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Temporal ranges of central nervous processing: clinical evidence

Abstract The organization of the time frames for perceiving, generating, and updating information in the CNS has as of yet received little attention despite its elementary character for human behavior. We investigated temporal epochs in perceiving, acting, and updating in patients with anterior and posterior lesions of the left and right hemisphere, in patients with lesions in the left hemisphere without aphasia, and in healthy controls. Three temporal ranges, 30, 300, and 3000 ms, were assessed with different psychophysical paradigms. Prolongation of the temporal perception of order (30 ms) was most pronounced with left posterior lesions, of repetitive action (300 ms) with left anterior lesions, and updating (3000 ms) with left and right anterior lesions. Temporal deficits are group as well as parameter specific. Our results support the notion of coordinated coexistence of different temporal mechanisms.

Introduction

The time needed to perceive, to act, and to update information is a crucial variable for any organism. However, temporal aspects of behavioral processes are only now attracting interest in neuroscience (e.g., Ivry 1996b; Pastor and Artieda 1996; Gibbon et al. 1997; Tallal et al. 1998) and have had as yet little impact on neuropsychological investigations. A general framework for the various results is provided by a dichotomy of mental functions into those that provide the content of our subjective experience (the “what”) and those that are considered to be the formal or logistical basis of mental processing (the “how”) (von Steinbüchel and Pöppel 1993). Awareness of this distinction can lead to a better understanding of the importance of the temporal nature of the ‘how’-functions. Concerning the diagnosis and eventual therapy of deficits of higher brain functions, it appears that

the idea of the ‘what’ and ‘how’ has not been duly considered. Little attention has been paid to those specific temporal changes of mental functions occurring after brain injuries.

Despite numerous neurophysiological and neuropharmacological experiments – predominantly in animals (e.g., Goldman-Rakic 1987; Gray and Singer 1989; Meck 1997) – and a large body of research with healthy humans (e.g., Efron 1963a; Fraisse 1984; Ingvar 1985), contemporary theoretical foundations (e.g., Fuster 1995; Ivry 1996a; Miall 1996; Pöppel 1997) and the assessment of altered temporal processing in patients with cortical lesions (Harrington et al. 1998) have been underrepresented. In this context, especially the ranges below 0.1 and between 1 s and 10 s need more attention. Although imaging techniques represent an important tool in brain research, methodological problems with behaviorally relevant investigations of high temporal resolution still exist. Therefore, the classical psychophysical approach remains important, especially when backed up by modern EEG/MEG-investigations (e.g., Joliot et al. 1994). Some of these research deficits have been considered before, e.g., in connection with two main concepts of temporal perception: succession and duration (Fraisse 1984; Block 1990).

The study reported here presents an attempt to gain insight into the basic behavioral effects of neocortical damage on three important temporal ranges, namely 30, 300, and 3000 ms. The short range is mainly associated with the perception of succession, and the long one with duration. The 300-ms range is associated with the timing of voluntary and repetitive movements. Five groups of age-matched patients with circumscribed focal lesions have been collected from various medical institutions in Bavaria. These 50 patients were compared with 17 neurologically healthy controls in three well-established psychophysical tasks, one for each temporal range. The issue of this approach is to present a more homogeneous view of temporal processes and their impairments than is possible in separate studies involving different subjects with different cerebral lesions. Furthermore, this study

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focuses on the consequences of damage to the pre- and postcentral regions of each cortical hemisphere, which still appear to be underrepresented in the literature. The main reason for this multi-range approach is to test the hypothesis that coexistent temporal mechanisms are co-ordinated, and e.g., possibly hierarchically organized.

There is detailed work on temporal processing in the basal ganglia (Malapani et al. 1993; O'Boyle et al. 1996) and in the cerebellum (Ivry 1996a; Nichelli et al. 1996). However, the temporal interplay of these structures, as well as that with the cortex, is still obscure. The fundamental inquiry is whether to assume a central timing authority or to invoke many (specialized) timing agents, which are distributed over various brain structures and co-ordinated by a still unknown process. One of the few models of timing is based on the concept of elementary temporal building blocks, from which the temporal units at different levels or temporal ranges are constructed (Pöppel 1997), in other words, a hierarchy of timing devices.

The main part of this report deals with the experiments that were performed to differentiate between the three temporal ranges. All three of them are structured as follows: first, the main results for healthy persons and, then, prominent pathological findings are reported, both according to the literature. Second, our own experiments are presented, which focus on pathological deviations. I will conclude with a brief comparison of the results from the three main sections and their compatibility, judged according to common concepts of timing. The section following immediately describes the composition of our patient groups.

Subjects

Our investigation of pathological changes on different levels of temporal processing in the central nervous system was performed by comparing five groups of patients with different lesion types. The prime criterion for patient selection was the comparability of focal lesions in the neocortical hemispheres.

We selected 50 patients with pre- or postcentral lesions in the left or right hemisphere. Seventeen patients hospitalized for orthopaedic problems (age 49.5 ± 12.0 years) without cerebral damage served as controls. Demographic data were recorded. The patients were assigned to one of five groups, according to the locations of the lesions as determined by CT- or MRI-scans. Patients with left-hemispheric cortical lesions predominantly showed Broca aphasia (seven patients, group 'LH.pre', 57.0 ± 7.4 years old) and Wernicke aphasia (17 patients, 'LH.post', 55.5 ± 8.7 years old), classified according to the "Aachener Aphasia Test" (Huber et al. 1983). A group of non-aphasic patients with predominantly left-sided subcortical lesions (nine patients, 'L.noAph', 48.7 ± 14.7 years old) was included to differentiate between subcortical and cortical temporal processing within the left hemisphere. In an attempt to outline the role of language-specific cortical areas, patients with right-

hemispheric lesions in areas corresponding to Broca's area (nine patients 'RH.pre', 48.2 ± 12.6 years old) and to Wernicke's area (eight patients, 'RH.post', 54.0 ± 8.4 years old) were also included. Due to logistical (concerning all experiments) or task-dependent problems (especially in the tapping tasks and tone reversals), not all patients participated in all experiments or trials.

Inclusion criteria were: (1) unilateral pathology as a consequence of ischemic infarction ($n=47$), insidious or massive haemorrhage ($n=3$), (2) right-handedness, (3) normal hearing according to audiometric testing, (4) age between 20 and 70 years, and non-verbal IQ greater than 85 (standard progressive matrices: Raven 1947). Exclusion criteria were: (1) infarction more recent than three months or older than four years, (2) repeated infarctions, (3) medication known to affect the speed of neural processing, and (4) memory problems or neurological disorders prior to the infarction.

Patients and controls were recruited from centers and hospitals affiliated with our university. Informed consent was obtained from all participants. Subjects were examined in 14 sessions – twice a week – of 1 h each.

Temporal range of event identification (30 ms)

Non-clinical research

The time epoch of 30 ms has been long known to play a major role in information processing. Neurophysiological, psychophysical, and neuropsychological investigations have demonstrated this time frame. Mach (1865) introduced the concept of a minimal interval of 30 ms, in 1864 von Baer presented the concept of the "perceivable moment" as the briefest sensible time frame for different species. On the basis of earlier experimental work, Hirsh (1959) and Fraisse (1963) presented a theoretical framework for temporal processing. Concurrently, a number of experimental investigations concerning simultaneity and sequentiality in perception resulted in basic insights into this temporal structure. Exponents of this research period were Hirsh and Sherrick (1961) and Efron (1963a,b), who found time intervals in this temporal range to be necessary to distinguish successive stimuli in their temporal order (see below) – widely independent of the sensory modality. Data from reaction-time experiments indicate a time grid with intervals of about 30 ms, within which a reaction is restricted to happen (Pöppel 1968, 1970). On the neurophysiological level, by investigation of invasively or noninvasively recorded mass potentials in various sensory modalities and brain regions, many researchers (e.g., Freeman 1975; Galambos et al. 1981; Eckhorn et al. 1988; Gray et al. 1989; Basar-Eroglu et al. 1996) found evidence for predominant activity in the γ -band with periods of approximately 30 ms. Whether these phenomena of similar periods actually result from the same neural mechanisms or serve the same purpose is as yet unknown. In more recent studies, brain activity around 40 Hz – measured with MEG-techniques – was

correlated with auditory perception around the temporal fusion limit (e.g., Pantev et al. 1991; Ribary et al. 1991; Joliot et al. 1994), and a characteristic neural signature for the perception of simultaneity and succession was found. The perception of succession of two events does not imply the recognition of their order. On a cognitive level, the temporal range of order discrimination also appears to be associated with speech reception and especially concerns the left-hemispheric analysis of rapid transitions of short speech-related events, such as changes between stop consonants and vowels (Studdert-Kennedy and Shankweiler 1970; Divenyi and Efron 1979; Schwartz and Tallal 1980). Astoundingly, behavioral experiments with animals (baboons) support the notion that this analysis of rapidly succeeding, speech-related events is lateralized to the left hemisphere (Pohl 1984).

Our own results were obtained with another experimental paradigm of auditory order thresholds. Therefore, this technique and the main results for healthy persons are described: If two consecutive clicks – or other very brief acoustic stimuli – are presented, one to each ear, one perceives a single auditory event for time intervals shorter than about 3 ms (auditory fusion). Two events are perceived for intervals between 3 and about 30 ms (Mills and Rollman 1980). For intervals longer than approximately 30 ms, one is able to indicate the ear to which the first click has been presented – the temporal order of the clicks. The so-called auditory order threshold (AOT) is the statistically determined click interval for which 75% of the sequences of the two clicks are correctly identified by the subjects. For children about 6 years old, the typical AOT is 170 ms (von Steinbüchel et al. submitted), and, for children about 8 years old, it is typically 109 ms (von Steinbüchel et al. 1998). Young adults (up to 25 years) show AOTs of 20–40 ms (Hirsh and Sherrick 1961; von Steinbüchel 1985; Lotze et al. 1998); older adults have AOTs around 60 ms (von Steinbüchel et al. 1996b).

Clinical research

Since the discovery of altered temporal auditory and visual fusion in patients with left hemispheric brain injuries (Battersby 1951; Lackner and Teuber 1973), the localization of lesions affecting such rapid processing was investigated. Efron (1963c) and Swisher and Hirsh (1972) found increased auditory and visual order thresholds (OT), especially for patients with lesions in cortical regions responsible for speech functions.

On the basis of investigations of patients with lesions in different cortical areas, Efron (1963c) associated general temporal processing with language function in the left hemisphere. Especially lesions in the superior temporal region that lead to fluent aphasia showed a major effect (Swisher and Hirsh 1972). This association has been supported by results from investigations of patients with aphasia who are impaired in the differentiation of certain stop-consonant/vowel transitions (Tallal and Newcombe 1978). Developmental dysphasics (Tallal and Pier-

cy 1973; Tallal and Stark 1981), as well as reading- and writing-impaired children (Tallal 1980; Reed 1989), also show degraded determination of the order of rapidly changing verbal or nonverbal acoustic stimuli. In their review, Farmer and Klein (1995) support Tallal's (1984) hypothesis that phonemic deficits, noted in many developmental dyslexics, can be viewed as symptom of a more general auditory deficit in rapid processing. For instance, significantly elevated AOTs have been observed in about one third of developmental dyslexics (von Steinbüchel et al. 1998). Based on the findings of Joliot et al. (1994), Llinás et al. (1997) performed an MEG-study on dyslexics and found the auditory temporal-fusion threshold to be shifted to greater time intervals; the temporal order threshold has not yet been investigated with these methods. We therefore decided to assess possible specific impairments on this psychologically elementary temporal level in our patient groups by determining auditory order thresholds. This method has been used and elaborated in our laboratory for many years, and it is generally accepted as an efficient and sensitive tool for the detection of low-level temporal-processing deficits. It should be pointed out that the determination of any sensory threshold generally implies the ability of subjects to distinguish between at least two stimulus qualities. However, for certain tasks, subjects can report on the perceived quality of each of these stimuli. One such task is the differentiation between two distinct auditory stimuli and the perception of their order. Therefore, we measured possible processing deficits both below as well as above the order threshold.

Methods and data evaluation

Auditory order thresholds (AOT) were determined with pairs of clicks (impulses of 1-ms duration) presented binaurally by headphones at a comfortable volume. A stimulus consisted of two consecutive and equally loud clicks – one for each ear – separated by an inter-stimulus interval (ISI) from the range of 10 to 200 ms. The stimuli were presented in randomized left-/right-ear order. After every stimulus pair (pair of clicks), the subject had to point to the ear where the first click was heard (forced choice). If the clicks were perceived as simultaneous, the subjects pointed to their forehead. On request, a stimulus was repeated up to three times before the final response. To minimize the data-acquisition time, a computerized adaptive procedure based on the maximum likelihood method, as described by Treutwein (1997), was used (Mates et al. 1998). A session ended when a certain stochastic criterion was reached (given the correct slope, guessing and lapsing rate were specified a priori; this corresponds to a 75% confidence with ± 10 ms steps around the threshold). Most subjects completed three sessions. The data were split with respect to the correctly recognised order of ear stimulation (first click to the left ear: 'L'; first click to the right ear: 'R') Clicks perceived as simultaneous were excluded as errors.

Binaural presentation was chosen for the identification of the two clicks because monaural presentation would necessitate different acoustic properties (e.g., tonality or intensity) for the two clicks. Consequently, they would be distinguished by cues other than or in addition to their temporal occurrence. However, with binaural presentation and quasi-dichotic stimuli (very short ISIs), the Kimura effect must be considered (Divenyi and Efron 1979). Kimura (1961) found, for the dichotic presentation of different short words, that those presented to the right ear were reproduced

Table 1 Number of subjects and sessions for the auditory order-threshold (AOT) experiments, *LH.pre* left-hemispheric cortical lesions showing Broca aphasia, *LH.post* left-hemispheric cortical lesions showing Wernicke aphasia, *L.noAph* non-aphasic left-sided

AOT	Healthy	LH.pre	LH.post	L.noAph	RH.pre	RH.post	Σ
Subjects	17	7	14	9	9	6	62
Sessions	47	20	37	26	25	16	171

correctly more often, particularly by patients with lesions in the left temporal lobe.

Due to logistic or task-dependent problems, not all patients could participate either in the experiment or in all of the three sessions. Analysis was based on data from the number of subjects and sessions listed in Table 1. (Less than 1.2% of the data were recognized as outliers.)

The mean AOTs and the corresponding standard deviations for all groups were computed separately for the conditions 'L' and 'R'. The differences of the group means were assessed – following one-way ANOVA – by multiple comparisons (P_{mc}) according to Scheffé. Additional paired t -tests (P_t) were performed to judge the within-group differences for the conditions 'L' and 'R'.

Results

According to their age, our healthy controls show the expected mean AOTs of about 60 ms. Under condition 'L' (grey bars), the 'LH.post'-group revealed a significantly elevated ($P_{mc} < 10^{-4}$) mean AOT in comparison to the groups 'Healthy', 'L.noAph', and 'RH.post' (Fig. 1). It must be emphasized that the group of patients with postcentral lesions in the left hemisphere – who show receptive language disorders – was the only one whose mean AOT differed significantly from that of the normal controls. Under condition 'R' (black bars), the mean AOT of the 'RH.post'-group is significantly below ($P_{mc} < 10^{-4}$) that of the groups 'LH.post' and 'RH.pre'. The apparent differences between the mean AOTs of the 'Healthy'- and the 'RH.post'-group were not significant at the 5% level. The differences between AOTs measured under the conditions 'L' and 'R' were not significant at an acceptable level, except for the 'LH.post'-group ($P_t < 10^{-4}$). Our results are compiled in Fig. 1.

Discussion

Auditory perception implies the functioning of the dedicated sensory, i.e., postcentral areas. Furthermore, analyses of rapid changes and succession is suspected to take place predominantly in the left cortical hemisphere (e.g., Efron 1963c; Hammond 1982; Nicholls 1996). Consequently, elevated AOTs for aphasic patients with lesions in the left hemisphere (von Steinbüchel 1985) and especially for patients with postcentral lesions were expected. Indeed, for our 'LH.post'-patients, on average doubled AOTs were found if the first click was presented to the left ear and a significantly less-pronounced elevation for the opposite order of presentation. This ear-disparity has been observed before for fusion thresholds (Lackner and Teu-

subcortical lesions, *RH.pre* right-hemispheric lesions in areas corresponding to Broca's area, *RH.post* right-hemispheric lesions in areas corresponding to Wernicke's area

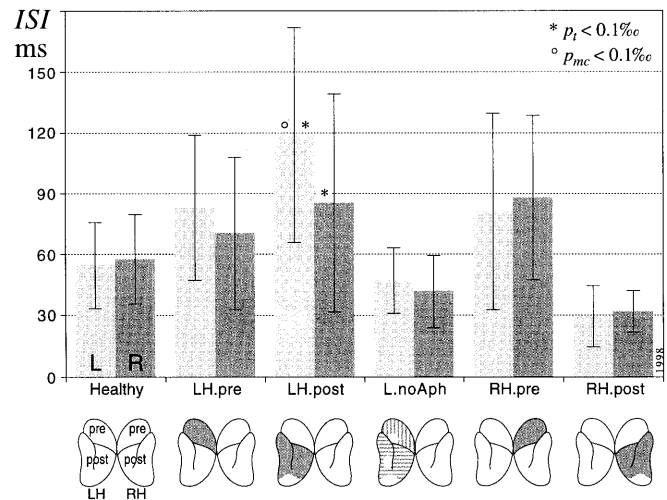


Fig. 1 Means and standard deviations of auditory order thresholds. ° Significances of multiple comparisons (P_{mc}) of all patient groups in comparison to the healthy controls, * significance of paired t -tests (P_t) for the conditions first click to the left ear (L, grey bars) or to the right ear (R, black bars). *ISI* inter-response intervals, *LH.pre* left-hemispheric cortical lesions showing Broca aphasia, *LH.post* left-hemispheric cortical lesions showing Wernicke aphasia, *L.noAph* non-aphasic left-sided subcortical lesions, *RH.pre* right-hemispheric lesions in areas corresponding to Broca's area, *RH.post* right-hemispheric lesions in areas corresponding to Wernicke's area (see shading in schematic brain diagrams)

ber 1973), and we tend to recognize it as the same as described by Kimura (1961). Based on her generally accepted view that (quasi) dichotic stimulation suppresses the ipsilateral auditory pathways, our main findings are summarized and explained in the following way. Considering the three auditory pathways (ipsilateral, contralateral, and callosal) to the left cortical hemisphere, we regard the callosal input as dominantly responsible for the task-specific deficits of our 'LH.post'-patients. Due to the widely suppressed ipsilateral pathway, signals from the left ear enter the post-central areas of the left hemisphere primarily via the callosum. This detour implies a neural shortening of the stimulus ISI for condition 'L' and its extension for condition 'R'. Consequently, the mean AOT is more elevated under the former than under the latter condition, which is evident from our data. This effect was not observed in our healthy controls; hence, it must be ascribed to the cortical lesions. The apparently low AOT of our 'RH.post'-group indicates that both the ipsilateral and the contralateral inputs to the left hemisphere – the (specialist) pathways for rapid auditory timing – are intact. This conclusion is based on the reasonable assumption that the

damaged right hemisphere prevents the suppression of the left ipsilateral pathway. The low AOTs observed for our patients with defects in the left brain, who show no aphasia ('L.noAph'), imply that they also use the ipsilateral pathway. However, the difference, in comparison to our normal controls, is not significant at all; hence this group can also be judged normal. Most important appears the significant AOT-difference in the 'LH.post'-patients (with Wernicke aphasia), implying a relation between fine temporal resolution and speech reception, which has been demonstrated by fusion-threshold data (Lackner and Teuber 1973). Finally, we ascribe the slightly, but not significantly elevated AOTs for our patients with precentral lesions to impairments of supra-ordinate temporal processes that supposedly take place in the prefrontal cortex (Fuster 1995). In this context, it should be mentioned that our data confirm findings of Swisher and Hirsh (1972), who reported that especially patients with nonfluent aphasia performed better in the perception of temporal order than patients with fluent aphasia.

These and related diagnostic findings point to an association between general temporal sequencing and certain language deficits, such as aphasia and developmental language-learning impairments. They suggest some nonverbal learning of fine temporal resolution. Yet, it took more than three decades for the first attempt to train patients with aphasia with nonverbal auditory feedback to improve their impaired identification of auditory temporal order (von Steinbüchel et al. 1985). By training, the elevated temporal-order threshold of aphasic patients was lowered to the range typical for healthy subjects, and speech reception was significantly improved. The discrimination of crucial stop-consonant/vowel syllables, such as /da/ and /ta/, which mainly differ in the transition time between the plosive and the vowel, was significantly improved in aphasic patients (von Steinbüchel 1987, 1995). It is known (Miller and Baer 1983) that the discrimination of such syllables is based on the onset of the voiced part, which is an acoustically well-defined feature, and that this analysis is crucially dependent upon structures located in the posterior parts of the left hemisphere (Philips et al. 1994). The notion of the trainability of impaired temporal processes, as applied to patients with aphasia, has been adopted for the treatment of children suffering from language-learning impairments. Such temporal training combined with linguistic training improved the ability to correctly recognize brief and fast sequences of speech and non-speech stimuli and enhanced speech production (Merzenich et al. 1996; Tallal et al. 1996, 1998).

Temporal range of repetitive movements (300–500 ms)

Non-clinical research

It is a well-accepted fact that movements are governed by interacting processes at various levels. Some of these elementary processes are quite regular or rhythmic, can

be characterized by their periods and are attributed to so-called central pattern generators (Ponder and Kennedy 1928; von Holst 1937; Cohen et al. 1988) or interval pacemakers (Treisman and Gormican 1988). Although it seems unrealistic to experimentally succeed in the isolated investigation of these processes, especially in complex organisms, there are some tasks that reveal specific motor rhythms, which can be accessed noninvasively. Although such rhythms cannot in general be attributed to a single generator, their behavioral importance, inter-individual presence as well as dominance (Frischeisen-Köhler 1933), and intra-individual constancy (Fraisse 1982) justifies their investigation. The free-running or the maximum-speed production of simple repetitive actions, such as finger tapping or hand and elbow movements, are such tasks. The maximum speed at which they can be performed appears to be similar (Keele 1986; Kunesch et al. 1989) and lies in a range of around 200 ms (Keele and Hawkins 1982; McManus et al. 1986; Shimoyama et al. 1990). Personally preferred tempi of such repetitive movements – which do not result from absolute mechanical or neural limits – show typical mean periods below 500 ms (Keele et al. 1985b; Kunesch et al. 1989; von Steinbüchel et al. 1992). Experimental evidence (e.g., Wyke 1967; Kimura and Archibald 1974) indicates that – independent of the hand – the left cortical hemisphere is mainly involved in the programming of hand and finger movements. This lateralization of neural processes that underlie various kinds of fine movements implies the general superiority of the left hemisphere for the serial processing also in the temporal range considered in this section and again especially for verbal and textual skills (Tzeng and Yang 1984). Interference between language and motor functions was observed by Keefe (1985) and Lewis and Christiansen (1989). Imaging studies show a possible association between the language domain and the motor domain, since the SMA (supplementary motor area) is activated during tapping movements at a pace corresponding to voluntary tapping with a frequency of 2 Hz (Boecker et al. 1994) and also during language tasks (Binder et al. 1997).

Our own investigations used finger tapping techniques, as described below:

1. To determine the personal tapping tempo, subjects were asked to tap on a button – usually with one of their index fingers – at a comfortable self-paced tempo. The intervals between consecutive taps are the so-called inter-tap or inter-response intervals (ITIs or IRIs). In general, the mean IRIs of a moderately long sequence (typically 100 taps or a duration shorter than 30 s) are relatively invariant for each subject, but show pronounced inter-individual variability. In general, IRIs for both hands range from 380 to 880 ms (Fraisse 1982). For right-handed adults of up to 40 years old, Collyer et al. (1994) reported two peaks in the frequency distribution of IRIs, one at 272 ms and the other at 450 ms. Our own investigations with subjects aged between 18 and 65 years old revealed median

Table 2 Number of subjects and trials for both tapping experiments. *pers.tap.* Tapping at a personally comfortable tempo, *max.tap.* maximum tapping tempo, all other abbreviations as in Table 1

	Healthy	LH.pre	LH.post	L.noAph	RH.pre	RH.post	Σ
pers.tap. subjects	14	6	14	7	7	4	52
pers.tap. trials	L:28/R:28	L:10	L:24	L:16	R:11	R:7	96
max.tap. subjects	16	6	16	9	8	7	62
max.tap. trials	L:80/R:80	L:30	L:80	L:42	R:40	R:35	305

IRIs of 522.5 ms (left hand) and 498.5 ms (right hand) (von Steinbüchel 1992). Those of students aged between 20 and 30 years old revealed mean IRIs of 465 ms (left hand) and 463 ms (right hand) (Scienza 1997).

- To determine the maximum tapping tempo, subjects were asked to tap as fast as possible. In general, the mean IRIs taken over several moderately long sequences (each of typically 50 taps or a duration of about 10 s) do not considerably differ among healthy subjects. McManus et al. (1986) found IRIs around 220 ms (left hand) and 180 ms (right hand) among a small number of young right handers. For more than 100 subjects aged 13–78 years old, Shimoyama et al. (1990) reported mean IRIs of 192.3 ms (left hand) and 178.6 ms (right hand). Our own investigations with subjects aged between 18 and 65 years old revealed mean IRIs of 200.8 ms (left hand) and 165.8 ms (right hand) (von Steinbüchel 1992). Those of students aged between 20 and 30 years old showed mean IRIs of 181 ms (left hand) and 165 ms (right hand) (Scienza 1997).

Clinical research

The timing aspects associated with the well-known motor impairments caused by damage to the basal ganglia (e.g., Nakamura et al. 1978; Benecke et al. 1987; Pastor et al. 1992) and the cerebellum (e.g., Marsden et al. 1977; Ivry and Keele 1989) are well described. There is now an increasing interest in cortical deficits in motor timing. Harrington and Haaland (1991) and Haaland and Harrington (1994) observed disturbed motor sequencing in patients with lesions in the left hemisphere, which they attributed to deficits in motor programming. When comparing the reproduction of complex hand movements as well as the formation of certain hand or finger configurations by patients with either left or right hemispheric lesions, the left-hemispheric – all patients with aphasia – appeared impaired (Kimura and Archibald 1974). Patients with callosal disconnection syndrome can reproduce fast repetitive patterns (period ≈ 0.2 s, i.e., about maximum tapping tempo) with both hands, but are impaired in reproducing slower patterns (period ≈ 1 s) with their left hand (Kashiwagi et al. 1989). This finding implies that the left hemisphere is important for the timing of certain voluntarily controlled repetitive movements.

To assess possible impairments on this temporal level in our patient groups, we first asked the patients to tap at their preferred rate and later to tap as fast as possible.

Personal finger tapping has been chosen because of the surprising constancy of the preferred tempi when produced by healthy subjects and because this task is so simple and easy for patients. Maximum tapping can be regarded as a reference experiment. For many years, various tapping paradigms have been used and refined in our laboratory, and they are generally accepted as a reliable tool for the detection of deficits of repetitive fine movements.

Methods and data evaluation

The subjects were instructed to tap regularly with their index fingers on an electronic precision button. The first task always was to tap at a personally comfortable tempo (personal or self-paced tapping tempo). The second was to tap as fast as possible (maximum tapping tempo). Data acquisition and evaluation of the inter-response intervals were computer assisted. For both tasks, patient data are presented that were obtained exclusively from experiments with the index fingers ipsilateral to the damaged brain sides. Data from the neurologically healthy controls were obtained from tapping with the left as well as the right index finger. For the first task, most subjects completed two succeeding trials, each with 99 recorded IRIs. For the second task, most subjects participated in five trials, for which the number of taps during 10 s was recorded. Then the average tapping interval was determined as 10 s divided by the number of taps.

Due to logistic or task-dependent problems, not all of our patients participated in the tapping experiments or in all of the sessions. Analysis was based on data from the numbers of subjects and sessions listed in Table 2. Except for the 'L.noAph'-group (4.4%), less than 2.3% of the IRIs – mostly due to key-slips or pauses – were recognized as outliers of the personal tapping results. Owing to the different data acquisition used for the second task, outliers were not detected.

For the results from personal tapping, the mean inter-response interval and the standard deviation were determined separately for each subject, which resulted in 38 samples for the ipsilateral hands of the patients and 2×14 samples for both hands of the healthy controls. Most of the corresponding sample histograms (bin width 20 ms) are approximately unimodal as well as symmetric. (Half of the data samples show a modulus of the skewness well below 0.25, and only 15% exceed the value of 0.5. The modulus of the difference between mean and median is below 1% for about 80% and exceeds 2% only for about 3% of the samples.) However, due to the considerable variance of the individual interval distributions – especially of their means – within every group, the group results were not compared on the basis of point estimates of their combined samples, but on the percentages of subjects whose mean IRIs fall into one of four temporal categories (see Fig. 2). For the results from maximum tapping, the mean tapping intervals and the corresponding standard deviations for all trials and subjects were computed for every group. Then, the means of the groups whose members had tapped with the same hand separately were compared – after a one-way ANOVA – by multiple comparisons (P_{mc}) according to Scheffé.

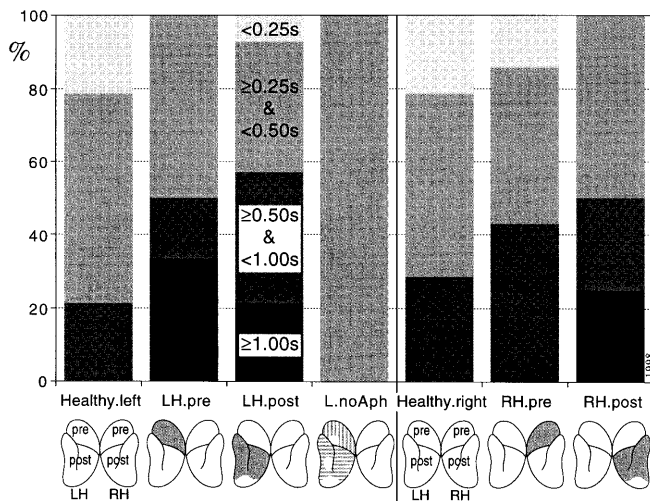


Fig. 2 Percentages of subjects whose mean inter-response intervals during personal tapping fall into one of the four specified temporal ranges. Tapping was performed with the index fingers ipsilateral to the side of the lesion. Abbreviations as in Fig. 1

Results

The IRI-histogram (bin width 10 ms) for our 'Healthy both'-group (data from both hands merged) shows three peaks with centers at 200, 300, and 370 ms. The IRI-histograms of the data from sessions performed with the left or right hand look roughly alike. About half of the healthy-subjects' performance differed significantly ($P_t < 10^{-4}$) between their left and right hands, and only 14% showed significances at levels $P_t > 0.1$, according to a paired t -test. A quarter of our healthy normals produced mean IRIs above 500 ms. A careful comparison of the IRI-histograms of our six groups of subjects led to the categorization of the individual mean IRIs in four time ranges, as indicated in Fig. 2. A pronounced increase of the percentage of patients with mean IRIs above 500 ms was observed for the groups with left-hemispheric cortical lesions. For both groups with right-hemispheric cortical lesions, this increase was less salient, which was partly due to the greater percentage of healthy subjects in this category. From our four groups with cortical lesions, the 'RH.pre'-group behaved most closely to normal. The 'L.noAph'-group was unique in showing an IRI-histogram that was roughly unimodal and symmetric with the mean at 293 ± 38.5 ms. The notably higher number of outliers is exclusively due to sporadic key-sticks, which appear typical for this group. The IRI-histograms for the remaining groups are all multi-modal, but highly dissimilar.

The results from the maximum-speed tapping task – revealing surprisingly similar mean tapping intervals – are compiled in the following Table 3.

Differences were significant neither among the groups of subjects who have tapped with their left hands ($P_{mc} < 0.995$) nor among the groups of subjects who tapped with their right hands ($P_{mc} < 0.6$). The difference between the mean intervals produced by the healthy subjects with their right and left hands is significant ($P_t < 0.006$), according to a paired t -test.

Discussion

Our findings suggest that voluntary tapping performance is mainly affected by left hemispheric lesions, whereas maximum tapping was not significantly affected by the defects in our patients. This result is known (Kashiwagi et al. 1989) and not that surprising, since voluntary actions per definition are aware and, therefore, associated with cortical processes. Inspired by various considerations (e.g., Kornhuber 1971), we assume that, compared with maximum tapping where whole sequences of essentially ballistic taps are controlled by cerebellar-cortical loops, in personal tapping the timing of every single tap is under cortical command or under the control of cortical and basal structures. The timing of the repetitive movement in maximum tapping most probably is controlled by the cerebellum (Brooks 1984), which, in turn, is assumed to be coarsely supervised by cortical circuits (initiation and veto, e.g., Ivry 1996b). Furthermore, the maximum tapping speed is thought to be near the mechanical and neural limits and can merely be increased by training, which might explain the shorter intervals produced with the right hands. However, the hypothesis of a strict functional and anatomical dissociation of the neural substrate underlying the execution of these two tasks must be modified. For instance, in sensorimotor synchronization tasks where finger taps must be synchronized with periodic auditory stimuli, patients with cerebellar lesions (Ivry et al. 1988) and patients with Parkinson's disease (Freeman et al. 1993; O'Boyle et al. 1996) perform with higher variability.

The effect of left hemispheric lesions on the personal tapping tempo conforms well with results from previous research. This hemisphere appears specialized for the production and control of sequential events. While defects in precentral areas of the left hemisphere – with their direct access to motor functions – can easily be imagined to influence the personal tapping performance, the role of the postcentral structures of both hemispheres

Table 3 Mean tapping intervals and standard deviations from maximum tapping (*Max.Tap.*). L Left, R right, other abbreviations as in Table 1

<i>Max. Tap.</i>	Healthy.L	LH.pre	LH.post	L.noAph	Healthy.R	RH.pre	RH.post
Mean [ms]	208	212	208	209	189	189	200
Standard deviation	8.0	13.0	8.0	10.6	5.9	8.4	8.9

is less obvious. We suggest that they are involved in the acoustic as well as proprioceptive feedback during tapping. Damage to these structures is assumed to lead to discrepancies in the timing of action and the sensory feedback, to which the brain reacts with slowed action.

The astoundingly uniform behavior of the patients in the 'L.noAph'-group gives rise to many speculations. Further experiments and more detailed lesion analyses are needed for sound interpretations of these results. However, this extraordinary group result indicates that the changes in the other left-hemispheric groups are of cortical origin.

Our healthy subjects produced results that did not widely deviate from those described in the literature. However, a numerical difference of the position of the maxima in the IRI-histogram that have been found by Collyer et al. (1994) is evident. Furthermore, a local maximum at 200 ms was reached by some of our subjects, who definitely regarded this maximum as their comfortable personal tapping tempo.

Temporal range of gestalt formation (3 s)

Non-clinical research

For logical reasons, any successful behavior in complex environments requires – for analysis and planning – parallel, i.e., atemporal access to neurally salient, but not necessarily aware events and brain states. For economical reasons, these simultaneously available events must be limited to a behaviorally relevant time interval. In other words, the brain analyzes the syntax and deduces the basic semantics inherent to these events within a shifting time window, whose extent is expected to be optimized with respect to cost and benefit (Glünder 1993; Schill and Zetsche 1995). Association appears to be an important and universal process, which acts on these chunks of selected events. Events that occur during such an interval and that are made simultaneously available, selectively activate neural assemblies, which essentially consist of previously learned synaptic interconnections (Hebb 1949; Braitenberg 1978). Active assemblies must be reset after an appropriate time, which is probably the same duration as the aforementioned temporal window. We propose active resets instead of satiation or neural fatigue (Köhler 1940; Hochberg 1950). Most of the supra-ordinate temporal functions that appear necessary for managing such processes are thought to be located in the prefrontal cortex (Fuster 1995). The introduced temporal intervals can be recognized as forming an aware temporal unit, a moment in the literal sense, the psychological present, or *nowness*. Of course, the psychological and philosophical consequences of these elementary requirements have long been discussed. James (1890) and Stern (1897) predicted the length of the interval to be only a few seconds. Other early estimates were made by Vierordt (1868) and Woodrow (1935), who found that intervals of up to

about 3 s are generally overestimated, and, above this so-called indifference interval of typically 3 s, they are underestimated. According to extensive investigations by Fraise (1963), the psychological present has no fixed duration, but typically lasts 2–3 s and hardly exceeds 5 s (Fraise 1978, 1984). Basic research on the perception of time intervals performed by Bechinger et al. in 1968 determined – out of a spectrum of intervals from 50 ms to 10 s – the optimum interval to be 2 s.

Numerous investigations dealing with the temporal range from about 1–10 s can be split into holistic behavioral and detailed analytic studies. The former deal, among others, with the duration of elementary movement stereotypes and their inter-cultural constancy (Schleidt and Kien 1997) and with phrases and pauses in normal speech (Kowal et al. 1975), in rhymes (Turner and Pöppel 1988), and in music (Pöppel 1988; Epstein 1989). The latter comprise various forms of time estimation and their influence on the perception of duration (Vierordt 1868; Woodrow 1935; Pöppel 1971; Aschoff 1984; Block 1989; Zakay 1993), of sensorimotor synchronization (Mates et al. 1994), of temporal patterning (Woodrow 1909; Kastenholz 1922; Szelag et al. 1996), of perceptual reversals (Borsellino et al. 1972; Holt and Matson 1976; Gómez et al. 1995), and also of either short-term, working, or procedural memory and time in animals (Jacobson 1935; Goldman-Rakic 1987; Olton 1989) and humans (Lashley 1951; Peterson and Peterson 1959; Sternberg 1966; Baddley et al. 1975; Fraise 1985). Unfortunately, some approaches in this field do not sufficiently differentiate memory effects, such as the remembered number or kind of salient events, from the results of short-term analyses, such as associations, judgments, and decisions, which are often simply called temporal grouping effects. Despite many investigations with widely different methods, converging evidence for significant changes in perception and behavior have been observed that occur at time intervals or durations of about 3 s. Additional evidence for a rather regular modulation of neocortical activity in the 3-s range that can be associated with processes, such as the reset of assemblies, comes from neuropsychological investigations, especially of the auditory system (Elbert et al. 1991; Sams et al. 1993).

Our own investigations were carried out with perceptual reversals of ambiguous figures, optic as well as acoustic. The technique and the main results for healthy subjects are described below: If one is principally able to perceive the different aspects of ambiguous stimuli, then, at least after some minutes of initial observation, one generally reports regular perceptual reversals. Although many suitable ambiguous figures are known – optic as well as acoustic – most of the investigations known to us are based on the Necker cube (Necker 1832). Borsellino et al. (1972) confirm the finding of Washburn et al. (1931) concerning the existence of slow and fast subjects. The former produce irregular reversal intervals with modes of up to 8 s; the latter produce regular intervals with modes of about 2.5 s. Holt and Matson (1976)

Table 4. Number of subjects participating in the perceptual reversal experiments. Abbreviations as in Table 1

Subjects	Healthy	LH.pre	LH.post	L.noAph	RH.pre	RH.post	Σ
Necker	13	4	14	8	8	8	55
Rubin	14	6	15	9	8	8	60
Syllables	11	2	6	5	6	5	35
Tones	7	0	3	5	5	5	25

report an age effect: middle-aged people are fastest with a mean interval of around 1.5 s; subjects aged 55–65 years old report mean intervals of about 3 s. Depending on how their student subjects were instructed, Gómez et al. (1995) obtained different reversal intervals. With the instruction to maintain each percept as long as possible, the mean interval was 2.9 s and without, 1.7 s. Scotto and Oliva (1990) measured intervals from 2 to 8 s for student subjects and noticed influences of the viewing conditions, especially of eye movements. Results from our own laboratory conform well with most of the findings cited above (Pöppel 1987; Radilowa and Pöppel 1990). For neurologically healthy subjects (age 41.4 \pm 15.0), the following mean reversal intervals were found for two optic and two acoustic figures: Necker cube: 3.0 s, Rubin vase: 2.4 s, syllables ‘so-ma/ma-so’ 3.2 s, and two tones ‘high-low/low-high’ 5.0 s (von Steinbüchel et al. 1993, 1996b).

Clinical research

As one might expect, processing in the temporal range from one to a few seconds, with its immediate behavioral aspects, is disturbed by brain damage outside the neocortex, especially in the basal ganglia (Pastor et al. 1992) and the cerebellum (Nichelli et al. 1996; Malapani et al. 1997). Only few studies deal with impairments due to neocortical defects. Their influence on the comparison or reproduction of time intervals has mostly been determined in temporal ranges below 1 s (Ivry and Keele 1989; Harrington et al. 1998) or beyond 8 s (Petrovici and Schneider 1994; Shaw and Aggleton 1994; Damasceno 1996). Damasceno (1996), as well as Harrington et al. (1998), found lesions in the right cortical hemisphere to cause pronounced overestimation of time intervals. However, Nichelli et al. (1995) reported underestimation in patients with frontal lobe lesions in the same time ranges, without considering the time range in-between. For Alzheimer patients, Nichelli et al. (1993) reported prolonged reproduction with increased variance of optically and acoustically defined intervals of 1 s.

Some authors observed that patients with cortical lesions – especially in the frontal lobe – have severe difficulties in shifting from one aspect to another during perceptual reversal tasks (Cohen 1959; Teuber 1964; Ricci and Blundo 1990). Unfortunately, quantitative results from longer trials under established conditions are scarce. No significant lateralization was found by Ricci and Blundo, but Meenan and Miller (1994) reported a signif-

icant slowing of the reversals for patients with lesions in the right frontal lobe, which was exclusively due to the more than two-fold prolongation of the interval during which the second aspect was perceived. Pöppel et al. (1978) investigated a patient with bilateral occipital infarction, who showed reversal intervals of more than 10 s for the Necker cube.

To investigate changes in cortical processing at the time interval of about 3 s and to minimize the aforementioned confusion with memory effects, we decided to assess possible impairments through the analysis of reversal times reported during the perception of ambiguous figures. Reasonable caveats remain, such as the interference with attention (Horlitz and O’Leary 1993), the inability of certain patients to see reversals at all, and the impossibility to determine fast and slow subjects by their impairment. The lack of alternative investigative methods, the easy application, and the existing experience in our laboratory were further arguments for this method.

Methods and data evaluation

For the optic tasks, subjects were seated 1 m from black and white drawings, either of the Necker cube (12 \times 12 cm²) or the Rubin vase (12 \times 17 cm²). The subjects could view each drawing freely. For the acoustic tasks, subjects listened with both ears to a sequence either of two tones – 250 Hz for 393 ms followed by 1.3 kHz for 393 ms, separated by 40 ms – or of two similarly timed and synthesized syllables, which have different meanings according to their grouping, e.g., ‘so-ma/’/ma-so’. Both stimuli were played back from tape by loudspeaker at a comfortable volume. Each of the four stimuli was presented three times for 1 min, with intervening pauses of 1 min. Subjects had to report immediately – by pressing a button – when they “could no longer prevent” the new percept. The mean duration of constant percepts, i.e., the length of the reversal intervals, averaged over the 3-min stimulus presentation, was calculated independent of the perceived aspect, order, or meaning. Subjects were informed about the character and especially the reversibility of the stimuli. Only subjects perceiving both perspectives after short familiarization were included in the trials and instructed not to induce reversals by strategies (e.g., by eye blinking).

Due to logistic or task-dependent problems, only some of our patients could participate in all of the reversal experiments. Their numbers are given in Table 4. Less than 2.5% of all the raw data was recognized as outliers.

The mean durations and the corresponding standard deviations for all groups and stimuli were computed and compared by use of unpaired *t*-tests (P_t) and – following one-way ANOVA – multiple comparisons (P_{mc}) according to Bonferroni/Dunn. The *t*-tests were performed for the mean duration of each patient group and that of the healthy subjects, but not between the means of the patient groups. Furthermore, the means for the Necker cube, Rubin vase, and the ‘so-ma/ma-so’-stimulus were compared separately for each patient group by multiple comparisons as well.

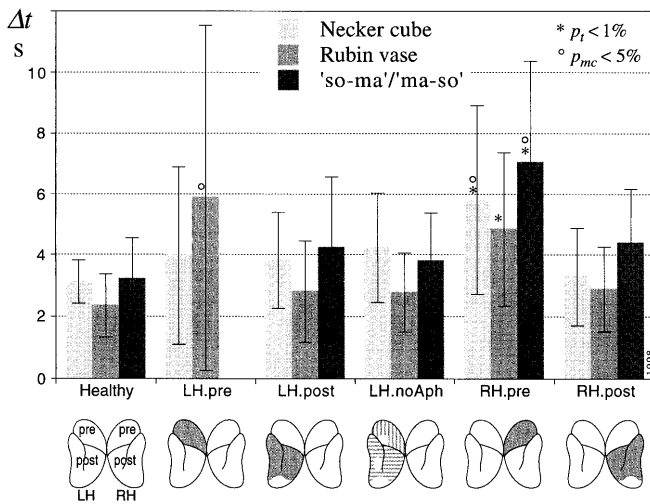


Fig. 3 Mean duration of reversal intervals and standard deviations. * Significances of unpaired t -tests (P_t) between each patient group and the healthy controls, ° significances of multiple comparisons (P_{mc}) for all patient groups as compared with the healthy controls. *so-ma/ma-so* Syllables used in the acoustic tasks

Results

Our results depend partly on the quality of the stimuli. Generally, visual reversals were perceived more easily than auditory ones. Even among the 14 healthy subjects, only 11 reported reversals for the 'so-ma/ma-so'- and seven for the 'tones'-stimulus. The latter did not evoke reversals in any of our 'LH.pre'-patients. For all other groups, no significant differences in the lengths of their mean durations was found, neither by unpaired t -tests nor by multiple comparisons. Only two of our 'LH.pre'-patients reported reversals for the 'so-ma/ma-so'-stimulus. Therefore, this and all of the 'tones'-results are not included in Fig. 3. Within each patient group, the results do not significantly ($P_{mc} < 0.05$) depend on the quality of the three remaining and depicted stimuli. As expected, our neurologically healthy subjects reported durations between 1.5 and 4.5 s, depending on their age.

Although the average durations of reversals for patients with precentral lesions, either in the left or right hemisphere, appear elevated for all three tasks, only the latter are significantly different from the healthy controls ($P_t < 0.01$), according to unpaired t -tests. By multiple comparisons, significant differences were found between the mean durations reported by 'RH.pre'-patients for the Necker cube and the 'so-ma/ma-so'-stimulus, as well as by 'LH.pre'-patients for the Rubin vase and the corresponding values of the healthy controls ($P_{mc} < 0.05$). All other comparisons deliver significances on at least a factor of three higher levels. The high standard deviations that resulted from the investigations of four 'LH.pre'-patients for the Necker cube and six 'LH.pre'-patients for the Rubin vase are remarkable.

Discussion

Our findings support the notion that mainly precentral cortical lesions significantly alter the performance in reversal tasks, but with different effects according to the damaged hemisphere. Our observations of significantly prolonged reversal intervals for patients with precentral lesions in the right hemisphere conforms with those of Meenan and Miller (1994). Patients with precentral defects in the left hemisphere clearly produced unreliable data and showed considerable difficulties in perceiving reversals, most pronounced for the acoustic stimuli. These effects have been observed by several authors (Cohen 1959; Teuber 1964; Ricci and Blundo 1990), but we cannot confirm their conclusion that there is no significant lateralization. We conjecture that right-hemispheric lesions slow down modulatory systems responsible for the succession of Gestalts, but we cannot differentiate whether fully developed Gestalts persist longer or whether their development is slowed. In the case of left-hemispheric lesions, we assume problems with the extraction and (temporal) analysis of salient events from which Gestalts usually are constructed (Fuster 1995). Although the frontal hemispheres appear to be involved in different aspects of temporal segmentation and Gestalt formation, it is also evident that both hemispheres perform co-operatively, and that lesions on one side necessarily effect the function of the other.

Comparisons with results from reproductions of time intervals are difficult due to the lack of agreement in the literature and because the investigated range of time intervals is different. The results of Damasceno (1996) and Harrington et al. (1998) – who reported an overestimation for patients with lesions in the right hemisphere – as well as Nichelli et al. (1993) – who reported prolonged reproduction with increased variance for Alzheimer patients – generally conform with ours. In this context, we would like to point out that the reproduction of time intervals clearly is a voluntary task, because the required decisions explicitly result from cognitive processes and strategies. Consequently, access to the proposed temporal mechanism is less available than to perceptual reversals. If subjects really avoid influencing the reversal times, we judge reversals as essentially involuntary and, therefore, expect to directly access an important temporal aspect of Gestalt formation.

Conclusion

There are several general aspects of our study that should be explained and summarized. In contrast to many patient studies, in which mainly one parameter is tested in few patients, we report group-specific deficits with respect to several parameters. The main advantage of our extended approach lies in the general result that temporal deficits are group as well as parameter specific. On this basis, we can logically rule out a single central timing authority. Yet the model of temporal building

blocks as a basis of temporal hierarchy (Pöppel 1997) remains possible, if unlikely. The character of our three experiments leads us to conjecture that distinct timing agents for sensory (AOT), sensorimotor (tapping), and more cognitive (perceptual reversals) tasks exist. The nature of the underlying mechanisms is not clear, but oscillatory processes and interval timer mechanisms, as proposed in the literature, might be invoked: For the 30-ms range, fundamental temporal units – system states provided by an oscillatory process with a period of 30 ms – are assumed (Pöppel et al. 1990; Pöppel 1997). For the 300-ms range up to the seconds range, internal oscillators are postulated, which trigger impulses with a regular frequency in which the number of accumulated pulses in a counter represents the time elapsed (Macar 1985; Treisman et al. 1990, 1992; Miall 1996). In the middle range around 300 ms, temporal processing can alternatively also be explained by specific interval timers – non-oscillatory timing mechanisms in which intervals of different durations are processed by distinct sets of duration (Ivry 1996a).

Coordination of these three timing agents appears to be intuitively necessary, since the behavioral consequences would otherwise be disastrous. It may well be that one of the timing agents also has the co-ordinating competence, without necessarily being situated on a hierarchically higher level.

In specific therapy, we see opportunities for all three timing agents (von Steinbüchel et al. 1996a), and it remains an open question whether there is any transfer of training results among them. The specific application of our tasks for diagnosis of cortical defects has to be further investigated on the individual-patient level. However, there are segregating effects, which appear significant for larger samples of patients.

Finally, we would like to emphasize that our results essentially confirm and complement the few existing investigations concerning timing functions and their impairments in the neocortex. In the field of timing mechanisms, however, further research, especially concerning the interplay of the timing agents (including those suspected in the basal ganglia and the cerebellum) is necessary. The complexity of the brain requires adequate approaches that deliver more than monocausal explanations of its function and malfunction. Our investigation of different ranges of temporal processes with an acceptable number of patient groups can be regarded as a step in this direction.

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