PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The challenge of non-invasive cognitive physiology of the human brain: how to negotiate the irrelevant background noise without spoiling the recorded data through electronic averaging

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THE ROYAL SOCIETY

The challenge of non-invasive cognitive physiology of the human brain: how to negotiate the irrelevant background noise without spoiling the recorded data through electronic averaging

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Brain mechanisms involved in selective attention in humans can be studied by measures of regional blood flow and metabolism (by positron emission tomography) which help identify the various locations with enhanced activities over a period of time of seconds. The physiological measures provided by scalp-recorded brain electrical potentials have a better resolution (milliseconds) and can reveal the actual sequences of distinct neural events and their precise timing. We studied selective attention to sensory inputs from fingers because the brain somatic representations are deployed over the brain convexity under the scalp thereby making it possible to assess distinct stages of cortical processing and representation through their characteristic scalp topographies. In the electrical response to a finger input attended by the subject, the well-known P_{300} manifests a widespread inhibitory mechanism which is released after a target stimulus has been identified. P_{300} is preceded by distinct cognitive electrogeneses such as P_{40}, P_{100} and N_{140} which can be differentiated from the control (obligatory) profile by superimposition or electronic subtraction. The first cortical response N_{20} is stable across conditions, suggesting that the first afferent thalamocortical volley is not affected by selective attention. At the next stage of modality-specific cortex in which the sensory features are processed and represented, responses were enhanced (cognitive P_{40}) only a very few milliseconds after arrival of the afferent volley at the cortex, thus documenting a remarkable precocity of attention gain control in the somatic modality. The physiology of selective attention also provides useful cues in relation to non-target inputs which the subject must differentiate in order to perform the task. When having to tell fingers apart, the brain strategy for non-target fingers is not to inhibit or filter them out, but rather to submit their input to several processing operations that are actually enhanced when the discrimination from targets becomes more difficult. While resolving a number of such issues, averaged data cannot disclose the flexibility of brain mechanisms nor the detailed features of cognitive electrogeneses because response variations along time have been ironed out by the bulk treatment.

We attempted to address the remarkable versatility of humans in dealing with their sensory environment under ecological conditions by studying single non-averaged responses. We identified distinct cognitive P_{40}, P_{100}, N_{140} and P_{300} electrogeneses in spite of the noise by numerically assessing their characteristic scalp topography signatures. Single-trial data suggest reconsiderations of current psychophysiological issues. The study of non-averaged responses can clarify issues raised by averaging studies as illustrated by our recent study of cognitive brain potentials for finger stimuli which remain outside the subject's awareness. This has to do with the physiological basis of the 'cognitive unconscious', that is, current mental processes lying on the fringe or outside of phenomenal awareness and voluntary control, but which can influence ongoing behaviour. Averaged data suggest that, in selective auditory attention, the subject may not notice mild concomitant finger inputs. The study of non-averaged responses documents the optional and independent occurrence of the cognitive P_{40}, P_{100} and N_{140} (but not P_{300}) electrogeneses while the finger inputs remain outside phenomenal awareness.

These results suggest that the subject unconsciously assigns limited cognitive resources to distinct somatic cortical areas thereby submitting finger inputs to an intermittent curtailed surveillance which can remain on the fringe or outside consciousness. The study of cognitive electrogeneses in single non-averaged responses is making possible a neurophysiology of cognition in real time.

Keywords: physiology of cognition; non-averaged brain potentials; brain imaging; perceptual processing; cognitive unconscious; selective attention

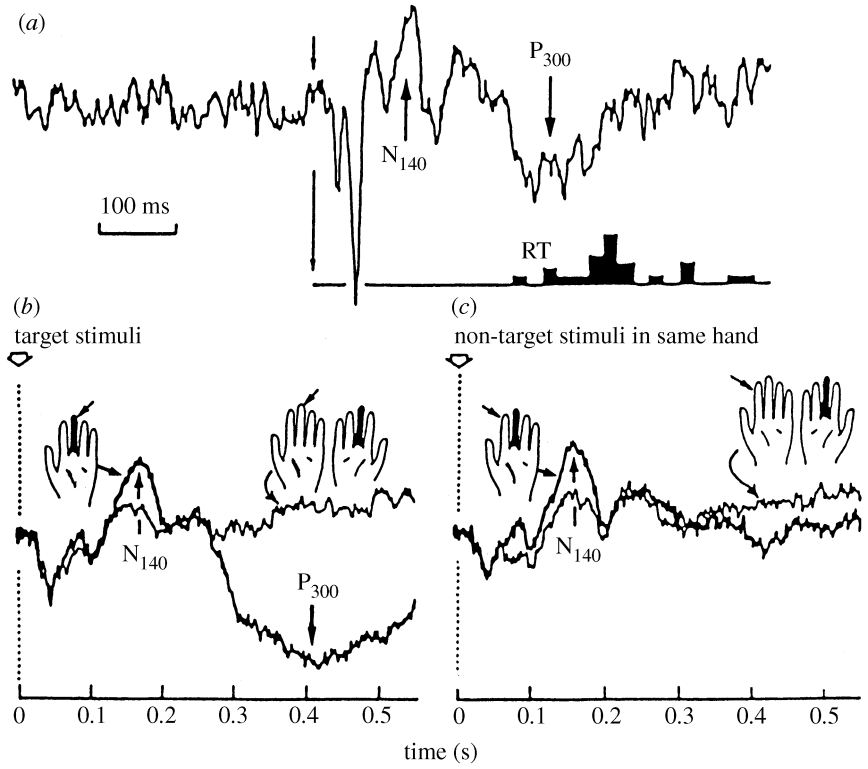

Figure 1. (*a*) Average of 200 target responses to a brief electrical stimulus delivered to the left third finger. Derivation from the right parietal scalp using a right ear lobe reference. Negativity at the scalp electrode drives the trace upwards in this and all subsequent figures. The subject detected only 56% of the stimuli which had a very small near-threshold intensity. Reaction times (RT) were concomitant with the P_{300} component, which was preceded by an N_{140} negative component. From Desmedt *et al.* (1965, fig. 7). (*b*,*c*) Intramodality selective attention in forced pace task. Four near-threshold electrical stimuli were delivered to fingers II and III of either hand, respectively, in a randomly intermixed series at intervals varying between 250 and 570 ms. In any attention run, one of the four fingers was designated as target and counted mentally. The task was difficult and only highly motivated subjects performed with less than 5% errors. In the hand figurines, the attended (target) finger is in black. Small arrows point to the finger evoking each response. (*b*) Grand average of 560 responses to the left target third finger (thicker trace), superimposed on the response (thinner trace) to the same left finger in other runs when the subject attended the right third finger now designated as target. (*c*) Grand average of 560 responses to the left non-target index finger adjacent to the target (thicker trace), superimposed on the response (thinner trace) to the same left index finger when the subject attended the right hand target. Derivations from the right parietal scalp with ear lobe reference. N_{140} was present in both target (*b*) and non-target (*c*) responses while P_{300} only occurred for targets (*b*). From Desmedt & Robertson (1977).

1. AVERAGED EVENT-RELATED POTENTIALS AND SELECTIVE ATTENTION

Methods for measuring regional cerebral blood flow and metabolism by positron emission tomography provide invaluable data about where in the human brain activities are enhanced during selective attention (Raichle 1994; Price *et al.* 1996). However, cognitive tasks induce rather small regional cerebral blood flow changes (about 10%) and data usually require to be averaged across experimental runs and/or subjects. In addition, one must subtract 'control' data acquired under different experimental parameters which are thought to provide appropriate baseline conditions. The choice of such control data is rather critical for the end results and may sometimes lead to controversies between groups. Also, the anatomical imaging methods have a limited time-resolution (in the range of seconds) and cannot document the actual sequences and time-features of the enhanced effects recorded throughout the brain.

Scalp-recorded electrical potentials provide more precise (millisecond range) physiological measures of these sequences and they can reveal the actual time-course of neural processing events along pathways and cerebral areas, for example when the subject identifies relevant 'target' sensory inputs in a randomly intermixed sequence of stimuli. Many studies have been devoted to the prominent P_{300} (P for positive, peak at about 300 ms) component (Sutton *et al.* 1965; Desmedt *et al.* 1965) which is generated over rather wide cortical areas after detection of a significant environmental event in any sensory modality (Ford *et al.* 1973; Callaway *et al.* 1978; Squires *et al.* 1975; Knight *et al.* 1981; Begleiter *et al.* 1983; Yamaguchi & Knight 1991). The subject's behavioural response (e.g. button press reaction time) is usually concomitant with the P_{300} (figure 1*a*) (Ritter *et al.* 1972). A negative decision does not elicit a P_{300} (Hillyard *et al.* 1971). P_{300} also occurs in mammals tested with similar attention paradigms (Paller *et al.* 1988). Briefly put, P_{300} manifests a widespread inhibitory mechanism (Desmedt & Debecker 1979; Desmedt 1981) which is released after an attended stimulus has been identified and the currently active brain circuits must be cleared for the next task.

Thus, P_{300} is a rather 'late' event in the perceptual sequence and it is preceded by the processing operations that are manifested by distinct cognitive electrogeneses at different latencies (figures 1–5). In experiments with intermixed series of sensory stimuli, the non-target inputs do not call for any response, but the subject must of course differentiate them from the targets in order to perform the task. It is in a way not surprising that sizeable cognitive electrogeneses, such as N_{140}, appear in non-target responses, even though there is no subsequent P_{300} (figure 1*c*) (Desmedt & Robertson 1977). The non-target processing leading to a decision of 'correct rejection' indeed involves sizeable short-latency cognitive activities not followed by P_{300} (Hillyard *et al.* 1971).

Considering such data, it is rather surprising that many studies have been overlooking the fact that the so-called 'irrelevant' non-target responses cannot provide any foolproof baseline for assessing the target profiles (e.g. Hillyard 1981; Desmedt & Tomberg 1991).

In an attempt to remove these ambiguities we revised protocols to include a second condition with separate runs during each of which one of the experimental stimuli was delivered singly in a mismatch-free series while the subject was reading a book (Desmedt & Tomberg 1989, 1991). The controls provided by this second condition also avoided unwanted habituation or rate effects by using randomly varying inter-stimulus intervals exceeding 1.4 s (Tomberg *et al.* 1989). Any enhancement of responses to either attended or not-attended stimuli could then be clearly differentiated by superimposition on the control baseline (obligatory) profile (figure 2*b*,*d*) or by electronic subtraction of the control averaged response (figure 2*c*,*e*).

We call 'cognitive' any of these optional brain electrogeneses which can be identified as significantly diverging enhancements from the control baseline. We think of them as resulting from the allocation of a surplus of resources to the processing activities in specific cortical areas. 'Resources' are viewed as related to the physiological mechanisms whereby certain neurons in definite cortical columns receive a surplus of subliminal synaptic excitation and/or neuromodulations (Mountcastle 1998). Such effects must play an essential role in governing the nature and level of the perceptual processing of any sensory input. They are presumably organized from the mid-dorsolateral prefrontal cortex, which is endowed with executive functions for putting the current processing into context and for updating relevant information along time (Luria 1966; Milner 1982; Fuster 1989; Kornhuber 1993; Knight & Grabowecky 1995; Goldman-Rakic 1996; Tomberg 1999*b*). As discussed below, the allocation of cognitive resources does not necessarily lead to conscious awareness. These brief targeted effects related to specific perceptual operations are to be distinguished from the slower widespread regulations of the level of the brain excitatory state, as in sleep, waking or arousal (Steriade *et al.* 1993, 1996).

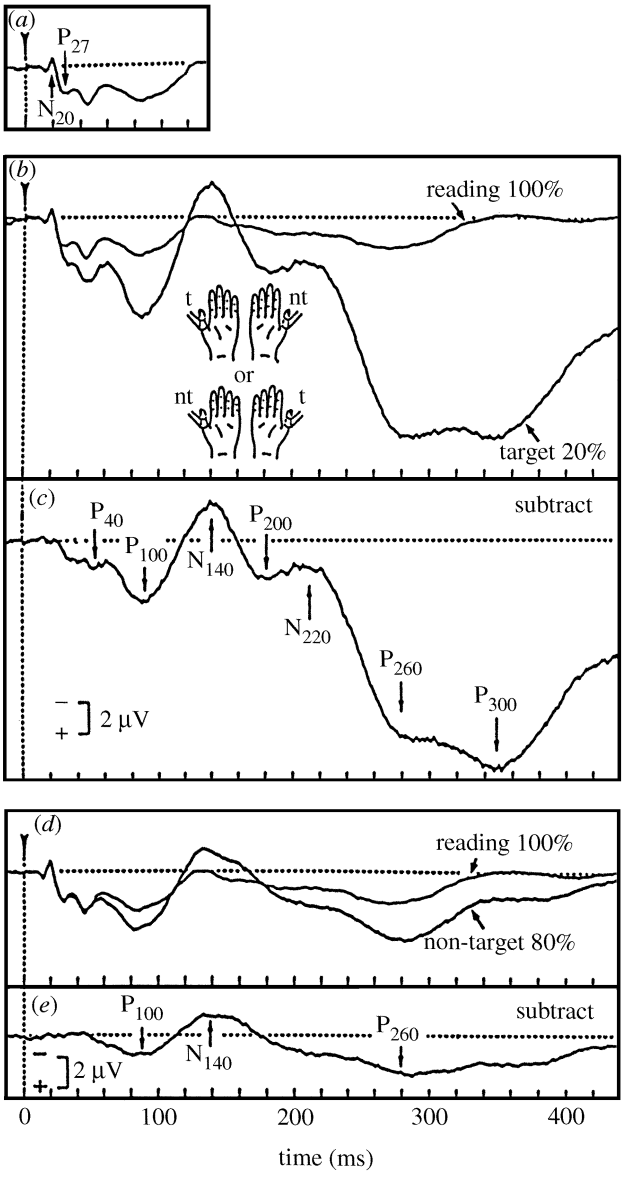

Figure 2. Grand average responses evoked from the contralateral thumb in nine normal adults. Randomly intermixed mild electrical stimuli to the right or the left thumb. Right ear lobe reference. In the different runs assembled, either the right or the left thumb received 20% of the stimuli and was designated as target while the opposite thumb received 80% of the stimuli and was designated as non-target (hand figurines in (*b*)). In the control runs, 100% of physically identical stimuli were delivered either to the left or to the right thumb and neglected by the subject, who was reading a book. (*a*) Control response with the short-latency (obligatory) N_{20} and P_{27} components. (*b*) Target response superimposed on the control response. (*c*) Subtraction of target minus control. (*d*) Non-target response superimposed on the control response. (*e*) Subtraction of non-target minus control. From Desmedt & Tomberg (1991).

2. THE EARLIEST ELECTRICAL SIGNS OF BRAIN PROCESSING IN ATTENTION

When the thalamocortical volley generated by a finger stimulus arrives at the cortex it evokes an N_{20} component (surface-negative at contralateral parietal electrodes) which is generated by area 3b at a depth of about 30 mm in the posterior wall of the central sulcus (see Desmedt 1988). The N_{20} showed strictly no change in voltage, latency or profile, whether evoked by attended or unattended finger stimuli (figure 2*b*,*c*). It was annihilated by the subtraction target minus control responses (figure 2*c*,*e*) (Desmedt & Tomberg 1989, 1991).

The remarkable stability of the first cortical N_{20} response across conditions suggested that somatic attention did not affect the earliest thalamocortical volley arriving at the primary projection cortex. This finding apparently falsifies the Crick (1984) thalamic 'searchlight' hypothesis for the somatic modality in which the first cortical response can be readily identified and titrated with great precision.

By contrast, selective attention to target finger inputs enhanced the subsequent P_{27} parietal positivity which is generated by areas 1 (and 2) in the postcentral gyrus, i.e. at the second stage of modality-specific cortex (figures 2*a*,*b* and 3). A large cognitive P_{40} was disclosed by the difference of target and control responses (figure 2*c*) (Desmedt & Tomberg 1989). Tactile features of the skin are known to be processed and represented in area 1, which receives corticocortical connections from the primary 3b area as well as direct thalamocortical axons from the ventro-posterior (VP) thalamic nucleus (figure 3) (Kaas & Pons 1988).

It is well established that the volley of action potentials conducted from the finger along the afferent pathway takes as much as about 18 ms to reach the postcentral cortex, and that small variations thereof are related to the length of the arm in different subjects (Desmedt 1988, fig. 4). The enhancement of the cognitive P_{30}–P_{40} can be identified at a latency as short as 23–26 ms, only a very few milliseconds after the peak of the N_{20} response (median delay 6 ms, figure 3*d*). In this figure, inter-individual variations in afferent conduction time have of course been removed by only taking into account the transit times from the N_{20} peak to the onset of the cognitive enhancement in target responses.

These data provide strong evidence for a remarkable precocity of cortical attention gain control in the somatic modality. 'Early' effects recorded so far apparently start only at 50–70 ms for the auditory modality and at 70–90 ms for the visual modality (see Hillyard *et al.* 1995).

3. TELLING FINGERS APART: BRAIN PROCESSING STRATEGIES

Psychological theories of attention have been arguing about the level, early versus late, beyond which relevant and irrelevant sensory stimuli are treated differentially (see Kahneman & Treisman 1984) and proponents of an early selection have postulated that irrelevant inputs might be suppressed at a quite early stage so as to alleviate the computational load required for a response.

When a subject is dealing with a randomly intermixed series of inputs from different fingers, the brain strategies for telling fingers apart appear to be quite different from the classical psychological models of selection. We found no evidence for any short-latency cognitive potential being present in both target and non-target responses while subsequent cognitive components would occur only in target responses, but not in the non-targets (hypothesis of early selection); neither did the target and non-target responses display any identical set of early and late cognitive components (hypothesis of late selection).

In fact, the short-latency cognitive P_{40} was rarely seen in non-target responses. Its early part, which can be called a cognitive P_{30}, virtually never occurred in non-targets, but

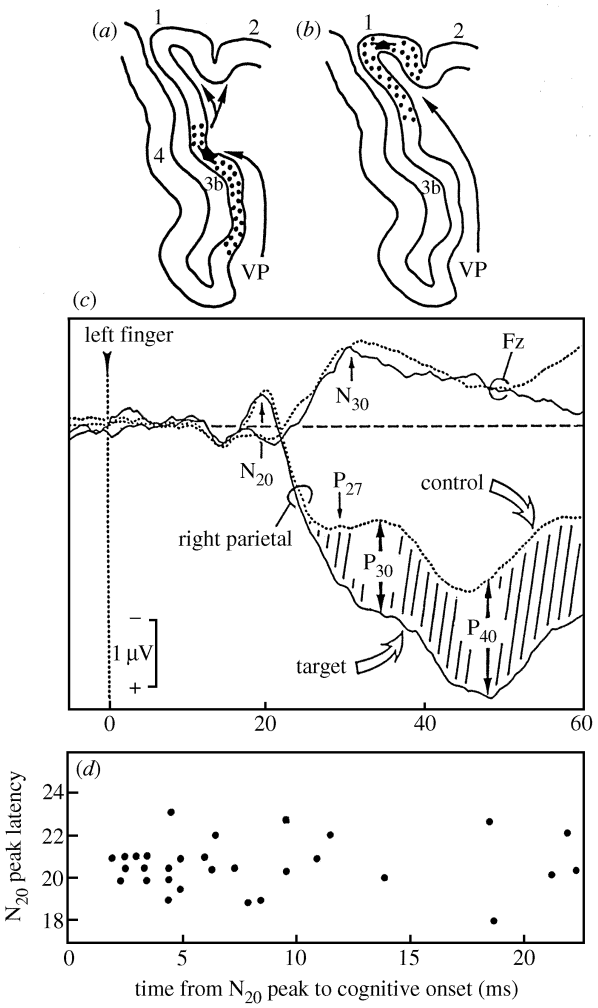

Figure 3. (*a*,*b*) Sketch of a transverse section through the central sulcus (posterior wall to the right) of the human brain (based on a histological section kindly provided by Dr Albert Galaburda, Boston, MA). (*a*) Area 3b (stipple) with black arrow showing approximate level of the equivalent cortical dipole (surface-positive, bottom-negative) which generates the primary N_{20} recorded as a negative component on the parietal scalp. (*b*) Area 1 (stipple) with equivalent cortical dipole generating the P_{27} recorded as a positive component on the parietal scalp. The ventro-posterior (VP) thalamic nucleus projects to areas 3b and 1. Area 3b sends corticocortical axons to areas 1 and 2. (*c*) Superimposed grand average responses to near-threshold stimuli to the left thumb, either in attention runs when the thumb stimuli are targets attended by the subject (intermixed series of two stimuli, $p = 0.2$, full line), or in control runs when physically identical thumb stimuli are neglected by the subject, who was reading a book ($p = 1.0$, dotted line). The early N_{30} component recorded at mid-frontal Fz is unaffected by attention. The right parietal traces disclose a stable N_{20} followed by early attention enhancements labelled P_{30} and P_{40}. The cognition-related enhancement starts at 26 ms in this example. From Tomberg *et al.* (1990). (*d*) Transit time from the N_{20} peak (ordinate) to the onset of cognitive deviation of the target from control averaged traces (abscissa) in 31 subjects of whom 14 showed a transit time between 2 and 5 ms only. From Desmedt & Tomberg (1989).

it was observed in targets. It is interesting that the later part of P_{40} could actually be enhanced in averaged non-targets by making it more difficult to differentiate fingers, for example in runs with a non-target index finger adjacent

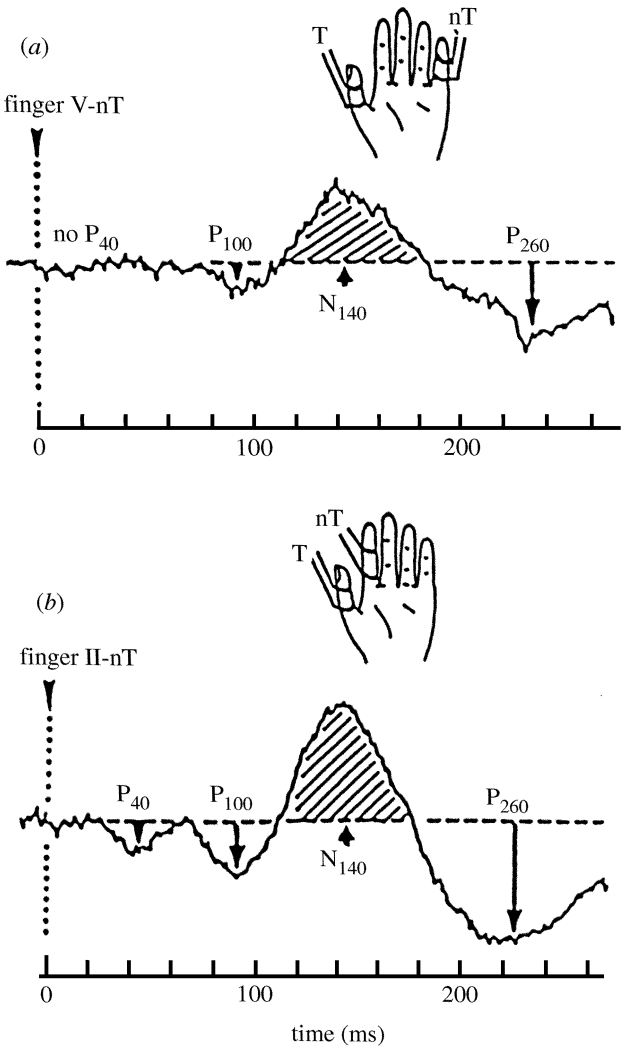

Figure 4. Effect of difficulty of the selective attention task on the 'unattended' non-target averaged responses. Series of randomly intermixed near-threshold stimuli were delivered to the left target thumb ($p = 0.2$) and to either the left non-target fifth finger (*a*) or index finger (*b*) ($p = 0.8$). The traces shown result from the subtraction non-target response minus control response ($p = 1.0$, subject reading a book). The discrimination is more difficult for adjacent fingers (*b*) when a cognitive P_{40} is recorded while the subsequent cognitive components are further enhanced. From Desmedt & Tomberg (1991).

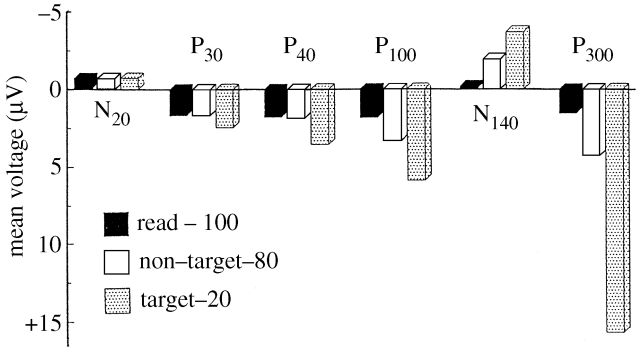

Figure 5. Mean voltage (measured from pre-stimulus baseline, microvolts) of components in grand averaged responses from 23 normal young adults. Series of randomly intermixed stimuli to two fingers of the same or opposite hands. Control runs ($p = 1.0$, read-100, black), and runs with non-target ($p = 0.8$, white) or target ($p = 0.2$, light stipple) responses. No change for N_{20} throughout conditions. All cognitive components from P_{30} to P_{300} were enhanced for targets ($p < 0.001$). For non-targets the components at 25–40 ms showed no significant change ($p > 0.05$), while subsequent components were enhanced when the target and non-target fingers were on the same hand ($p < 0.001$). From Desmedt & Tomberg (1989, tables I and II).

to the thumb target (figure 4*b*). P_{40} was absent for the non-target fifth finger (figure 4*a*), which was easier to differentiate from the thumb target (Desmedt & Tomberg 1989). Also, larger cognitive P_{100}, N_{140} and P_{260} were recorded for the non-target index finger than for the non-target fifth finger (figure 4). None of these non-target responses disclosed any P_{300}.

In a series of 23 normal adults, grand averages of responses to physically identical finger stimuli showed striking differences in component voltage between control, non-targets and targets (figure 5). All components except N_{20} were significantly enhanced in targets. For non-targets the components at 25–40 ms showed no significant change ($p > 0.05$), while all subsequent components were enhanced when the non-target fingers were on the same hand as the targets ($p > 0.001$) (Desmedt & Tomberg 1989). The data of figure 5 assemble non-target components on the same and opposite hands as the target.

For telling fingers apart the actual brain strategy for non-target stimuli was thus not to inhibit or filter them out, but rather to submit them to several cognitive processing operations that were actually enhanced as the discrimination from targets became more difficult.

In other words, the non-targets which tended to interfere with target identification in the intermixed sequence will be allocated a larger, not a smaller, share of cognitive resources. It seems remarkable that rather large cognitive brain electrogeneses (figures 2–5) have to be engaged for telling apart objects so intimately known to the subject as his or her own fingers.

4. SINGLE NON-AVERAGED RESPONSES VERSUS AVERAGED DATA

The current methods based on the electronic averaging of recorded data and on the subtraction of data acquired in different experimental runs (or in different subjects) impose obvious, though little acknowledged, limitations to studies of the dynamics of brain processing. It is well known that noise transients will not be eliminated through averaging unless they are random and many. More serious uncertainties arise from the fact that human subjects are eminently versatile and efficient in dealing with their environment. They quickly learn alternative ways to handle problems in daily living or of the kind used in experimental attention tasks. While a single verbal instruction expressed in two or three words can thoroughly switch the perceptual behaviour for the next run, subjects may only follow such instructions up to a point and their mind may be transiently committed to a variable extent to many shifting items during the prescribed task.

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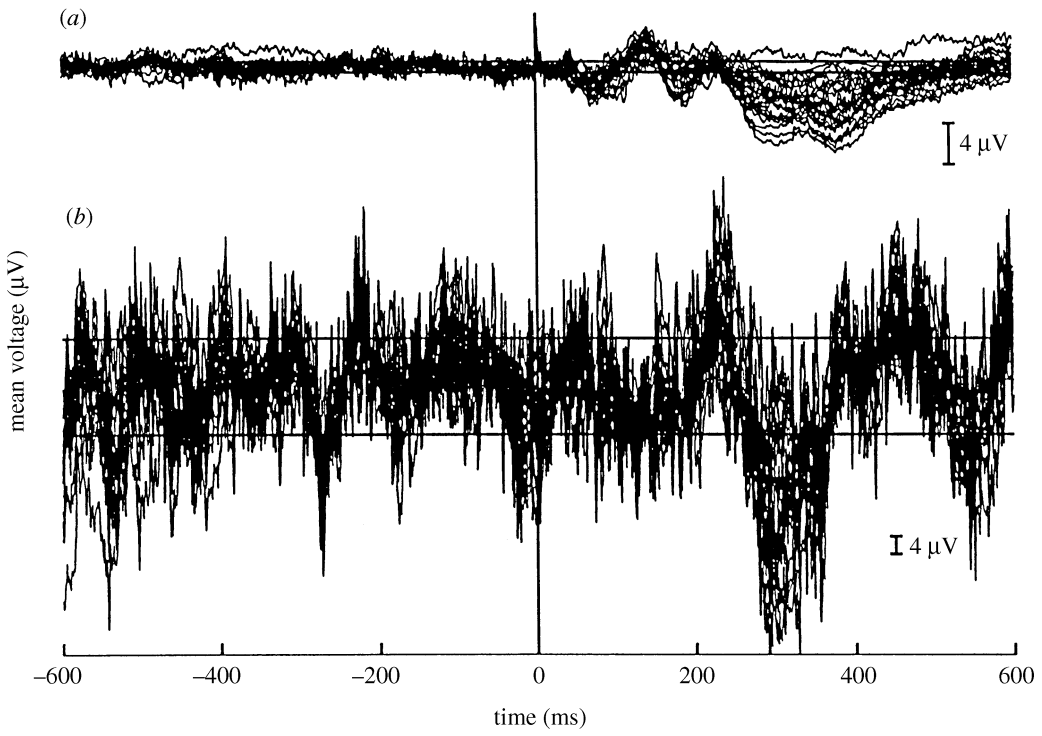

Figure 6. (*a*) Averaged response ($N = 39$) to a target finger stimulus delivered at time 0. (*b*) Single non-averaged response from the same run at reduced amplification. Standard deviation of the mean voltage of the traces increases from 0.5 μV (*a*) to 9 μV (*b*). Superimposed 28 scalp recordings.

When considering such fleeting parameters along time, it seems obvious that the methods of averaging and subtraction only provide a very rough approximation to the real thing. Data provided by these methods cannot avoid missing pertinent features of the physiology of cognitive brain processing. For example, the above results based on averaged data no doubt provide clear evidence about significant features of the somatic cognitive electrogeneses, but they ignore the variations along time even though these are quite significant for the study of brain cognition.

An obvious alternative is to use non-averaged data, but it is then necessary to deal with brain responses flooded by large noise transients (figure 6) which the averaging method was actually designed to reduce. The standard deviation of the mean voltage of a single trace may indeed exceed by a factor of 20 or more that of the same set of data submitted to electronic averaging.

Our proposed solution has been to accept the noise in non-averaged data and to design a method making use of those features of the scalp topographies which appear to be characteristic for each electrogenesis. It seemed wise to study the somatic cortex, which is deployed over the brain convexity and thus more accessible to a detailed analysis of the topographical signature of the potential fields generated by distinct cortical areas (Desmedt 1988). Mild stimulation of single fingers also helped assess their brain responses, which are clearly lateralized over the scalp surface.

The feasibility of the single response approach and its validation for the cognitive P_{40} are briefly summarized in figure 7 (Tomberg & Desmedt 1996). Starting from a grand average of 2760 responses to a left target finger stimulus (in 23 normal adults), the set of electrode voltages at the P_{40} peak latency was used to define a template of standard P_{40} scalp topography (figure 7*a*,*b*). The $\mathcal{Z}$-estimator of Desmedt & Chalklin (1989) was adapted for numerically assessing the detailed congruence between the set of template voltages and the non-averaged response voltages at each millisecond along time (figure 7*c*,*d*). $\mathcal{Z}$ can vary between −1 and 1, and a $\mathcal{Z}$ threshold of 0.96 has been documented as indicating a significant level of congruence between the voltage gradients of any two such maps, irrespective of their absolute voltages.

In figure 7*d*, the $\mathcal{Z}$ estimation for the contralateral parietal electrodes exceeded 0.96 between 26 and 55 ms. Interestingly, the $\mathcal{Z}$-test was not passed by even larger subsequent positivities nor indeed at any time at the ipsilateral scalp. Colour maps at different latencies during P_{40} showed large irregular noise transients as well as variations in the P_{40} voltage, but the core positivities at the P_{40} scalp focus remained fairly consistent.

5. SINGLE-TRIAL DATA SUGGEST THE RECONSIDERATION OF PSYCHOPHYSIOLOGICAL ISSUES

These and more recent studies (Tomberg 1999*b*; Tomberg & Desmedt 1996, 1998) have validated methods for identifying distinct electrogeneses in single responses. These methods help resolve issues hitherto considered to be out of reach and they lead to new ways of conceiving cognitive physiology in humans.

A few examples will be mentioned. The actual validity of so-called control responses should be tested by scrutinizing single trials and checking whether trials with unsuspected cognitive electrogeneses may have been collapsed into the

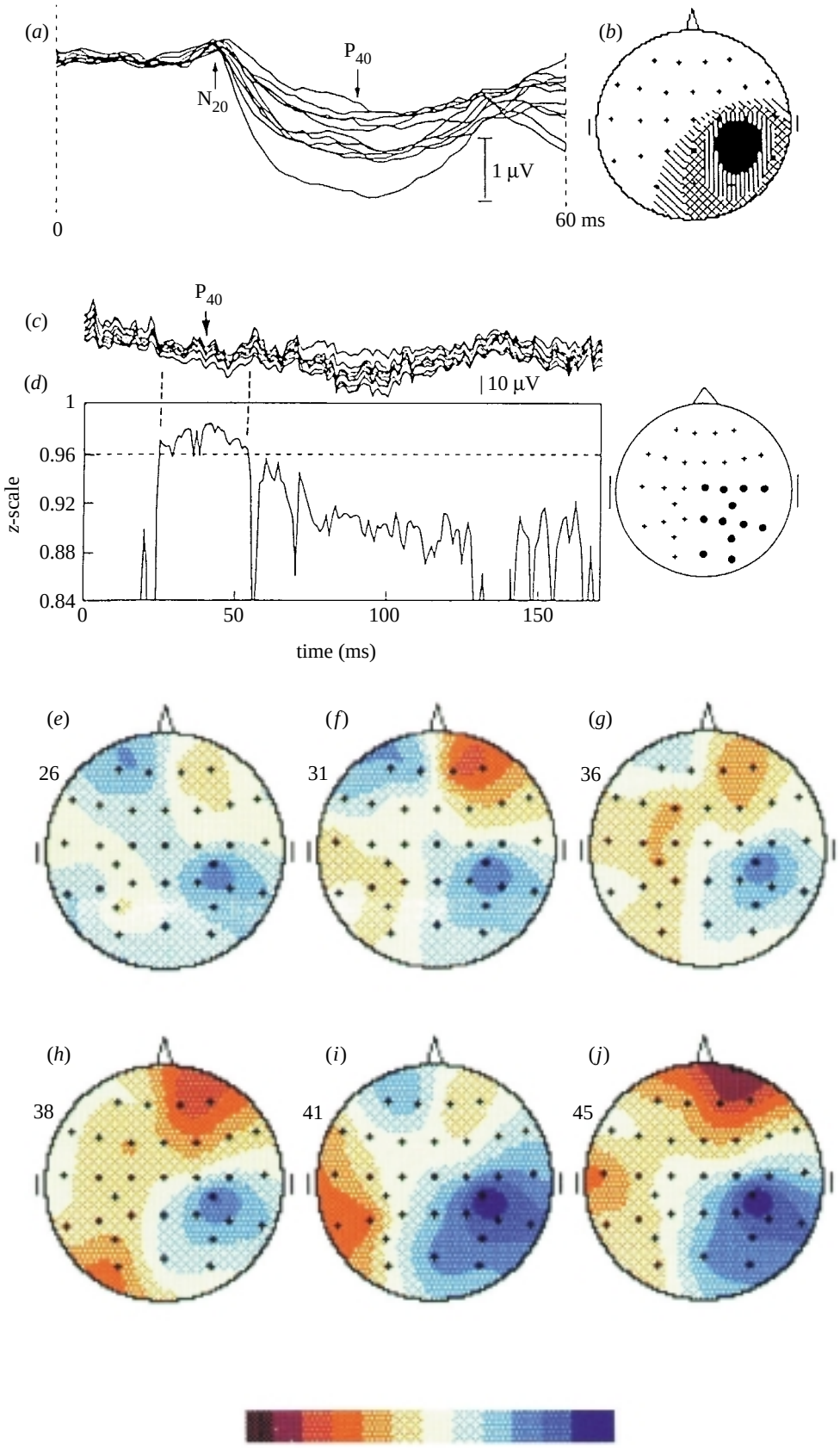

Figure 7. (*a*) Superimposed right parietal traces of a grand average of 2760 responses to a left target finger stimulus in 23 young adults. (*b*) Scalp map at 40 ms latency (four voltage steps of 0.5 μV). (*c*) Superimposed parietal traces (recorded from scalp electrodes with larger dots in figurine) of a single non-averaged response to a left finger target. (*d*) Z-test comparison of this response with the grand average template. Abscissa, time in milliseconds. Ordinate, Z-scale from 0.84 to 1, with horizontal dotted line at 0.96. (*e–j*) Scalp maps of the same P_{40} at the latencies indicated (milliseconds). Voltage steps of 2.5 μV (blue for positive, red for negative). From Tomberg & Desmedt (1996).

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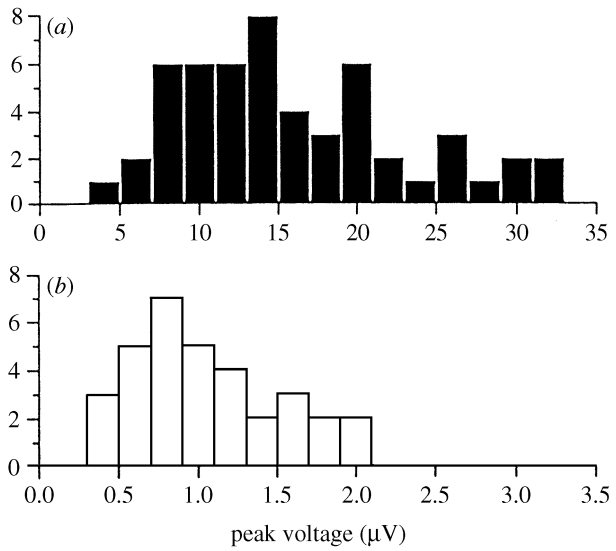

Figure 8. Histograms of cognitive P_{40} voltage (microvolts) for single non-averaged responses (*a*) and for averaged responses (*b*). Notice the difference in abscissa: to 35 μV (*a*) or 3.5 μV (*b*). From Tomberg & Desmedt (1996).

average thereby upsetting the control. This is pertinent when assessing differences between grand average profiles.

When averaged target and non-target responses show differences in distinct cognitive components (figures 2, 4 and 5) the question arises whether these may reflect stability of actual response profiles, or rather result from the intermittent presence and/or time-varying features of the single responses assembled in the average. No matter which of these alternatives is eventually substantiated by single-trial studies, current issues and interpretations will require reassessments.

Some results for the cognitive P_{40} in the detailed study of 145 single target responses already raise quite unforeseen questions. The cognitive P_{40} was found to occur in only one-third of the target responses and its voltage was quite large, ranging from 4 to 33 μV, thus about 12 times greater than the voltage recorded for averaged P_{40} (figure 8). The intermittency of P_{40} and its variations in latency and duration in single target responses provide an explanation as to why the P_{40} voltage is so much reduced by averaging (Tomberg & Desmedt 1996). Needless to say, the large voltage of the single cognitive P_{40} was a welcome bonus which helped in coming to terms with the noise in non-averaged responses. Another finding was that for a target response to include a P_{40} did have behavioural significance. The subject's reaction time for a single target trial with P_{40} was on average 19% shorter than for target trials without P_{40} (Tomberg & Desmedt 1996).

The presence of a cognitive P_{40} in a response is thought to manifest priming of the somatic postcentral areas 1 and 2 as a result of corticocortical interactions with the dorsolateral prefrontal area 46, which, briefly put, is involved in the temporal integration of behaviour (Luria 1966; Milner 1982; Fuster 1989; Kornhuber 1993; Knight & Grabowecky 1995; Goldman-Rakic 1996; Tomberg 1999*a*). The long-range interactions between these prefrontal and parietal areas are also manifested by the transient corticocortical 40 Hz phase-locking ('binding'), which has been related to the conscious perception of a target input (Desmedt & Tomberg 1994).

6. PHYSIOLOGY OF THE 'COGNITIVE UNCONSCIOUS'

The impact of non-averaged responses for clarifying issues raised by averaging studies can be shown by our recent study of cognitive brain potentials for mild finger stimuli which remain outside the subject's awareness.

These issues have to do with the physiological basis of the 'cognitive unconscious' (Kihlstrom 1987) which encompasses current mental processes lying on the fringe or outside of phenomenal awareness and voluntary control, but which can nevertheless influence ongoing behaviour. While the literature of perception and cognition actually documents a pervasive influence of unconscious contexts in normal human behaviour (Piaget 1973; Dixon 1981; Marcel 1983; Tranel & Damasio 1985; Baars 1988; Searle 1992; Kihlstrom 1993; Reber 1993), the underlying brain mechanisms are still obscure.

In a first series of experiments with averaged potentials, each run involved the delivery of randomly intermixed sequences of four stimuli (figure 9*a*): brief tone pips at 1000 Hz ($p = 0.15$) and at 900 Hz ($p = 0.55$) to the left ear, and electrical pulses to the left thumb ($p = 0.15$) and to the fifth finger ($p = 0.15$). The frequent pips served as non-targets to be neglected throughout. The contralateral parietal responses to the finger stimuli were averaged across appropriate runs.

In the somatic attention runs (figure 9*b*), the subject had to ignore the acoustic pips, identify all the finger stimuli and lift the right index finger for each of these targets. The grand average response presented a characteristic profile with sizeable cognitive P_{40}, P_{100}, N_{140}, P_{200} and P_{300} electrogeneses, well identified against the smaller control profile (figure 9*b*). Reaction times were concomitant with the P_{300}. In alternate auditory attention runs, the infrequent target pips had to be identified by the subject, who, on subsequent debriefing, stated not to have been consciously aware of the mild randomly intermixed finger stimuli. The latter nevertheless elicited small, but significant cognitive P_{40} and P_{100} in the 15 runs collapsed in the grand average of figure 9*c*, and a cognitive P_{100} not preceded by P_{40} in the 14 other runs collapsed in the average of figure 9*d*. A small N_{140} was noticed, but no P_{300} was detected in any of these runs (Tomberg 1999*a*).

These averaged data apparently suggest that, while the subject selectively attended the auditory target pips, the infrequent finger input might have been submitted to some incomplete processing unnoticed by the subject.

This issue has been clarified by the study of single non-averaged responses. Randomly intermixed sequences of mild stimuli to three fingers with probabilities of 0.2, 0.2 and 0.6 were delivered while the subject was asked to daydream in a relaxed but detailed manner about a wide variety of past and future personal items or events. On subsequent debriefing, the subjects stated not to have been consciously aware of the finger stimuli. In over 80% of the single trials no cognitive potentials were identified by the Z-method used with templates for the cognitive P_{40},

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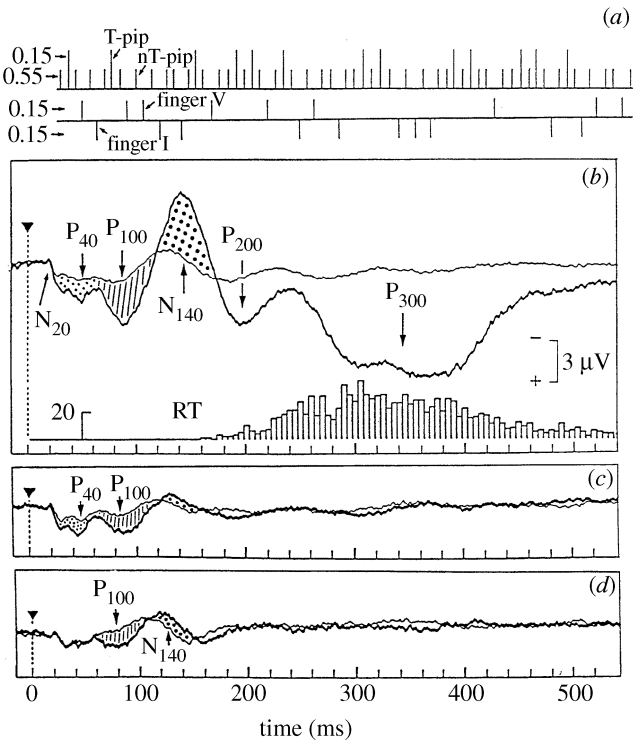

Figure 9. (*a*) Sample of the randomly intermixed sequence of four sensory stimuli: brief acoustic pips at 1000 or 900 Hz to the left ear and electrical pulses to the left fingers I and V. Probabilities of each of four stimuli indicated on the left side. (*b–d*) Grand averages of the responses (thicker trace) to finger stimuli recorded from the right parietal scalp (right ear lobe reference). Superimposition of control responses (thinner trace) to physically identical stimuli delivered in a homogeneous series ($p = 1.0$) while the subject is reading a book. (*b*) Selective attention to the finger stimuli. Cognitive components identified by difference with superimposed control trace. Histogram of reaction times (RT). (*c*, *d*) Selective attention to the infrequent target acoustic pips. The averaged responses to the finger stimuli still show small cognitive components, but no P_{300}. The runs with identified P_{40} were assembled in one grand average (*c*) while the runs without any clear P_{40} were assembled in another average (*d*). From Tomberg (1999*a*).

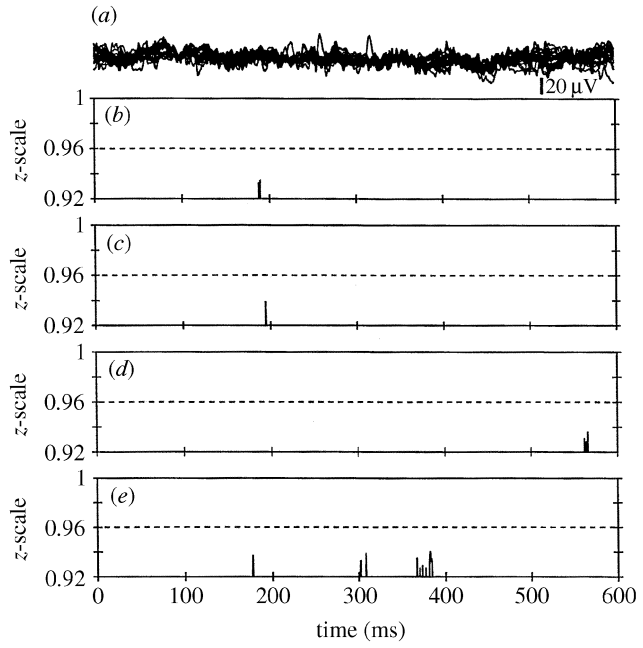

Figure 10. Single non-averaged response to a finger stimulus under no-task condition. (*a*) Superimposed 28 scalp traces. (*b–e*) Z-tests for P_{40} (*b*), P_{100} (*c*), N_{140} (*d*) and P_{300} (*e*) identify no cognitive component in this response. From Tomberg (1999*a*).

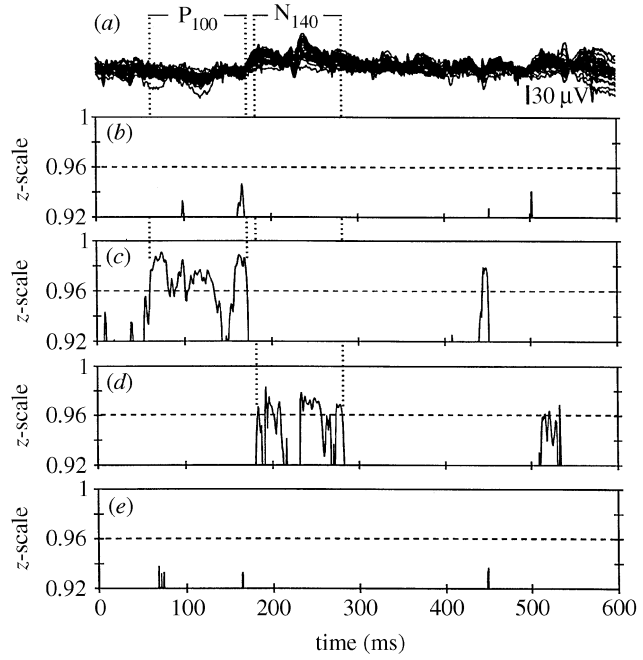

Figure 11. Single non-averaged response to a near-threshold finger stimulus under no-task condition. (*a*) Superimposed 28 scalp traces. (*b*) Z-test with P_{40} template is negative. (*c*) Z-test with P_{100} template identifies a cognitive P_{100} of 153 ms duration. (*d*) Z-test with N_{140} template identifies a cognitive N_{140} of 136 ms duration. (*e*) Z-test discloses no P_{300}. From Tomberg (1999*a*).

P_{100}, N_{140} and P_{300} (figure 10). However, occasional trials unambiguously disclosed genuine cognitive P_{100} (figure 11*c*) and N_{140} (figure 11*d*) electrogeneses, but no P_{300} (figure 11*e*). P_{40} was missing from this trial (figure 11*b*). Due to the background noise the Z-profiles presented noticeable transient irregularities, but the Z-threshold of 0.96 was practically satisfied over 153 ms for P_{100} (figure 11*c*) and 136 ms for N_{140} (figure 11*d*). Occasional brief upswings of the Z above 0.96 also occurred in relation to some of the noise transients. In another trial of the same run only a cognitive P_{100} of 86 ms duration was identified (figure 12*c*) while the other cognitive components as well as the P_{300} were all found to be missing.

If the method of averaging had been used, all the single trials would have collapsed whether or not they included any cognitive activities, thereby making it impossible to resolve the issue. The study of each single response actually disclosed unsuspected variabilities of features and provided strong evidence that optional partial cognitive processing of a finger input did occur outside any deliberate attention on the part of the subject. The data also documented the optional and mutually independent occurrence of the cognitive P_{40}, P_{100} and N_{140} electrogeneses while the finger inputs remained outside phenomenal awareness.

These results suggest that the subject would, from time to time, unconsciously assign some limited cognitive

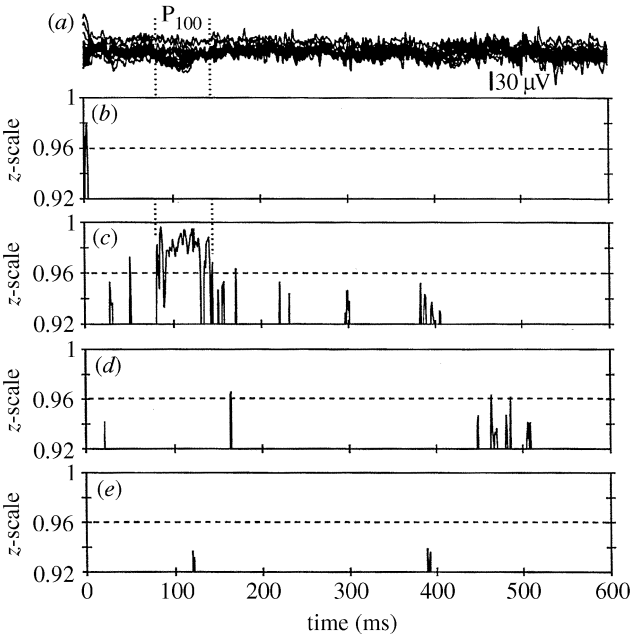

Figure 12. Single non-averaged response to a finger stimulus under no-task condition. (*a*) Superimposed 28 scalp traces. (*b*) $\mathcal{Z}$-test for P_{40} is negative. (*c*) $\mathcal{Z}$-test identifies a cognitive P_{100} of 86 ms duration. (*d*, *e*) $\mathcal{Z}$-tests identify no N_{140}, nor any P_{300}. From Tomberg (1999*a*).

resources to distinct somatic cortical areas thereby submitting finger inputs to an intermittent curtailed surveillance which can remain on the fringe or outside consciousness (Tomberg 1999*a*). This interpretation is indeed consistent with the fact that these single responses did not include any P_{300}, which makes sense in so far as the P_{300} appears to be released after a conscious perceptual decision (Desmedt & Debecker 1979; Desmedt 1981). In a recent study of non-averaged responses, the transient 40 Hz binding between parietal and prefrontal areas, which may manifest an essential feature of the perceptual processing of attended target input, was found to be inhibited and disrupted by the P_{300} (Tomberg & Desmedt 1998).

Thus, the study of non-averaged responses provides unique assistance for understanding the physiological mechanisms underlying the psychological phenomena of the 'cognitive unconscious' and implicit perception. The ability to identify distinct cognitive electrogeneses such as P_{40}, P_{100} and P_{300} in spite of the noise through assessment of their topographical patterns in the single non-averaged response is making it possible to study the neurophysiology of cognition in real time.

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