

A hybrid model for the neural representation of complex mental processing in the human brain

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Abstract In the present conceptual review several theoretical and empirical sources of information were integrated, and a hybrid model of the neural representation of complex mental processing in the human brain was proposed. Based on empirical evidence for strategy-related and inter-individually different task-related brain activation networks, and further based on empirical evidence for a remarkable overlap of fronto-parietal activation networks across different complex mental processes, it was concluded by the author that there might be innate and modular organized neuro-developmental starting regions, for example, in intra-parietal, and both medial and middle frontal brain regions, from which the neural organization of different kinds of complex mental processes emerge differently during individually shaped learning histories. Thus, the here proposed model provides a hybrid of both massive modular and holistic concepts of idiosyncratic brain physiological elaboration of complex mental processing. It is further concluded that 3-D information, obtained by respective methodological approaches, are not appropriate to identify the non-linear spatio-temporal dynamics of complex mental process-related brain activity in a sufficient way. How different participating network parts communicate with each other seems to be an indispensable aspect, which has to be considered in particular to

improve our understanding of the neural organization of complex cognition.

Keywords Complex mental processing · Neural hybrid model · Individuality · Brain development · Modular neural organisation

What is a complex mental process?

It seems to be impossible to find a model that appropriately describes all necessary components, which are involved during complex mental processing as, for example, in complex mental calculation (e.g., Dehaene 1992; Dehaene and Cohen 1995; Arsalidou and Taylor 2011). However, the proposal of appropriate models is an important basis for further hypotheses testing. They support the verification of new methodological approaches for the analyses of data obtained during complex mental processing. Several cognitive sub-elements such as long term memory (LTM) retrieval, appliance of different mental algorithms, and working memory (WM) processing including information of different modalities (e.g., visuo-spatial and verbal) (e.g., Baddeley 1992, 1997) are involved in complex mental processing potentially varying from experimental trial to trial and also varying in its composition from individual to individual. The more complex a process is the more sources of variability and the more dimensions it might bear. Therefore, one of the biggest challenges for modelling and testing aspects of complex mental processing seems to be related to intra- and inter-individual differences (e.g., Fehr 2011; Fehr et al. 2011, 2003; Achtziger et al. 2009; Regenbogen et al. 2010; Reinvang et al. 2003; Feredoes and Postle 2007; Miller et al. 2012). What, if we need a single model for each individual, which, furthermore, dynamically

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alters over time due to changing compositions of mental sub-elements varying with applied mental strategy and/or alterations related to physiological brain development (e.g., Fehr 2008a, 2009, 2011; Fehr et al. 2008b, 2011)? Such an assumption does not seem to provide the best basis for a handy working hypothesis, which can easily be tested by contemporary methodological approaches. Therefore, in the present conceptual review information from several theoretical and empirical sources were combined to emphasize a potential principle that might generally explain the neural organisation of all or at least of most complex mental processes.

The following section focuses on two different concepts proposed for the organisation of complex systems: a network and a modular based concept. The reflection of these both concepts will provide the theoretical basis for an integration of empirical data discussed later in the present conceptual review.

Is there a functional and structural modularity in neural systems?

Beside problems of consistently localizing neural correlates of complex mental processing in the brain (e.g., Fehr 2008a, 2011; Fehr et al. 2003, 2008b, 2011; Achziger et al. 2009; Regenbogen et al. 2010; Reinvang et al. 2003; Feredoes and Postle 2007), it seems that there are two opposing theoretical views concerning the question of how mental processing architecture is organized in functional neuroanatomic equivalents. For some low-level processes (e.g., sensory input and motor processing) an innate basis of isomorphic cerebral representation might be given, which is in line with massive modularists' or localisationists' view (see Barrett and Kurzban 2006; Bassett and Gazzaniga 2011). Localisationists, in contrast to network theoreticians, however, tend to "extrapolate evidence from primary areas to upper associative areas" (see Fuster 2006). This might prominently originate from an over-interpretation of some behavioral results correlating with cortical lesions in neurological patients, which have, according to Fuster, incorrectly led to the assumption that not only complex sensory features (located in primary sensory cortices) or basic action-related (primary motor cortex) concepts, but also *specific cognitive functions*, are represented comparably in associative areas. Joaquín Fuster stated (2006): "..., some neuroscientists have been led to believe that there are cortical modules or 'centres' for perception, memory, language, attention, and executive control, among other cognitive functions. And thus, a more or less academically condoned "neo-phrenology" has emerged." Analogous to the historical concept of *phrenology* introduced by Franz Joseph Gall at the beginning of the nineteenth century, which according to quasi empirical

observations assumed a relationship between head form and the localization of specific mental functions, this means that brain functions are assumed to be strictly separable into cognitive domains. Furthermore, these cognitive domains are assumed to be related to discrete areas of the cerebral cortex that are morphologically localizable by 3-D, or say Cartesian, rules.

In contrast to this massive modular view, Fuster (see 2006 for review) developed a whole brain network concept of mental processing architecture. The elements, which represent "sub-modules" of mental information processing, were termed *cognits*. Cognits might be understood as portions of *memory*, which are organized as widely distributed neural sub-networks inseparably associated with others (see also Basar 2004, 2005, 2006, 2011). The hierarchical order of cognits emerges from their developmental dynamics. At lowest level there are cognits located in primary cortices (so-called *phyletic memories*). Adjacent to primary cortices in the brain, more abstract and individual cognits will be elaborated during ontogenesis, depending on perceptual or motor experiences. At highest level, cognits driven by and related to experience will develop into hetero-modal frontal, parietal and temporal association cortices representing complex cortico-cortical connected networks hosting higher conceptual concepts. Fuster distinguishes between perceptual cognits, located in post-rolandic brain regions and executive cognits, located in pre-rolandic brain regions. Together both these classes of cognits form the basis for perception–action cycles acting via reciprocal cortico-cortical connections. Automatic, instinctive, or well-rehearsed behaviors have been proposed to be adaptively integrated at lower cortical levels (e.g., basal ganglia). Higher level processing, requiring semantic information at conceptual levels too, for example, form new "gestalts" of action, has been suggested to prominently be located in iso-cortical association cortices (see also Basar 2004).

Memory, as a putatively important basis for complex mental processing, was typically described as including LTM and WM modules (e.g., Baddeley 1992, 1997). According to contemporary models, LTM consists of declarative and non-declarative or procedural components. WM was discussed to be composed of at least three sub-systems, an articulatory loop system, a visual scratchpad module, and a so-called central executive component coordinating the latter two sub-systems. However, there is also the concept of phyletic, perceptual, and executive memories, as outlined above (Fuster 2006), and model assumptions about relationships between memory complexity and neural network communication (e.g., Mizraji et al. 2009; Bassett and Gazzaniga 2011), which can be linked to certain oscillatory and evoked EEG parameters such as, e.g., alpha, gamma, theta and delta frequency band

activity, and different ERP characteristics (for an extensive introduction and review see Basar 2004, 2005, 2006, 2011; see also Yener and Basar 2010).

Beside somewhat diverging cognitive model assumptions about memory organization, there is only little consensus about where memory is located in the brain. Despite a certain agreement that the hippocampal formation and adjacent medio-temporal regions seem to be more or less inevitably linked to memory processing, especially during consolidation of new declarative memories, principally each neuron of the neural system can potentially be part of each existing memory (sub-)network in the brain (Basar 2005, 2006, 2011). Neurons in brain stem and particularly in the reticular system, limbic system, thalamus with multiple afferent and efferent connections from and to, e.g., neo-cortical association, but also to primary, cortices, the cerebellum, and multiple neo-cortical regions, which are highly interconnected (compare Basar 1999, 2011), provide a quasi unlimited basis for physiologically based memory formations in the brain. And this is a big challenge for any proposed modular organized functional neuroanatomic memory model, but also for the respective methodological approaches to prove these and alternative network models.

However, as one of the basic scientific aims is the reduction of data masses—especially in the psychophysiological research domain—to avoid the interpretation of redundant information, and, of course, to make phenomena more comprehensive to a broader audience, modular views of neural brain functioning still belong to the most popular ones. Most models describing complex mental processes such as, for example, mental arithmetic, consist of modules (or sub-elements), which have been more or less clearly defined by several features and communication characteristics (Dehaene 1992; Dehaene and Cohen 1995). Therefore, *modularism*, as a related concept, which is often used to explain respective psychophysiological entities as localizable in a Cartesian (say 3-D) way, should shortly be introduced at this place.

Among others, there is one central problem when authors address the topic of *modularity*: it is easy to fill books with all the existing facets of views concerning the *modularity* notion in the different scientific domains. Also in the neurosciences *modularity in functional neuroanatomy* is a central topic of an ongoing debate (e.g., Bassett and Gazzaniga 2011). According to psychological notations, and as putatively most psychologists would agree that the mind has some internal structure, different modular systems have independently been defined for different cognitive sub-systems (or cognitive levels) as language (Fodor 1983), “theory of mind” (Baron-Cohen 1995; Leslie 1994; Scholl and Leslie 1999), spatial orientation (Hermer and Spelke 1996), number processing (Dehaene 1992; Dehaene and Cohen 1995), different emotional information processing

systems (e.g., Buss 1992; Öhman and Mineka 2001; Rozin et al. 2000), face recognition (Duchaine et al. 2004; Kanwisher 2000), and other putatively modular composed emotional and/or cognitive sub-systems. All these models were prominently based on theoretical assumptions revealed or inferred by introspective intuition, lesion studies on cognitive and/or emotionally impaired patients, and empirical data obtained by psychophysiological and behavioral studies. The broad variety of sources, from which information has been integrated, inevitably leads to a certain variety of the principles attributed to the proposed model sub-components. Thus, to find a general explanation of what a modular arrangement has to be is not trivial. A common approach, however, defining properties for a modular organization of a system was proposed by Fodor (1983).

Fodor (1983) introduced a concept of modularity that consists of several features assumed to be necessary for a modular system such as for example *domain specificity* and *fixed neural localization*. All modularists would for sure agree that the presence of some of the features proposed by Fodor are sufficient for defining a modular system, but not all are necessary at the same time. And furthermore, some modularists might for sure accept different arrangements or compositions of sub-sets of the proposed features to be sufficient for a modular system. In particular this makes a general definition of modularity extremely difficult or even impossible. Nevertheless, modular model assumptions are popular as they seem to provide an efficient and comprehensible basis for the explanation of complex systems such as the human brain and its highly integrated functional properties, and, there is empirical evidence that apparently support this trend.

For instance, case studies on patients with lesions have shown that specific cognitive impairments are sometimes directly linked to sub-elements proposed in psychological, mental processing models, a modular view of, e.g., human numerical cognition seems to be largely justified. Unfortunately, patients included in case studies show remarkable inter-individual differences (Caramazza 1986) because the spatial distributions of lesions in different patients are only coarsely comparable. Furthermore, selective impairment related to a specific traumatized brain region does not justify the sufficiency of the respective region for a specific mental process, but at best that this region seems to be a necessary part of a broader process-related neural network. Nevertheless, as Barrett and Kurzban (2006) postulated, most psychologists might generally agree that because *cognitive architecture* is instantiated in *neural architecture*, the two will be isomorphic at some level (see also Marr 1982). But, at macroscopic level, there is no reason to assume that there must be spatial units or chunks of brain tissue that neatly correspond to information-processing

units (compare Atmanspacher and Rotter 2008; Lo 2010). What, if there are many facets of modular architectures varying with respective specific mental processes, individually different learning histories, daily or situational preferred mental strategies, different cultures, and many other aspects? This idea is substantiated by studies showing that the spatial organization of functional neuroanatomic correlates associated with complex mental processing shifts, for example, after practicing and/or strategy adaptation (e.g., Raichle et al. 1994; Sakai et al. 1998; Houdé et al. 2000; Fehr et al. 2008b; see also Fehr 2008a, 2011; Fehr et al. 2010, 2011).

In the following the above-introduced concepts for the neural organization of complex mental processing will be discussed and critically reflected on the basis of empirical neurophysiological data related to mental arithmetic, a prominent prototype of complex mental processing. Furthermore, methodological thoughts on how, for example, the impact of individual characteristics of complex cognition on the respective neural correlates can be handled appropriately will be discussed. As not all neuroscientists are familiar with all kinds of the here mentioned approaches of non-invasive human neuroscience, some of the most prominent methods are shortly introduced in Box 1.

Mental arithmetic as a prototype of complex mental processing and its neural organization

As mental arithmetic involves LTM retrieval, the appliance of different mental algorithms, WM processing in different modalities (verbal, visual, spatial), and the production of respective responses, this process is referred to as a prototype of complex mental processing in the present discussion. First, basic principles of mental arithmetic are introduced, and thereafter, contemporary assumptions about the neural representation of mental arithmetic processing and related functional neurophysiological data will be presented.

Dehaene (1992) introduced the so-called *triple-code-model* of number processing, which integrates assumptions about the processing of spoken numbers, recalling numerical knowledge, calculation, and comparing magnitudes. This model is still deemed to be the putatively most appropriate approach to integrate the results of the majority of publications addressing the topic at the moment. Furthermore, this model has been discussed, adapted and improved since 1992 (e.g., Dehaene and Cohen 1995; Pinel et al. 1999; Dehaene 1996; Dehaene et al. 2003, 2004; Arsalidou and Taylor 2011). As its label already suggests, the *triple-code-model* is based on the assumption that there are three different mental number representation codes: (1) an *auditory verbal word frame*, which recruits general

language modules to create and manipulate verbal number codes represented by word sequences (e.g., /seven//100/), (2) a *visual Arabic number form*, which manipulates numbers on a spatially extended representational medium, and (3) an *analogue magnitude code*, which is suggested to represent numerical quantities as inherent variable distributions of activation over an oriented analogical number line. But, how are these proposed modules of mental arithmetic evolve during ontogeny, and furthermore, how are they organized in the neural system?

Simple abstract number representations have been reported to be present even in preverbal children (Wynn 1992, 2000) as well as in primates (Hauser et al. 1996; Nieder 2005; Nieder et al. 2006), a phenomenon that might indicate a genetically determined and evolutionary developed basic concept of the representation of small numerosities in the brain (for integrative review, see Dehaene et al. 2004). Subitizing, discussed as a given skill for the very fast processing of small numerosities (between 3 and 5) (Mandler and Shebo 1982), might provide a good explanation for an innate rudimentary present cognitive number module working in a perceptual spatial encoding style: it has been suggested that during subitizing, the recognition of invariant canonical *spatial* configurations might be processed very fast and in parallel (all contextual features at once) at a pre-attentive level for different arrangements of objects. The mental processing of large numbers and arithmetic operations, however, has to be learned individually, and hence, this provides a potential source for individual differences in the respective neural representation.

The above-introduced “triple code model” by Dehaene (1992) suggests three ‘frames’ associated with number processing, which are located in distinct regions of the brain and that can be dissociated by both function and location in the neural system (Dehaene and Cohen 1995; Pinel et al. 1999; Dehaene 1996). Representation of magnitude is assumed to be processed in bi-hemispheric parietal regions, and is activated automatically when stimuli involve numbers, number comparisons, approximations and/or estimation procedures. Left and right inferior occipital regions are assumed to be involved in the processing of written Arabic numerals and left perisylvian regions when numbers are represented in written or spoken forms. Additionally, left perisylvian regions might be involved in the access of arithmetic facts that have been memorized in association with structures in the basal ganglia. A detailed review (Dehaene et al. 2003) led to the conclusion that parietal brain activation in number-related tasks might be segregated to three distinct sites: the superior posterior parietal lobule, which is associated with visuo-spatial processing; the left angular gyrus, where verbal processing of numbers takes place; and the horizontal

Box 1 Several non-invasive methods in human brain sciences—temporal and spatial resolution

	MRI (magnetic resonance imaging)	PET (positron emission tomography)	fMRI (functional magnetic resonance imaging)	EEG/MEG (electro-encephalography/magneto-encephalography)
spatial resolution	very good	good	very good	surface: very good central structures: none
temporal resolution	none	very poor	poor	optimal

MRI (magnetic resonance imaging) MRI measurements of the brain provide detailed information about individual neuroanatomy on the basis of, e.g., the distribution of H-nuclei in biological tissue. Furthermore, MRI images provide an excellent basis for the superposition of functional data from, e.g., fMRI and biosignalanalysis (EEG and MEG). For detailed introduction to MRI see, e.g., Sanders (1995)

PET (positron emission tomography) PET measurements provide information about regional blood flow and metabolism in the brain. As PET is using weak radioactive metabolites and substances that decay rather slowly, functional PET-data can only be obtained in experimental block designs. This is a serious limitation for most psychophysiological examinations. Detailed information and an extensive introduction to PET is, e.g., published by Hartshorne (1995)

fMRI (functional magnetic resonance imaging) most fMRI-studies are based on the so-called blood oxygen level dependent (BOLD) effect. Oxygenized blood shows different magnetic resonance properties than de-oxygenized blood. As active brain regions are characterized by larger metabolism rate, more oxygenized blood is needed and therefore these regions show enhanced blood volume and oxygenized blood flow. Magnetic resonance data obtained from activated brain regions show specific temporal characteristics, which can be modeled by the so-called hemodynamic response function. Using general linear model statistics, a brain region can be identified as being activated by particular events or mental processes according to its signal time course. As the hemodynamic response is rather slow (~ 10 s), and as whole brain fMRI data can only be obtained in about 2-s intervals, the method does however not provide very good time resolution (for more detailed information and introduction see, e.g., Sanders and Orrison 1995; Logothetis et al. 2001)

EEG (electroencephalography) EEG data are obtained by electrodes placed on the surface of the scalp. The obtained electrical signals refer to extra-cellular mass activity of asymmetric dendrite trees all over the brain. Localization of underlying generators is very good at the surface but becomes impossible towards the center of the brain volume. For more detailed information and introduction to EEG see Basar (1980, 2004, 2011) and Rüsseler and Münte (2008)

MEG (magnetoencephalography) MEG data are obtained by so-called SQUIDs (superconducting quantum interference devices) from outside the head. Most of the MEG signal is assumed to be produced by intra-cellular mass activity of asymmetric dendrite trees tangentially oriented to the SQUID-sensors. Comparable to EEG, localization of underlying generators is very good at the surface but becomes impossible towards the center of the brain volume (for more detailed information to MEG see, e.g., Lewine and Orrison 1995; Fehr 2008b)

segment of the intra-parietal sulcus, where numerical quantity is processed (see also Dehaene et al. 2004).

In two studies, conducted by Fehr et al. (2007, 2008a), the four basic arithmetic operations addition, subtraction, multiplication, and division were examined by means of functional magnetic resonance imaging (fMRI). Despite that the operation-specific activation patterns seem to be rather comparable in principle, but not strictly overlapping in the same regions, overall conjunction analyses across all operations and two different task presentation modalities (auditory and visual) consistently revealed common activations only in superior medial frontal and right parietal regions, when contrasting complex and simple task conditions (see Fig. 1 for illustration).

A schematic overview for operation and presentation modality related activation foci is given in Fig. 2. From a macroscopic point of view, it might be concluded that different arithmetic operations are rather processed in similar, but not in identical neural networks. This assumption is confirmed by somewhat heterogeneous results reported by different functional neuroimaging studies on mental arithmetic (Arsalidou and Taylor 2011; Fehr et al. 2007). In conclusion, the processing of mental

arithmetic seems to be somewhat modular organized according to the model assumptions of, e.g., Dehaene and Cohen (1995), however, there is also empirical evidence for considerable sources of variability, incompatible with an assumption of a massive modular neural organization of complex mental arithmetic processing. Two potential reasons for that, individuality and variations in mental strategy, will be addressed in the following section.

Individual differences and/or applied strategies in complex mental processing modulate brain physiological parameters

In several studies, individual variation in different brain activation parameters has been discussed as a considerable source of statistical inconsistency (e.g., Fehr, et al. 2003; Achtziger et al. 2009; Regenbogen et al. 2010; Reinvang et al. 2003; Burbaud et al. 2000; Feredoes and Postle 2007; Nunez-Pena et al. 2006; Thirion et al. 2007). The consideration of individual cognitive and physiological profiles is almost always ignored in contemporary neuro-cognitive studies. However, this bears the risk of potential

visual & auditory presentation modalities (complex > simple tasks)
 conjunction analysis {null}: addition, subtraction, multiplication and division

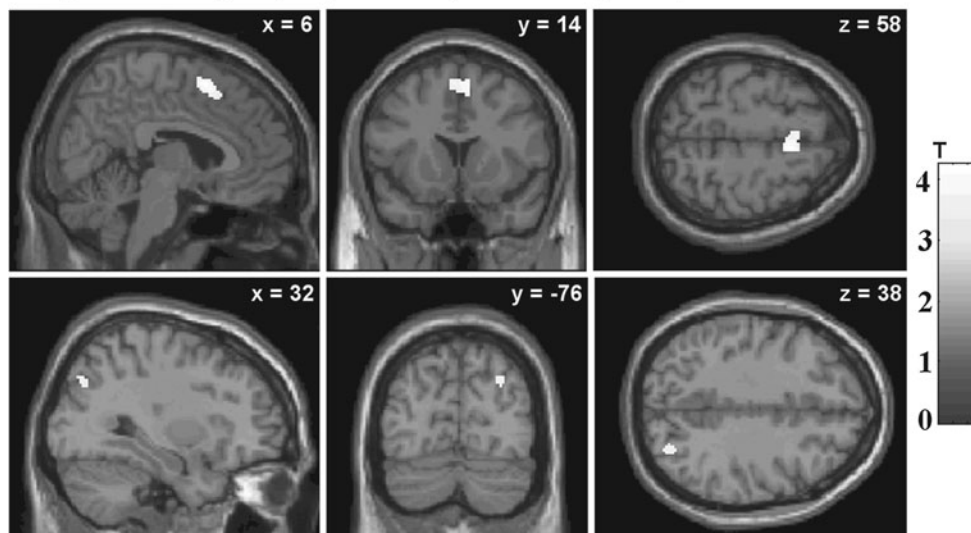


Fig. 1 Conjunction {null} including complex versus simple addition, subtraction, multiplication and division task contrasts for both auditory and visual task modalities ($p < .001$, uncorrected, $k > 9$)

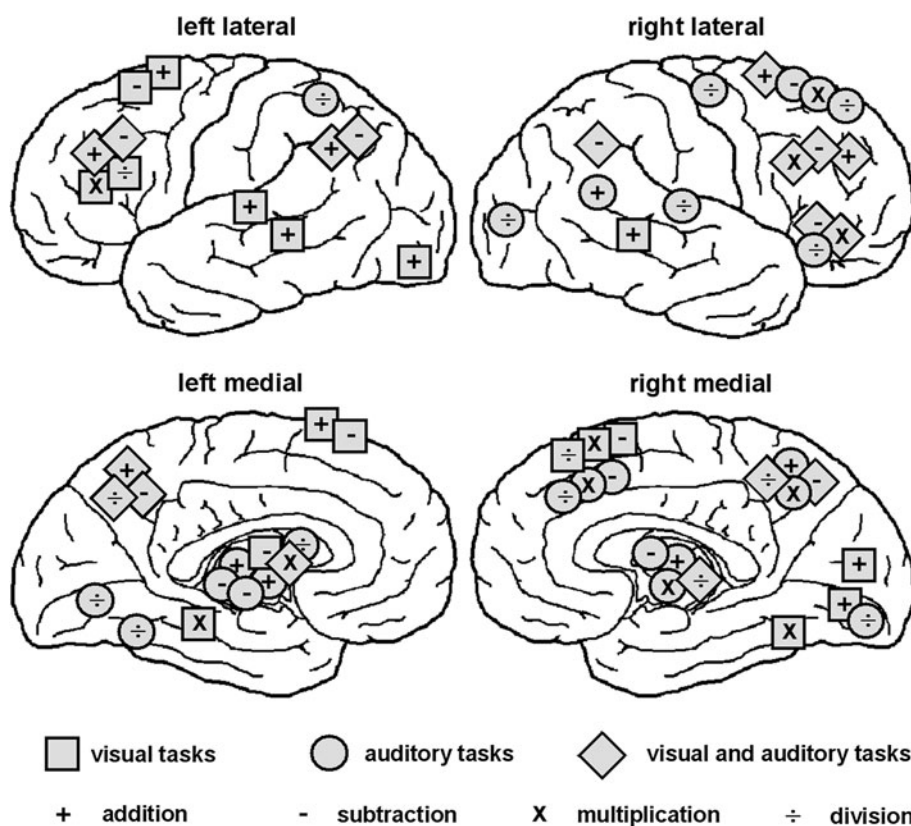


Fig. 2 Complex versus simple mental arithmetic—schematic overview of the fMRI activation foci reported by Fehr et al. (2007, 2008a), Fehr (2008a)

miss-interpretation of physiological activation patterns revealed by group-analyses because these results are often interpreted as complete task-processing-related neural

networks sufficiently reflecting a specific complex mental process. In Fig. 3, rendered statistics of individual fMRI activation patterns obtained from 11 individuals are

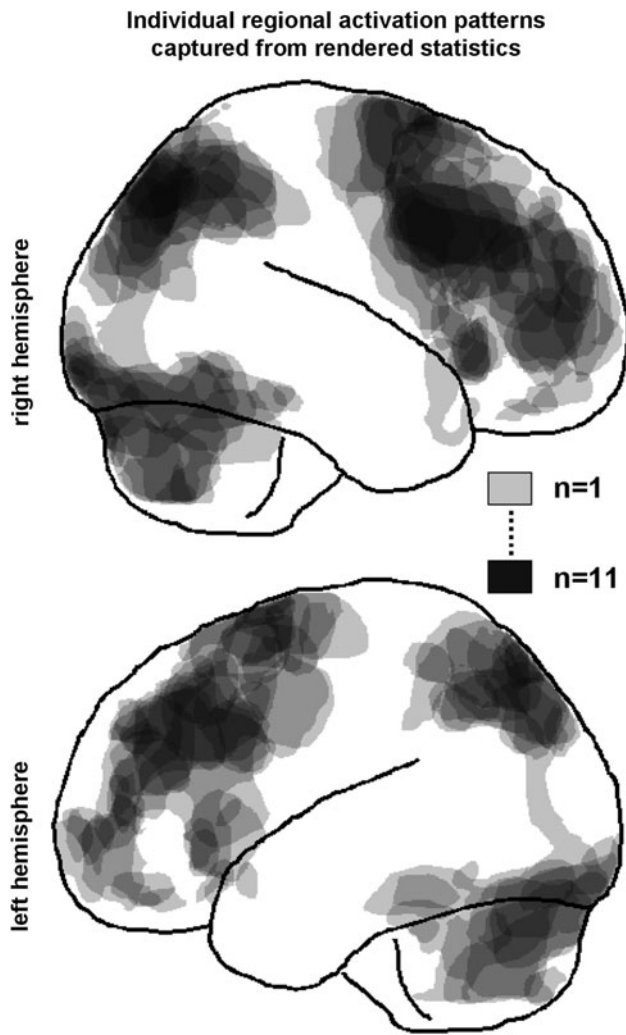


Fig. 3 Complex versus simple mental calculation ($p < .0001$, FWE-corrected): areas were captured from rendered statistic views (original data: Fehr et al. (2007, 2008a), Fehr (2008a) and superimposed; the darker the shadings the more individuals showed significant differences in the particular region

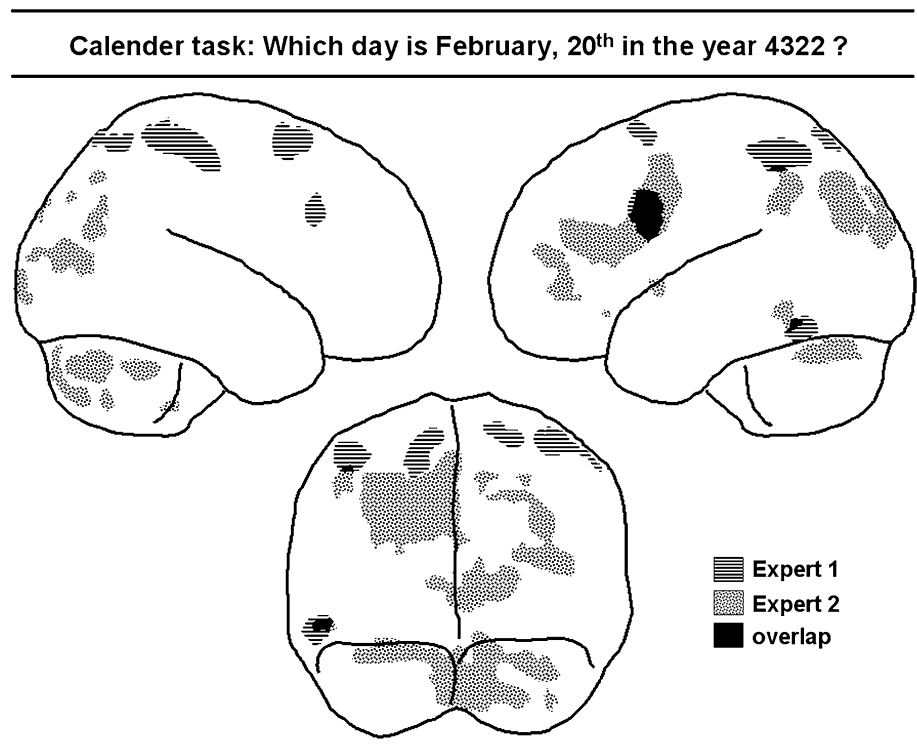
superimposed to illustrate individual differences in mental arithmetic processing (see also Fehr 2008a). These data illustrate that there is only moderate consistent overlap of activation between all individuals.

Individual differences in brain activation patterns might be due to different applied calculation strategies (Fehr et al. 2008b, 2011; Fehr 2011). Related to the cognitive number processing domain, handling simple one-digit problems is developed during childhood, starting with counting strategies and ending up with memory retrieval based strategies (see Ashcraft 1982, 1987; Siegler and Shrager 1984). Selected strategies used by children even vary across experimental trials in one experimental session (Siegler and Shrager 1984). Adults, usually only sometimes confronted with mental arithmetic problems (mostly solved by

using electronic calculators), might also apply varying strategies for different more complex arithmetic operations depending on their individual learning histories. There are several studies confirming that applied strategy can vary between individuals and that this can have considerable influence on brain activation (e.g., Burbaud et al. 2000; Nunez-Pena et al. 2006; Fehr et al. 2011). For example, Burbaud et al. (2000) showed that study participants who reported different strategies (described as visual or verbal) showed different brain regions to be activated during serial subtraction tasks. Assuming the participants were really able to appropriately determine, which calculation strategy they *mainly* applied, there is no warranty that they did not apply varying strategies from trial to trial. The assumption of individually different processing strategies across calculation trials becomes even more evident when considering the different codes, utilized for numerical magnitude processing, represented by symbolic or approximate quantity representations proposed by Dehaene (1992). These codes might dynamically be involved and trans-coded one into the other in a varying manner intra- and inter-individually within and between mental calculation trials (compare also Fehr et al. 2010).

Extrapolating the conclusions above from mental arithmetic to other complex mental processes, some further empirical data from different mental domains should be mentioned at this place. Houdé et al. (2000) applied a deductive reasoning task with negative conditionals. Study participants were presented with a rule such as “If there is not a red square at the left, then there is a yellow circle on the right”. Functional neuroimaging data indicated that brain activity shifted from prominently posterior to pre-frontal locations, after training. This regional activation shift was interpreted as reflecting a shift from a perceptual to an executive mental strategy. This result makes an exclusive determination of a putative existing functional neuro-anatomic equivalent (or module) for the processing of a certain mental task at least difficult. Analogously to the study of Houdé et al. (2000), Adleman et al. (2002) showed that during brain development from childhood through adolescence to early adulthood, Stroop-task related fMRI activation patterns seem to develop from posterior to more anterior brain regions. These data, however, involve an additional brain developmental component, which might not be separable from an assumable cognitive strategy shift from perceptual (posterior) to more executive (frontal) processing during learning history. However, a recent study further substantiates the assumption that individual strategy largely modulates brain activation patterns (Fehr et al. 2011). Two calendar calculation experts successfully solved the same tasks using different strategies and recruiting almost completely different neural resources (see Fig. 4 for illustration).

Fig. 4 Calendar versus baseline task contrasts for two calendar experts successfully solving the same tasks: Rendered statistics superimposed on MNI standard brain ($p < .05$, FWE-corrected); free according to Fehr et al. (2011)



Summarizing, individual differences in learning history (e.g., see Houdé and Tzourio-Mazoyer 2003; Johnson 2001), psychological strategies (Burbaud et al. 2000; Fehr et al. 2011), developmental status (Adleman et al. 2002; Casey et al. 2002), and other factors have been shown to considerably influence the spatial organization of neural networks related to complex mental processing. It might be questioned, whether statistically survived multi-trial based activation patterns, revealed by means of temporal and/or spatial averaging procedures in biosignalanalysis or neuroimaging, really reflect the examined mental process at cortical level; or whether these neurophysiological results just reflect a fragmentary subset of all of the potentially involved mental sub-processes. More precisely, it might be argued that we do only interpret the activations of some shared neural tissue, meaning junctions, intersections, or say nodal points, recruited by various different processes that are, however, each distributed at completely different locations invisible for our “trivialized” and/or “inappropriate” statistical approaches. It could further be argued that *single trial—single individual data analysis* might be the first choice of future data analyses strategies in order to examine complex mental processes.

In the following section, another central problem of inferring mental processes from revealed activation patterns on the basis of group analyses will be addressed before the previously discussed aspects will be integrated into a general hybrid model for complex mental processing.

Can specific mental processes be concluded from brain activation patterns? The inverse problem of functional neuroimaging

Many neuroimaging studies, addressing complex mental processing, present large, similarly distributed activation patterns in, for example, fronto-parietal association cortices. These patterns have also been suggested to constitute a network activated during WM and visuo-spatial attention processing (e.g., Corbetta et al. 1993; Goldman-Rakic 1984; Nobre et al. 1997). Different cognitive functions have been proposed to temporally be controlled in parallel within neural systems (e.g., Basar 1999, 2004, 2011), linking posterior parietal, prefrontal and related sub-cortical structures (Goldman-Rakic 1988). This fronto-parietal association network, mostly activated in combination with basal ganglia, cerebellum and inferior temporal association cortices, has been reported to be activated by a large variety of tasks addressing complex mental processes from different mental domains such as attention, mental arithmetic, WM, and others (e.g., Valera et al. 2005; Chochon et al. 1999; Corbetta et al. 1993; Nobre et al. 1997, Fehr et al. 2007, 2008a). This kind of principally common recruitment of neural resources by different cognitive processes, however, in combination with large individual differences in psychophysiological measurements provide a serious problem for the inference of mental processes from given brain activation patterns (compare also

Poldrack 2006; Fehr 2009, 2011). This problem is discussed by the following example:

Figure 5 illustrates adumbrated brain activation patterns of 11 individuals performing mental arithmetic superimposed on group statistical functional imaging data of three additional studies (Glabus et al. 2003; Lee et al. 2006; Rombouts et al. 2001) applying experimental designs addressing different cognitive domains: (1) An fMRI study by Glabus et al. (2003) examining WM processing during a 2-back task; (2) a study by Lee et al. (2006), who contrasted fMRI activation during a complex and a simple intelligence task, based on Raven's Advanced Progressive Matrices; (3) a further completely different study by Rombouts et al. (2001), who contrasted, among others, the

encoding of unfamiliar with the encoding of familiar color pictures showing complex motives like landscapes. The illustration (see Fig. 5) documents that it would not be possible to conclude, which specific mental process, mental arithmetic or one of the respective tasks mentioned above, was performed, on the basis of a given individual or group-related activation pattern as presented in the illustration.

As brain activation related to complex mental processing must be assumed to be largely modulated by individual properties as applied strategies, it should be argued that specific task processing (e.g., mental arithmetic or other complex mental processes involving multiple cognitive sub-components) cannot be identified by respective task-related 3-D brain activation patterns, neither on individual nor on group statistical level. Additional information on behavioural level is necessary to make further inferences. Concluding from both the previous and the present section, it seems that it is rather something about the *HOW* a process was performed, but not *WHAT* specific process was performed, which can be inferred from brain activation patterns revealed by, e.g., functional neuroimaging (e.g., Fehr 2008a, b, 2011; compare also Poldrack 2006). The *HOW* can further be sub-divided in individual strategic preference (e.g., perisylvian activations might reflect language involvement, and inferior occipito-temporal activations might reflect visual processing style) and actual communications between neural networks reflected in oscillatory activations across different frequencies (Basar 2006, 2011; compare also Colliaux et al. 2009; Wang 2007; and see also next section for further discussion). The more complex a mental process is structured by its mental architecture, the less modular and the more holistic and individual it appears to be organized in neural network structures distributed all over the brain. In the next section, some suggestions are given on how the potentially shared neural networks recruited by different mental processes might further be characterized by their process-related dynamic communication properties.

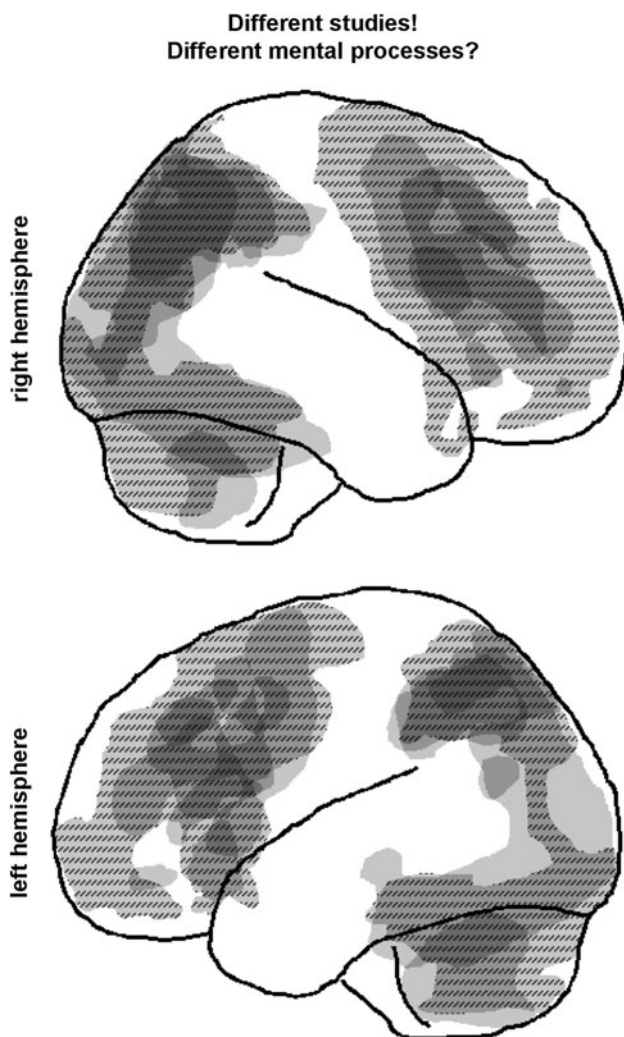


Fig. 5 Superimposed activation patterns revealed by three different neuroimaging studies examining complex mental processes (Glabus et al. 2003; Lee et al. 2006; Rombouts et al. 2001); darker shadings indicate overlapping activations. Regions, which have been shown to be activated for 11 single participants (mental arithmetic task performance), have additionally been included and are indicated by hatched areas

Spatio-temporal processing dynamics as an indispensable source of information for the characterization of complex mental processing in the brain

From the very beginning of postnatal development, in preverbal infants, rudimentary forms of numerical representations related to numerical processing (e.g., Wynn 1992, 2000; Hauser et al. 1996) might innately be organized in inter-individual comparable, thus modular organized, brain regions (e.g., in predominantly intra-parietal areas, see Nieder 2005; Nieder et al. 2006). Neural networks storing these rudimentary forms of numerical

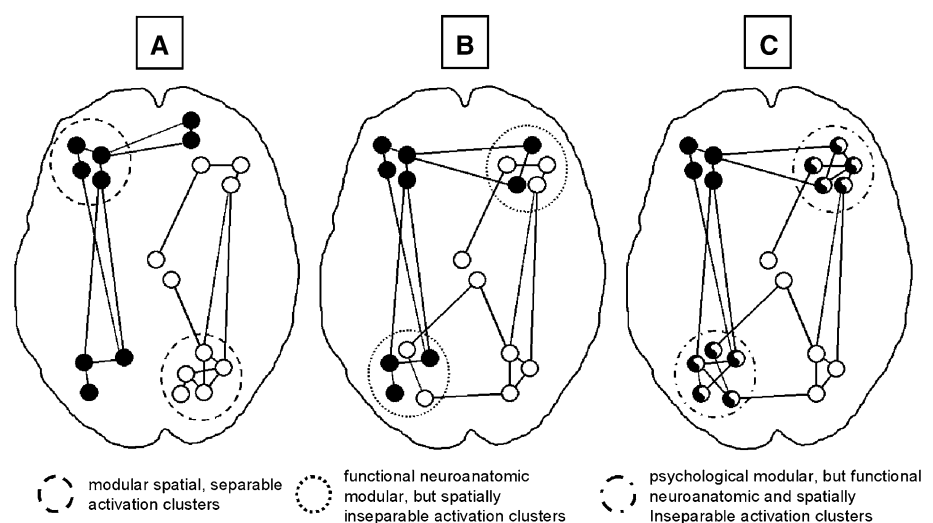
information might analogously be organized as primary sensory or motor cortices, and furthermore, the initial numerical information stored in these brain regions, say intra-parietal areas, might be characterized analogously to phyletic memories as proposed by Fuster (2006). Later on, during individual development and learning history, the distribution of respective neural networks might become more and more individually distinct organized in widespread neural networks, across hetero-modal frontal, parietal and temporal association cortices (compare Fuster 2006; and next section of the present conceptual review). The course of this development might especially be dependent on individual learning history and a contextually modulated and developed preference for particular idiosyncratic complex mental processing strategies (i.e., for a discussion about individual cognitive style see Miller et al. 2012). This assumption would predict that there might be a certain overlap of neural network recruitment during mental arithmetic across individuals, but also across different tasks involving similar mental sub-processes (see also the two previous sections). Following this line of argumentation, different complex mental processes cannot be differentiated on a psychophysiological level just based on brain activation patterns. Additional information is needed to characterize both the dynamics of network communication and its individual entities (compare also Poldrack 2006).

Spatial overlap of brain activation patterns, for example, as revealed by means of functional neuroimaging (see also previous section), does not necessarily provide convincing evidence that the potentially inferred regional located processes interact with each other following a unique communication principle or that they are morphologically hosted in common neural networks (see Fig. 6 for a schematic illustration of hypothetical regional morphological neural network compositions). Possibly, these networks

communicate with a completely different oscillatory code (see also Basar 2005, 2006, 2011; compare also Singer 2009). Basar (2006) stated: “The oscillations in the different frequency bands are like the phonemes in a language. Superimposed oscillatory responses are the words. The selectively distributed parallel processing pathways are the syntax of the brain language. And the whole brain-work that follows the super-synergy is the sentences and the discourse in the language of the brain.” Thus, not only the Cartesian-like 3-dimensional location, but also the oscillatory language of the brain that is spoken across respective neuronal networks, provides an additional modular and/or holistic aspect in the 4th dimension of the characterization of different complex mental processes and related memory concepts (compare Basar 2004, 2011). In conclusion, for a *sufficient* analysis of brain activity, it is not enough to examine *WHERE* process-related activities can be found, it has also to be examined *HOW* these activated regions communicate with each other over time (e.g., Güntekin and Basar 2010).

A further critical point may also be the potential existence of further inter-individually different compositions of task-related oscillatory generators not detected by event-related oscillatory or fixed frequency range and averaged FFT (fast Fourier transform) group analyses. Possibly, temporal averaging procedures cancel task-related, say important, but inter-individually different oscillatory activities statistically out, as in the spatial domain averaging procedures analogously do by functional neuroimaging procedures. This would require the development of new non-linear methodological approaches on the basis of individual task-related oscillatory profiles. Fehr et al. (2003) and Achziger et al. (2009) successfully applied a multi-source density procedure on continuous individually band-pass filtered data to regionally discriminate different complex social cognitive processes. Individuals showed

Fig. 6 Neuroanatomic morphology of functional mental modularity—hypothetical assumptions



task-related generator activity in comparable regions, but in individually different combinations of frequency band ranges. Until respective task-related, but non-time-locked, methodological approaches are further developed appropriately, many questions addressing spatio-temporal dynamics of complex temporally nested compositions of mental sub-processes in complex cognition cannot sufficiently be answered. In the next section a general *hybrid* model of the neural organization of complex cognition in the human brain will be proposed.

A general hybrid model for the neural representation of complex mental processing

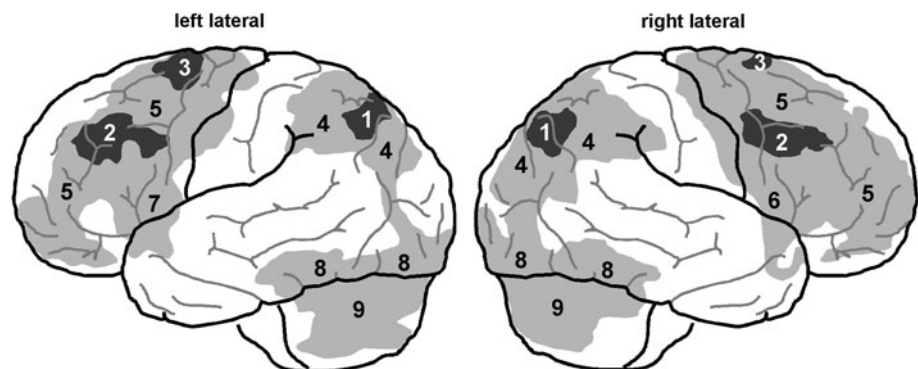
Dehaene (1992) proposed: “Number processing, in its fundamental form, seems intuitively linked to the ability to mentally manipulate sequences of words or symbols according to fixed trans-coding or calculation rules.” However, exactly this might analogously hold true for *different* forms of complex mental processing and can also be formulated in a more common way as follows: “Complex mental processes might generally be linked to the ability to mentally manipulate sequences of information (verbally, spatially, auditory, visually, symbolically, canonically, etc.) according to individually learned trans-coding rules and/or algorithms.” However, how might the necessary cognitive components for such processes be organized in the neural system?

Empirical data and theoretical approaches discussed in the present conceptual review might encourage to a certain extension of the memory-based cognit-model proposed by Fuster (2006). Assuming two further phyletic memory parts in middle and medial frontal (representing innate memories for rudimentary forms of information handling and manipulation, or say executive, skills) and in intra-parietal regions (representing innate memories for rudimentary forms of perceptual spatial and/or unspecific canonical processing skills as was discussed to represent a basis for, e.g., numerical processing) would potentially

provide a neuro-developmental basis for a general hybrid model for the neural organization of complex cognition. Such a model assumes, analogous to the model provided by Fuster (2006), that there are phyletic memories from the start of cognitive development, which will be differentiated during individual learning histories by recruiting and integrating more and more neural resources in hetero-modal association cortices and other regions of the brain (see Fig. 7 for an illustration of the model inferred from functional imaging data obtained during mental arithmetic processing). The here reported individual fMRI data support the proposed model assumptions, as inter-individual activation patterns show most consistent overlap in middle and medial frontal as well as in intra-parietal regions. This concept, describing a dynamically developing whole brain network, comprising both innate pre-determined neuro-developmental starting positions and inter-individually different and contextually shaped further recruitment of widely distributed neural resources, cannot be classified as either a *holistic* or a *massive modular* concept, but possibly as a *hybrid* of both.

Following references to digit labels are related to the illustration in Fig. 7. The proposed model, assumes that there are primary (labeled with the digits 1–3) and secondary (labeled with digits 4–9) regions, which might more or less consistently be involved inter- and intra-individually, according to, e.g., individual learning history, contextually or habitually applied strategy, developmental status, specific task requirements, and so on. The regions labeled with 1–3 might in its nature potentially be comparable to primary sensory or motor cortices, for which the accommodation of innate basic perceptual and/or executive memory units (phyletic memories) was proposed by Fuster (2006). A parietal located, modular organized center of non-verbal and/or spatially organized magnitude representation, innately present from the start of postnatal development (compare also Wynn 1992, 2000; Hauser et al. 1996; Nieder 2005; Nieder et al. 2006), might also contribute to a respective neuro-architectonical fundament of complex cognition. This fundament can be described as

Fig. 7 Proposal for a neuroanatomic model representing the 3-D localization of the neural architecture of complex mental arithmetic in neo-cortical and cerebellar regions. This model can potentially be generalized to different kinds of complex cognition. Labels 1–9 displayed in the figure are further explained in the text



a sort of primary number and/or spatial information processing cortex, from which the cortical organization of complex mental arithmetic processing, but also other complex spatial and/or canonical cognition, emerges, following the notions of dynamic brain development along the hetero-modal association cortices. This putative developing cortical representation might become, according to the notions of Fuster (2006), more and more abstract, and according to the notions of Basar (2005, 2006, 2011), more and more networked and inseparably organized (“whole brain work”), the larger the spatial distance to the primary region becomes. Thus, it seems that at least humans start with their neural architectural development of complex cognition at a massive modular stage, and further develop to a more and more abstract and holistic neural organization, recruiting more and more neural resources across hetero-modal association cortices.

Bilateral middle frontal regions, labeled with digit 2 (see Fig. 7) might represent an executive part of a primary fronto-parietal, visuo-spatial attention network, interacting with region 1 from the start of postnatal development. Furthermore, these lateral middle frontal regions might host a necessary component for mentally holding and manipulating all kinds of information (i.e., WM) in cooperation with parietal regions labeled as 1. That these fronto-lateral regions might innately be present in its functionality from the start of ontogenetic information processing development, at least in a rudimentary form, is corroborated by an interesting finding that neurons associated with WM performance could be located in homologous regions even in the brain of pigeons (Diekamp et al. 2002).

The superior medial frontal region, labeled with digit 3, might be related to supplementary motor functions, which may play a crucial role in the executive visuo-spatial processing triggered by executive task requirements (see Fehr et al. 2007 for the discussion about the involvement of motor system components and fronto-parietal visuo-spatial attention networks during mental arithmetic processing). The above mentioned “primary” middle frontal (2) and parietal (1) regions seem also to be involved in “completely different” complex mental processes, requiring visual encoding, visuo-spatial intelligence and WM (see also previous sections). Thus, complex mental arithmetic, but also other complex mental processes, might basically be coordinated and/or hosted by a visuo-spatial processing network in combination with motor processing networks.

Regions labeled as 4 and 5, adjacent to the rather regionally focused parietal (1), middle frontal (2) and superior/medial frontal (3) areas, might accommodate *individually* structured increments of the basic representations recruited during individual learning histories. Region 6 might be discussed to potentially represent a pendant to left hemispheric language processing regions or a

visuo-spatial form of the processing of verbal material as reflected by the activation of right hemispheric brain regions. Language processing, related to perisylvian regions, has been suggested to be involved in, e.g., mental calculation (see Dehaene 1992; Dehaene and Cohen 1995). The present model suggests region 7 (left inferior frontal) as optionally involved in mental arithmetic, depending on applied calculation strategies and/or other individual neural network properties.

Region 8 (inferior occipito-temporal) might be involved in inner representations and/or the identification of digits or numbers (see “triple code model”, Dehaene and Cohen 1995), or in a more common sense, individually learned object representation (e.g., Tyler et al. 2004 for a discussion about visual object representation in the brain). Cerebellar regions (labeled with digit 9) might, besides regions in the basal ganglia, which are not further discussed here, optionally be involved in, e.g., a motor network suggested to be related to mental arithmetic processing (e.g., Fehr et al. 2007), but also in other cognitive processes (for review see Justus and Ivry 2001).

Summary and final conclusions

The here proposed *general hybrid model for the neural representation of complex mental processing in the human brain* is based on both massive modular and holistic principles, and thus, it provides a hybrid of both. The degree of massive modular and holistic neural network organisation is supposed to be prominently related to developmental gradients of individual learning history.

Originally present massive modular parts of neural representations of complex mental processing, hosting a rudimentary and innate memory basis (phyletic memories) for further cognitive development, are still present during later development, but lose their importance in individual complex mental processing as more and more individually different strategic cognitive aspects, and therefore, individually different brain networks are involved. Therefore, most functional imaging studies on complex mental processes might only identify intersections of activated brain portions across individuals that potentially represent only the developmental origins of those regions, from which individually different process-related development initially emerged. The actual processing of the tasks might rather more validly be located in individually different adjacent and/or more widely distributed neural networks. Hence, so-called regions of interest analyses, which are often based on activation foci only obtained by respective group analyses, might provide an arbitrary basis of information, very unspecific to the complex mental process addressed, and might at best be related to group-related strategic

processing aspects (e.g., cognitive processing levels as spatial, visual, verbal, and others). This assumption is confirmed by studies considering individual differences in complex mental cognitive and emotional processing (e.g., Burbaud et al. 2000; Feredoes and Postle 2007; Regenbogen et al. 2010; Fehr et al. 2011, 2003; Achtziger et al. 2009; Miller et al. 2012; Thirion et al. 2007). If individuals in one examined sample apply rather different mental strategies in solving the same tasks, statistical power of group statistics can be expected to be reduced because of differences in mental strategy-related regional brain activation patterns across these individuals.

It is finally concluded that the corresponding functional imaging data in combination with theoretical assumptions derived from the respective literature, largely confirm the proposed view of a hybrid model, combining massive modular and holistic components in the neural architecture of complex mental processing. To further substantiate such a theory, however, nested studies, systematically varying partial features of complex mental processing are necessary. Both individual learning histories of examined study participants and the actually applied individual mental strategies must be considered as important covariates, and these factors should be modulated to prospectively examine their impact on cognitive brain dynamics. Experimental designs based on trial-related task processing should include analyses procedures sensitive for individual trial by trial variations in the temporal processing order of different related cognitive sub-elements, and therefore, of brain physiological correlates such as the respective process-related brain oscillations.

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