Sensory Discrimination and its Relationship to the Cerebral Processing of Infrequent Stimuli

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ABSTRACT: We recorded cerebral evoked potentials, back and forward averaged from the EMG onset of the responding muscle, in three reaction time tasks, each requiring an identical motor response to an identical stimulus but differing in the nature of the sensory discrimination required. Two types of stimuli were presented: a rare one to which the subject responded with finger-extension, and a frequent one to which no response was required. We found a close but variable relationship between the cerebral events associated with performance of a task and the timing of the motor response. As completion of the discrimination process was delayed relative to stimulus occurrence, EMG activity began later relative to the cerebral potentials. Moreover, we were able to record these cerebral events only from the response to the rare (unexpected) stimulus and not when subjects were required to respond to the frequent stimulus, suggesting that the sensory discrimination, in these experiments, is an event that occurred only in the processing of the unexpected stimulus.

RÉSUMÉ: La discrimination sensitive et sa relation à l'interprétation des stimuli rares au niveau cérébral. Nous avons enregistré les potentiels évoqués cérébraux, les potentiels évoqués cérébraux ont été enregistré sur une pérriode précedent et suivant le début de l'activité électromyographique des muscles réagissant, dans trois tâches réaction-temps, chacune de ces tâches demandant une réponse motrice identique à un stimulus identique, différent cependant dans la nature de la discrimination sensitive requise. Deux types de stimuli étaient présentés: un stimulus rare auquel le sujet répondait par une extension digitale et un stimulus fréquent auquel aucune réponse n'était requise. Nous avons observé une relation étroite mais variable entre les manifestations cérébrales associées à l'accomplissement d'une tâche et le moment de l'exécution de la réponse motrice. Comme l'achèvement du processus de discrimination était retardé par rapport au moment où le stimulus s'était produit, l'activité EMG commençait en retard par rapport aux potentiels cérébraux. De plus, nous avons pu enregistrer ces manifestations cérébrales seulement à partir de la réponse au stimulus rare (inattendu) et non quand les sujets devaient répondre au stimulus fréquent, suggérant que la discrimination sensitive, au cours de ces expériences, est un événement qui est survenu seulement dans le processus d'interprétation du stimulus inattendu.

When a subject is required to respond to an infrequently occurring target stimulus by performing a particular movement, the target stimulus will generate a series of long-latency "event-related" or "endogenous" cerebral evoked potentials (ERPs).[1,2]
The motor response is triggered after the stimulus has been discriminated by the subject as the one to which a response is required. This discrimination is a logical stage of information processing that the subject must complete before responding selectively to the target stimulus. For simplicity, the neural mechanisms underlying the ERP, sensory discrimination and the cerebral generation of a motor response can be regarded as discrete events, although each may in fact comprise a series of events or a network of interconnected neural activity extending over a considerable period of time, and perhaps reflecting substages of information processing. However, there must be some point in time following stimulus onset and preceding the

response when the subject has distinguished target from non-target stimuli with sufficient confidence to generate a correct response. For brevity, we will refer to the *completion* of this discrimination process as "sensory discrimination."

The discrimination process may, but does not necessarily, involve comparable neural processing of both target and non-target stimuli. For example, in a task requiring a target tone to be distinguished from a non-target flash, a subject may selectively attend to only the auditory sensory input and ignore the visual one. Thus, discrimination would be based on the fact that the two simuli occupy different sensory channels, and it would only require attention to, and processing of, a single channel. The concept of sensory channels can be broadened to include stimuli in the same sensory modality (e.g., a tone in the right or left ear, or a high or low pitched tone), if attention and processing can be confined to one of them. It could be argued that if a

discrimination is ever to be made, the two stimuli must ultimately occupy different channels. Some authors might prefer to reserve the word "discrimination" for situations in which two stimuli occupy sufficiently similar channels that they are processed similarly, at least initially, but this is difficult to define. In the present paper we have therefore used "discrimination" to mean the distinction between two stimuli irrespective of whether this is accomplished by attention to one or both of them.

It is not known if ERP components have any relationship either to this discrimination or to the decision to move. Several authors have shown that certain components of the ERP consistently precede the motor response and also have peak latencies that correlate with the response latency under their experimental conditions.[3,4,5,6,7,8] Others have shown that the peak latencies of several of the ERP components become longer as the difficulty of discrimination becomes harder[9,10,11,12,13,14] and suggested that certain ERP components specifically relate to these stages of information processing (i.e., to sensory discrimination or response selection). However, a component that consistently precedes the motor response in one experimental setting may follow it in another.

It is possible that the neural processing underlying sensory discrimination and that generating the ERP occur independently of each other despite their common link to the target stimulus. In other words, sensory discrimination and response selection lie on a branch of the stimulus processing sequence that is "in parallel" with the branch on which the ERP lies. The reported correlations between ERP component latencies and motor response latency would then be related to the time-locking of each parallel process to a common neural event preceding them (i.e., a branch point in the stimulus processing sequence). At the very least, the stimulus must initiate events that are common to both processing sequences, but if and where these sequences subsequently diverge is unknown.

An alternative interpretation is that the neural processing underlying sensory discrimination and that generating the ERP are intimately related but that the relationship between the two is not fixed. In this view these two processes occur along the same branch of the stimulus processing sequence (i.e., they are "in series"). Sensory discrimination is then not related to any specific ERP component, but relates to different components in different circumstances.

It is currently not possible to choose between these two models of neural organization. However, in the parallel model, if the ERP and the motor response are time-locked at all, the closeness of the association will depend upon the proximity of each to the common branch point. By contrast, in the serial model the time-locking will depend upon which ERP component or components most closely relate to the sensory discrimination preceding the response. We have therefore tried to distinguish between these two models experimentally, by varying the timing of sensory discrimination after onset of an identical target stimulus in three separate circumstances. Using this approach we compared the relationship of the ERP to this discrimination by back-averaging from the response. If the parallel model were correct, then the time-locking between the two processes should be looser when the discrimination is delayed since each would be more removed from the common branch point (either because of an increased number of intermediate stages or a greater delay at each stage), resulting in an

increased cumulative "jitter" between the two. If, however, the serial model were correct, then the time-locking of the two processes would remain tight although the sensory discrimination might be more tightly coupled to certain components in some circumstances.

METHODS

Six subjects (3 men and 3 women, aged 26-39 years) participated in this study which had the approval of the Committee on Human Research at this medical center. Each subject participated in three experiments involving tasks of increasing difficulty. In each experiment, subjects were presented binaurally with a sequence of 210 tones (65 dBHL) at a rate of one tone every 3.7 seconds. Subjects were required to distinguish the rare (target) tones which occurred on 14% of the trials from frequent (non-target) tones that occurred on 86% of the trials and to extend their right middle finger as quickly as possible after detecting a rare tone. The sequence of the tones was pseudorandom with the constraint that no two rare tones occurred consecutively, and the order of the target and non-target tones was the same in all experiments. Task requirements were changed although in each experiment the target tones (2000 Hz; 50 msec duration) were identical and in each the response (right middle finger extension) was the same. In the first task (Task 1) the frequent (non-target) tone had a frequency of 1000 Hz and a duration of 50 msec, in the second (Task 2) it was 2000 Hz and 100 msec, and in the third (Task 3) it was 2000 Hz and 65 msec. Performance on these tasks was excellent. No subject made more than two omission errors. On the first two tasks no one made any omission errors, whereas on the third task no one made more than three omission errors. Responses were recorded only to correct trials. Three subjects also participated in an additional experiment in which they extended their right middle finger in response to the frequent stimulus in the first discrimination-task.

These tasks involved somewhat different cognitive requirements. The first task required a pitch discrimination whereas the other two tasks involved discrimination on the basis of stimulus duration. In these latter tasks, target and non-target stimuli could not be distinguished until the stimulus had exceeded 50 msec, whereas in the first task the stimuli were distinct from their onset. This arrangement allowed us to satisfy the main requirements of the present experiments, that is, to delay unquestionably the discrimination of target from non-target relative to stimulus onset so that we could explore the relationship of the ERP to the EMG onset under different circumstances.

Responses were recorded (bandpass 1-40 Hz) from Fp1, Fp2, Fz, Cz, and Pz electrode placements on the scalp (International 10:20 system) with reference to linked mastoids, and back and forward averaged from EMG onset using a Nicolet Pathfinder II system. EMG was recorded from an active electrode situated over the motor point of the extensor digitorum for the middle finger with reference to an indifferent electrode placed on the ipsilateral hand. We also compared the relative timing of the response in the three tasks by recording the EMG activity from the responding muscle measured from the point of stimulus onset, and established the latency of the averaged EMG onset in each of the three conditions. Eye movements were monitored with the Fp1 and Fp2 electrodes. No consistent eye movement potentials were identified. In the first discrimination-

task, however, these scalp locations were active, and the cerebral origin of the potentials recorded was established in other ways.[15] In brief, one subject with particularly prominent potential changes at Fp1 and Fp2, was studied with electrodes placed supraorbitally, infraorbitally, and at the inner and outer canthus of the left eye, each referenced to an indifferent electrode on the hand. No potential phase reversals that were consistent with eye movements were detected by this approach. In another experiment we recorded the ongoing EEG and individual motor responses while simultaneously averaging the response and found no relationship of eye movements to finger movement.

Peak latencies were determined by extrapolating lines from the ascending and descending portions of the wave of interest and taking the latency at the point of interest. Amplitude of a component was measured as a peak-to-peak amplitude between the peak of interest and both the wave preceding it and that following it. Peak onset and offset were taken as the peak latency of the preceding and following waves respectively. Statistical analysis was performed using a repeated measures analysis of variance.

RESULTS

Grand average responses to the rare tones recorded for the three tasks are shown in Figure 1. In the first task, the response consists of a positive peak frontally followed by a positive peak parietally, separated by a small inflection. In the grand average tracings recorded from Cz (and to a lesser extent in recordings from Fz and Pz) the two positive components merge together to form a single complex that cannot be reliably separated. Because in an earlier experiment these two positivities, one frontal and one parietal, seemed to represent the P165 and P3 components of the event-related potential[15] (Figure 2) we have labeled them as such in these figures. In the responses recorded in the other discrimination-tasks a similar evoked potential complex is obtained at Fz, Cz, and Pz. The relationship of the EMG activity to this complex has, however, been considerably changed with different task requirements (Table 1). This effect is shown in Figure 3 where the cerebral responses recorded from Cz and the average EMG in the three tasks have been superimposed and aligned by the cerebral responses. This figure demonstrates that the timing of EMG activity has been delayed relative to the event-related cerebral activity, although the latter is little changed at Cz between conditions. The major differences in cerebral responses recorded in these three tasks is that the frontal positivity has become progressively less conspicuous, especially in the recordings at Fp1 and Fp2 ($p < 0.02$) in the second and third task-conditions. There were no other significant amplitude changes. Moreover, Table 1 shows that the onset of EMG activity following the stimulus has been delayed
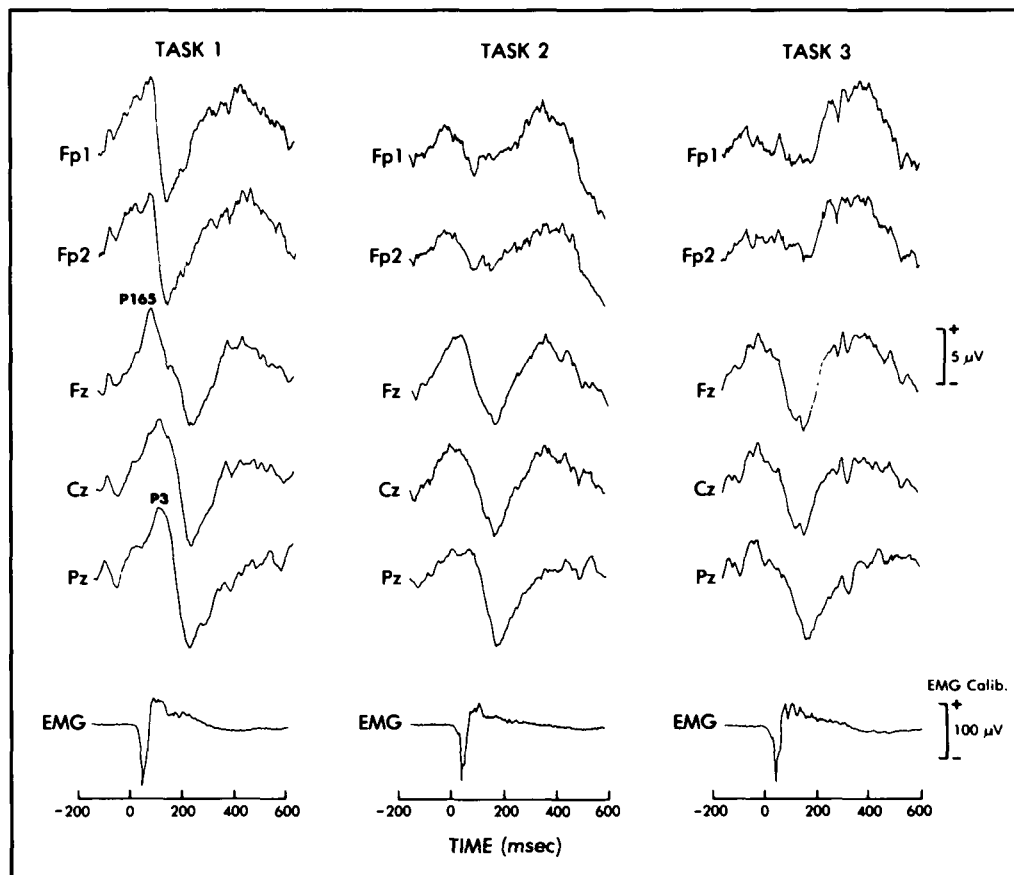

Figure 1 — Grand average cerebral evoked potential waveforms averaged from EMG onset of the motor response to the rare tone in three different discrimination-tasks. Responses were recorded from the electrode placements on the scalp indicated in the figure and referenced to linked mastoids. Averaged EMG was recorded from the motor point of the extensor digitorum and referenced to an electrode on the ipsilateral hand. In the first task the response consists of two positive peaks, one frontally (P165) and the other parietally (P3). In the responses recorded in the other tasks, the potentials recorded at Fz, Cz, and Pz, look similar, but at Fp1 and Fp2 the early positivity is considerably attenuated.
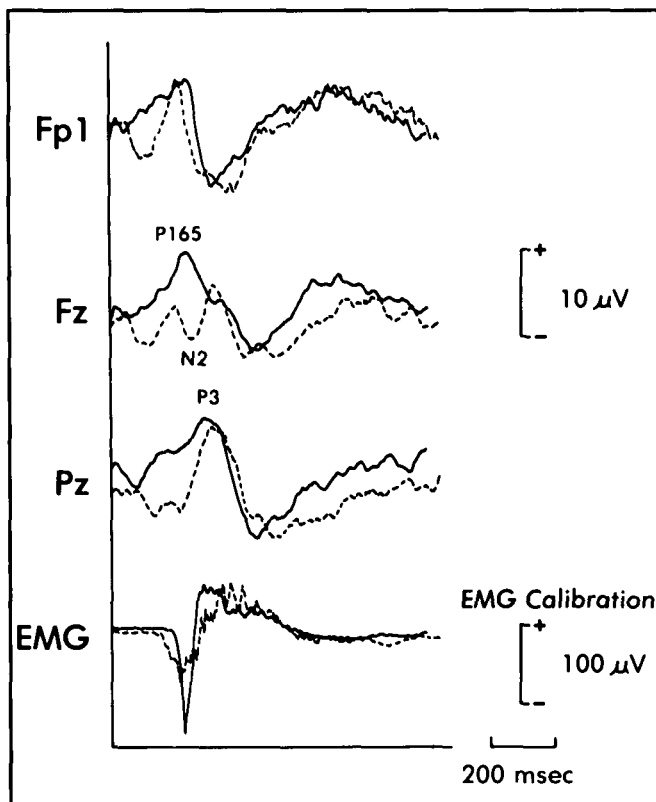
Figure 2 — *Response-synchronized waveforms (solid lines) and stimulus-synchronized difference waveforms (dashed lines) from the first-discrimination task have been superimposed and aligned by the compound muscle action potential produced by each averaging technique.[15] An early frontal positivity (P165) and later parietal positivity (P3) can be seen with essentially the same relationship to the motor response. In the response-synchronized average, however, there is a considerable attenuation of the early negativity (N2), especially at the Fz scalp location, and the two positive components merge to form a single complex.*

Figure 3 — *Grand average cerebral waveforms recorded from Cz with reference to linked mastoids, and the EMG of the responding muscle in three different discrimination-tasks. Responses were obtained by back averaging from the EMG onset of the motor response to the rare tone. The responses for the three tasks have been superimposed and aligned by the cerebral response. The cerebral response at Cz has been little changed by the changes in task requirements, but the relationship between this response and the EMG onset of the responding muscle has been altered considerably. As the sensory discrimination becomes more delayed, the onset of EMG activity occurs progressively later relative to the cerebral evoked potential.*

progressively in the three tasks. Since the response required was the same for each task this presumably reflects a delay in the sensory discrimination rather than in the execution of a response.

Figure 4 shows the response recorded in the first discrimination-task when subjects were asked to respond to either the frequent tone or the rare tone. Clear cerebral potentials can be seen in recordings back averaged from the response to the rare tones, whereas no reliable potentials could be identified in the recordings back averaged from the response to the frequent tone (and even if they are present, they are clearly markedly attenuated).

DISCUSSION

The fact that we were able to consistently record the ERP by back averaging from the EMG indicates that there is a close relationship between the cerebral events which are associated with the performance of a task and the timing of the motor response in all three tasks. This relationship is not fixed, but changes with task requirements. As the completion of the discrimination process is delayed, the entire cerebral response, averaged from the onset of EMG activity in the responding muscle, occurs earlier relative to the EMG activity. This change cannot be accounted for either by stimulus or response factors
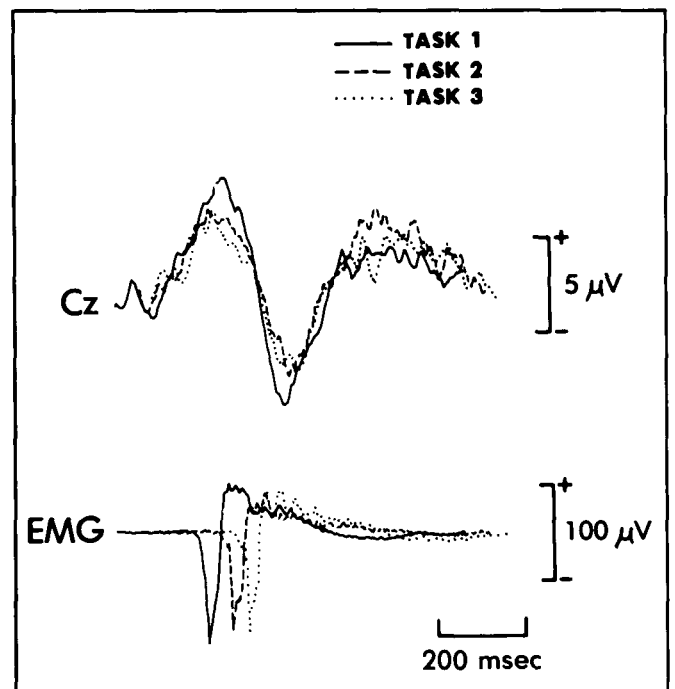
since both the target stimulus and the response itself were the same for each task.

The neural events underlying sensory discrimination must be in series with both the stimulus and the response. As mentioned in the introduction, if the ERP were on a separate parallel branch of the stimulus processing sequence from the branch on which sensory discrimination and response selection lay, then delaying the sensory discrimination should "jitter" the ERP relative to the response, since both will be further removed from their common neural generator (i.e., the branch point in Figure 5A). Consequently, back averaging from the movement should attenuate ERPs as task difficulty increases or if the sensory discrimination is delayed for other reasons. Since this did not occur (Figure 3), our findings suggest that the parallel model of neural organization is incorrect.

In addition we found a selective attenuation of the P165 component of the ERP relative to the P3 component when we back averaged from motor response in the second and third tasks (which were associated with a delay in initiating a motor response relative to stimulus onset). This suggests that the neural events that generate P3 are more time-locked to the motor response than those that generate P165 in these tasks. This observation again supports the serial model of neural organization (Figure 5B), in which the component most timelocked to the motor response should be that component closest to the time of sensory discrimination (i.e., P165 in the first task and P3 in the second and third tasks—see Figure 5). In contrast, under

Table 1: Relationship of Latency of Components of the Cerebral Responses to EMG Onset in Three Different Tasks Involving Recognition of an Identical Target Stimulus and Requiring an Identical Motor Response

	P165 onset[+] msec	P165 peak[+] msec	P3 peak[+] msec	P3 offset[+] msec	Motor latency* msec
Task 1	− 93 (25)	− 3 (51)	101 (21)	232 (18)	156 (32)
Task 2	−138 (28)	−77 (21)	76 (31)	166 (31)	257 (38)
Task 3	−152 (23)	−87 (30)	42 (43)	166 (26)	275 (47)
Significance**	p = .0148	p = .0171	p = .0089	p = .0006	p = .0001

[+] Values represent the mean latency of the component relative to the onset of the compound muscle action potential in the average EMG response. Values in parentheses represent standard deviations.

* The mean value of the onset of EMG activity in averaged EMG reponses using tone onset to trigger the averager. Values in parentheses represents standard deviations.

** p value obtained from the repeated measures analysis of variance described in text.
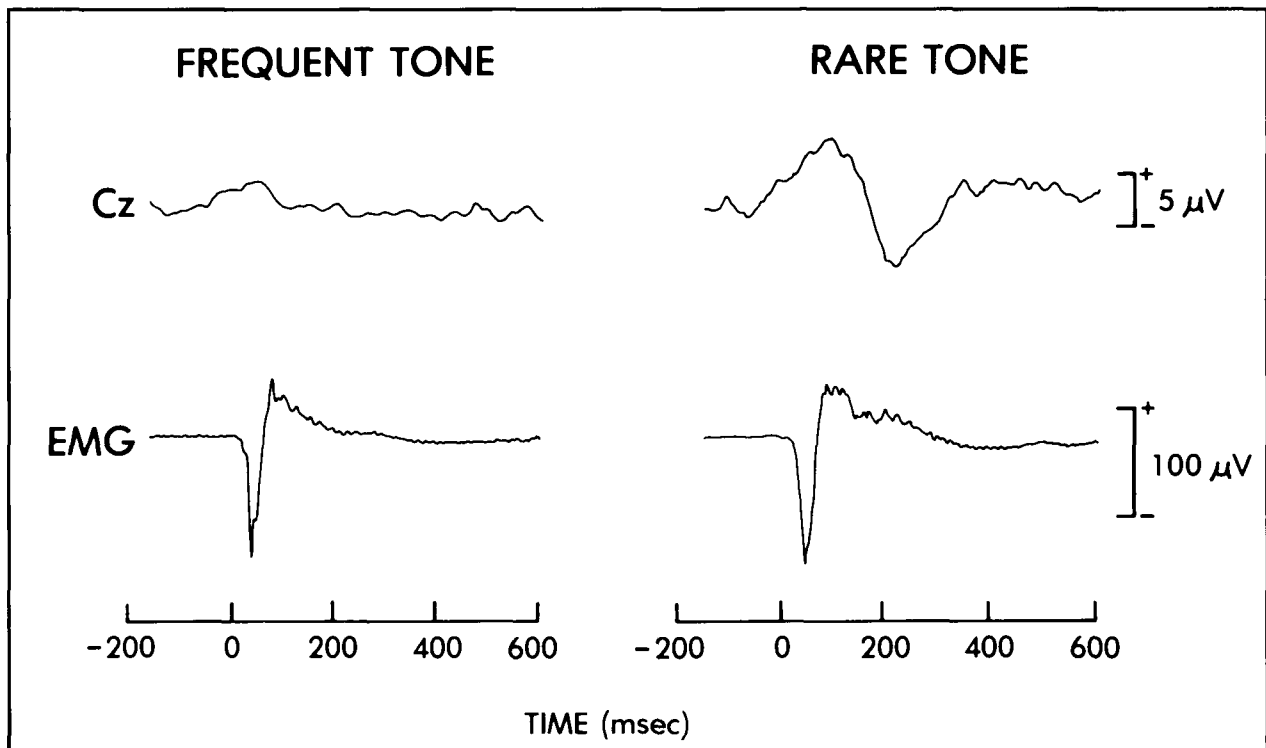

Figure 4 — Grand average cerebral responses recorded from Cz with reference to linked mastoids, and the EMG of the responding muscle in the first discrimination-task. Cerebral responses were obtained by back-averaging from the EMG onset of the motor response when subjects reacted to either the frequent tone (left) or the rare tone (right). In the rare tone average are the well formed responses shown previously in Figures 1 and 3. In the frequent tone average, however, we could identify no consistent cerebral response; even if the small deflections seen represent such a response, they are clearly markedly attenuated.

the parallel model, the component most time-locked to the motor response would be that component closest to the branch point (i.e., P165) in contrast to what we found (Figure 1). The frequency content (shape) of a wave may also affect how latency "jitter" influences amplitude; shorter duration waves will be disproportionately reduced compared to longer waves. This, however, should not have affected our results because the frequency of P165 and P3 was actually quite similar (Figure 2), but such an effect cannot be completely excluded.

Thus the present results suggest that the completion of the sensory discrimination process and response selection are occurring at variable points along a stimulus processing sequence which includes the ERP. These results also suggest that different levels of discrimination are occurring within the central

nervous system. On the one hand, there must be a neural distinction between the rare and frequent tone prior to appearance of any of the ERP components since these only occur as part of the cerebral response to the rare events. On the other hand, the subject does not generate a response to the rare tone during difficult tasks until later in the ERP sequence, suggesting that the completion of the discrimination process (and thus the decision to move) does not have a fixed time relationship to any initial discrimination between rare and frequent tones. One might speculate that following the initial discrimination a variable amount of confirmatory cerebral processing is required before the final decision is made and the response executed. This type of neural organization for information processing may explain why in some studies the response always follows
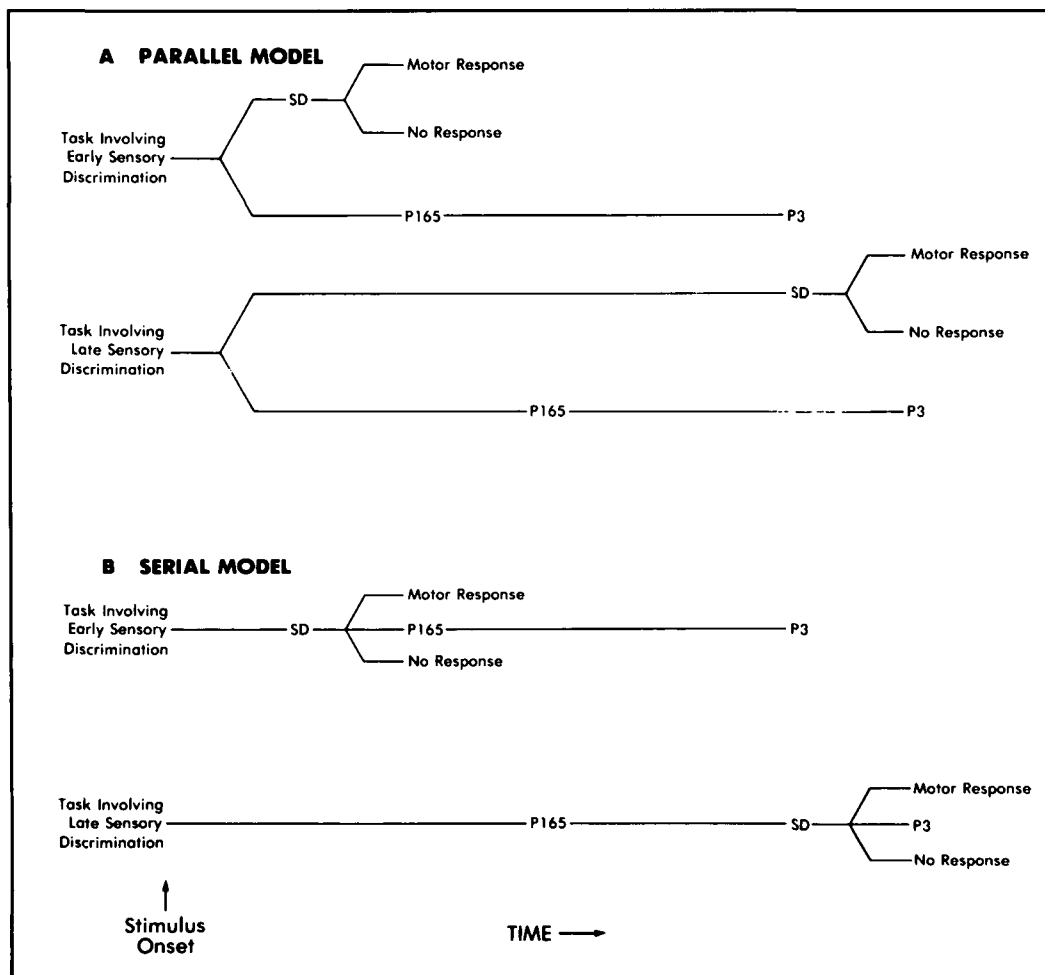
Figure 5 — Diagramatic representation of the two alternative schemes for the neural organization underlying completion of the sensory discrimination process (SD), response selection, and the ERP, considered in the text. Only the processing of the rare tone is depicted, and only the ERP components P165 and P3 are shown. Two levels of discrimination (early and late) are shown and the relative timing of events depicted in accordance with our experimental results. In A (parallel model), SD and response selection occur on a branch of the stimulus processing sequence parallel to the branch on which the ERP lies. In the task associated with early SD, our ability to record ERPs from the motor response depends upon the proximity of each to the branchpoint at which the parallel paths diverge. In the task with a delayed SD, both the ERPs and the motor response are delayed relative to stimulus onset and, in addition, the completion of the discrimination process has been delayed relative to the cerebral potentials so that now the response occurs well after the P165 latency. Under these conditions the cerebral and motor response have both been further removed from the branch point (and therefore should be less tightly coupled to each other) and recording from the motor response should attenuate the evoked potentials relative to the easy condition, particularly the later (more removed) components. In B (serial model), response selection, SD, and the ERPs occur on the same pathway. In the task with early SD the peak of P165 and the motor response occur together. In the other task SD does not occur until after completion of P165 and the response is considerably delayed relative to this cerebral potential; P3 may, however, be more tightly coupled to the motor response than P165, since it is closer to the branch point of the decision to respond. This model is not, however, entirely serial since a response is not always generated once the ERP has been evoked.

P3[5,6,16,17,18] whereas in others it seems more closely coupled to N2[7,8,19,20,21] or even earlier events.[22] These results also have other, more important implications. They suggest that specific components of the cerebral evoked potential are not related to specific stages of information processing in any consistent way, but rather that they have a variable relationship depending upon the nature of the task.

The fact that we were able to reliably record potentials by back averaging from the response to the unexpected rare tone implies that these potentials must be closely linked to the decision to move. The absence or marked attenuation of such potentials when we back averaged from the motor response to the frequent tone (Figure 3A) suggests another dimension to the neural organization of discrimination and response under our experimental conditions. If sensory discrimination were an event that occurred in the processing of both rare and frequent stimuli then the electrical accompaniments of this event should, if present at all, be equally recordable from the response to either stimulus. The fact that we could not do this from the response to frequent stimuli but could from the response to rare stimuli suggests that the complete (as opposed to any initial) sensory discrimination process only occurs in response to the rare stimuli. Thus when a subject makes a motor response to the frequent but not the rare stimulus, it is not a decision to move that guides the behavior, but rather a decision not to move to the rare (unexpected) stimulus. Our results were the

same even when the stimuli to be distinguished were different only in that one lasted longer than the other by 15 msec or more. This suggests that even when initial neural processing is similar, stimuli are still distinguished by attention to a single channel. This approach (i.e., a go/no-go decision based on recognition of only one of the two stimuli) may be more efficient than a choice-decision based on recognition of both stimuli. Such an organization might explain why event-related potentials, which have been closely linked to sensory discrimination and response selection by many investigators are recorded primarily in the potential evoked by the rare stimulus, even when the task is to respond to the frequent stimulus.

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