatic capture of attention. The existence of this component may provide an important tool for studying attentional control.