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NEURONAL VS. SUBJECTIVE TIMING FOR A CONSCIOUS SENSORY EXPERIENCE

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In order to investigate a relation between conscious experience and specific kinds of neuronal activities, it is virtually necessary to study brain function intracranially in the awake, responsive human subject. Obviously, any such direct experimental investigation is subject to the severe limitations imposed by the rights of the subject and the ethical responsibility not to add unwarranted risks to the therapy. However, it has been possible to utilize gainfully the opportunities afforded by the surgical implantation of electrodes intracranially for therapeutic purposes[1,2], in informed and consenting human subjects*. When electrode contacts are located in various parts of the cerebral somatosensory system, innocuous electrical stimulation procedures can be employed in a controlled fashion to manipulate and investigate neuronal function in a causative, rather than merely correlative, relationship to conscious sensory responses. A subdural stimulus to primary somatosensory cortex (S I) initiates an input different in its entry path and pattern from that generated by a peripheral sensory stimulus[3]. Nevertheless, we have found it possible to elicit conscious sensory experiences with natural-like somatosensory qualities in most subjects by careful regulation of electrical stimulus parameters (particularly of intensity, train duration, and pulse frequency) to near-liminal values[3,4,5]. This is in contrast to the paresthesias more commonly reported in the pioneering studies of Penfield and others[3].

Two temporal features for specifically required cerebral processes have emerged from the study. One presents a substantial minimum time period of activation of cerebral neuronal systems, in order to achieve an adequate state for production of a conscious sensory experience[3,4,6]. The other invokes a mechanism for referral of the subjective timing of

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*All the investigational procedures have been reviewed (in relation to any possible risk factors and to the conditions of informed consent) and approved by an independent Committee on Human Experimentation in Mt. Zion Hospital, in accordance with guidelines set out by the National Institutes of Health, U.S. Public Health Service.

the experience retroactively, to a time close to the initiation of the sensory signal[7].

Minimum train duration for effective stimuli. Discovery of these temporal features began with the finding that direct electrical stimulation of postcentral gyrus (S I cortex) required repetition of pulses for surprisingly long periods of time in order to elicit any conscious sensation. The minimum train duration (T.D.) of the stimulus varied with pulse intensity, but was generally about 0.5 sec for the liminal intensity below which nothing could be felt (Fig. 1)[4,8].

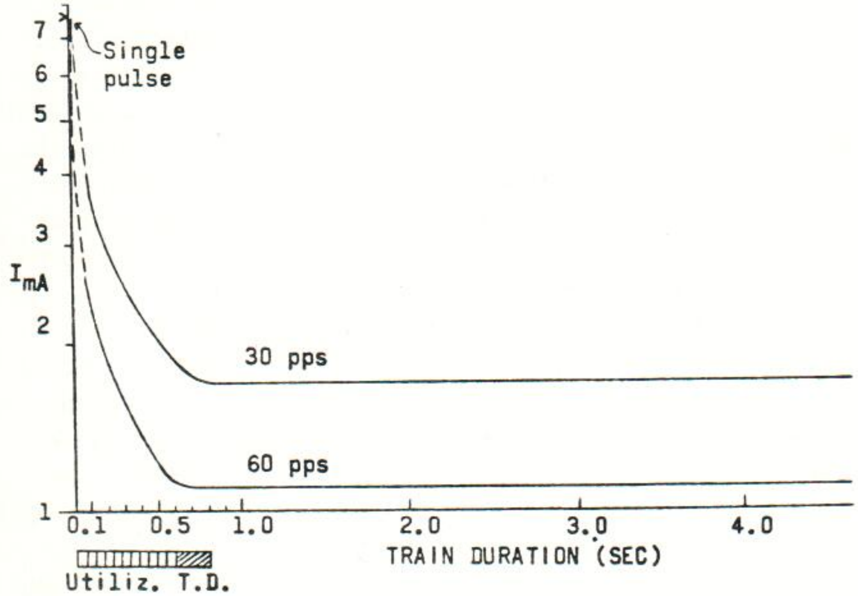

Fig. 1. Intensity/train duration combinations for stimuli (to postcentral gyrus) just adequate to elicit a threshold conscious experience of somatic sensation. Curves are presented for two different pulse repetition frequencies, employing rectangular pulses of 0.5 msec duration. (From Libet, 1966)[8].

This form of intensity-T.D. relationship, including the value of about 0.5 sec for utilization T.D. at liminal intensity, was independent of variations in other stimulus parameters, including pulse frequency. It was also found to hold for stimuli applied to subcortical sites in the specific projection system, i.e., in white matter below S I, and in brain stem targets judged to be n.VPL (or VPM) of thalamus or medial lemniscus (LM). However, this was in sharp contrast to stimuli in the periphery (skin or nerve)[4,6] and in dorsal columns[9]; at these levels a single pulse is quite effective and repetition is relatively inconsequential in its effects on threshold intensity.

Insufficiency of primary evoked response. Even though the initial stimulus pulses in the specific sensory system were ineffective for eliciting sensation, they nevertheless could elicit substantial electrophysiological responses. "Direct cortical responses" were recordable, adjacent to the stimulus at S I cortex, in response to the first as well as to each succeeding pulse of the stimulus train[3]. Also, a primary evoked potential response at S I, similar to that elicited by a peripheral sensory stimulus, is produced by a pulse in n.VPL or LM (Fig. 2). It followed from the latter that the cerebral

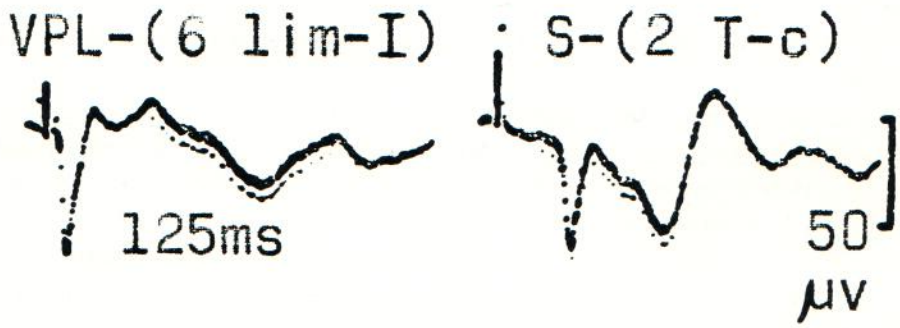

Fig. 2. Evoked potentials of somatosensory cortex, recorded subdurally, in response to thalamic (n.VPL) or skin stimuli in the same subject (patient with heredofamilial tremor). Each tracing is the average of 250 responses at 1.8 per sec; total trace length, 125 msec VPL: stimuli in ventral-posterolateral-nucleus of thalamus; subject reported not feeling any of these stimuli, although current pulses were at 6 times liminal-I for VPL electrode (liminal-I being minimum peak current per pulse to elicit sensation when delivering a > 0.5 sec train of pulses, 60 pps in this case; see Fig. 1). S: stimuli at skin; current at twice threshold, every stimulus pulse was felt. Note the shorter latency of the primary (surface positive) evoked response to VPL stimulus. (From Libet et al., 1967)[10].

processes associated with the primary evoked response of S I cortex to a specific projection volley, even in the context of awake and attentive brain function, were insufficient to induce a conscious sensory experience[5,6,10]. Also in accordance with this conclusion were the findings on evoked potentials recorded subdurally at S I cortex in response to single pulse stimuli to the skin. A pulse below threshold for producing any sensation could still elicit a primary evoked potential but little or no later components; a pulse at or above threshold elicited the later evoked components as well[10].

These findings led to the hypothesis that suitable neuronal "activations" at cerebral levels must proceed for a substantial minimum time period (of up to about 0.5 sec) in order to give rise to any conscious sensory experience. It was inferred that an adequate single volley of peripheral nerve impulses meets this requirement by its capability for eliciting a series of evoked cortical responses, early and late[5,10]. The later components have been thought to depend upon extralemniscal pathways[11] and presumably would not be elicited by a single volley generated in the specific lemniscal system well above the medullary nuclei. However, no definitive statement can presently be made about the ultimate locations and neuronal nature of any prolonged activations that may directly "represent" the conscious sensory experience[3,6].

Retroactive effects of a conditioning cortical stimulus, on a peripherally-induced sensation. How could one further test the possibility that the proposed hypothesis is in fact applicable to the case of a minimally adequate peripheral stimulus, a single threshold pulse to skin? The hypothesis would predict the existence of a period of up to 0.5 sec, following such a single pulse stimulus to skin, during which alterations of cortical activity might be able to modify the elaboration of the conscious sensory response to that pulse. It had been reported[12] that the conscious perception of a normally effective peripheral sensory stimulus could often be suppressed by simultaneous electrical stimulation of the appropriately related cortical sensory area. We were now able to show that such a suppression could also be retroactive. The delayed or conditioning stimulus consisted of a train of pulses applied to S I cortex; to be effective it had to have a minimal intensity of 1.1-1.2 times the liminal intensity needed for eliciting its own conscious sensation, and a train duration > 100 msec. The conscious experience normally elicited by a preceding test pulse to the skin could be abolished when the cortical conditioning train was begun after the skin pulse, up to 200 msec in most subjects, and up to 4-500 msec later in some[3,6]. To obtain this effect, the skin pulse itself had to be near threshold in intensity and also applied spatially in or adjacent to the peripheral field of the stimulated cortex (i.e., in or near the somatic area to which the sensation elicited by the cortical conditioning stimulus was referred). Retroactive inhibition producible by a peripheral (sensory) conditioning stimulus was of course already well-known[13], especially with visual stimuli. Our findings demonstrated that it could be initiated at the direct cortical site which received the afferent projection of the preceding sensory test stimulus and the quantitative timing relationships at the cortical level.

Retroactive enhancement was also detected in a number of subjects, perhaps in association with a somewhat different positioning of the cortical electrode. This type of conditioning effect was demonstrable when the test consisted of two separate pulses applied to the same site on the skin but delivered about 5 sec apart, and the subject asked to compare their subjective intensities. When the two delivered skin pulses were electrically equal or unequal (by about 10%), subjects reported them respectively to be subjectively equal or unequal (in the appropriate direction). However, if a conditioning cortical stimulus was begun at any time up to 200-500 msec following the second of two equal skin pulses, some subjects consistently reported that the second test pulse to the skin felt distinctly stronger than the first. (These same subjects never exhibited retroactive inhibition by the conditioning cortical stimulus, which was applied at the available electrode located on a fixed cortical site in each case.)

The finding of retroactive enhancement helps to select among some possible alternative interpretations of the retroactive actions. We must recognize that our operational definition of a conscious sensory experience is a report by the subject that he is presently aware of having had such an experience during the preceding test period, a few seconds earlier; this obviously adds the processes of short-term memory and of recallability to those that may be required to produce the subjective sensory experience. Generalized electroconvulsive shock treatment is known to produce some retroactive amnesia for recent events. In the case of retroactive inhibition by a cortical conditioning stimulus, it might be argued that there is in fact an early conscious experience of the test stimulus, but that the later cortical stimulus "disrupts" the processes of short-term memory for the experience. However, no such memory disruption could apply to retroactive enhancement. But, even for the case of retroactive enhancement, the view that there is no significant delay, for the conscious experience of a skin stimulus, may be retained by employing another sort of argument; it has been suggested that the experience of the test skin stimulus may later be reported as having been more intense, than it was in fact, because the delayed conditioning cortical stimulus may in the interim have induced some kind of "reinforcement" of the processes involved in recalling the intensity of the experience. Although this argument cannot be presently excluded, it introduces ad hoc assumptions and mechanisms that are not required by our hypothesis. Also, it does not explain why the initial primary cortical response, evoked by a stimulus to skin or to VPL/LM, elicits no conscious sensory experience at all (see above). We suggest that the simplest tenable conclusion from our findings on the retroactive effects of the cortical stimuli is that, as hypothesized, the threshold skin stimulus initiates cerebral processes which proceed for a substantial time before becoming adequate, and that during this delay period other imposed alterations in cortical activity can affect the nature of the conscious sensory experience that eventually "appears".

Is there a subjective delay for a peripheral sensation? We come now to the intriguing question of whether the *subjective experience* of a peripheral stimulus is actually delayed for the same substantial period of time that is postulated to be necessary for achieving the *neuronal adequacy* (to elicit the experience). It seemed to be impossible to establish experimentally the absolute timing of the subjective experience. Values that derive from the speed of any behavioral response to a stimulus, i.e., reaction time, may be invalid; clearly, it is possible for the subject to have made the response to a stimulus unconsciously and to have become subjectively aware of the stimulus afterwards. Instead, we adopted a procedure involving relative timing order of two sensory experiences. The validity of this procedure was based on the availability of a "reference" sensation elicited by a stimulus to S I cortex; since a minimum or utilization T.D. is known to be required in this case, in order to produce any conscious sensation, it seemed reasonable to assume that this subjective experience could not begin before the end of such a stimulus train (though it might begin after the end). The single test pulse at threshold intensity to the skin can be delivered at any desired time relative to the end of the minimum T.D. applied to S I cortex (see Fig. 3), and the subject asked to report which of the two sensations appeared first, that elicited at the skin or the one (recognizably different) elicited by the liminal cortical stimulus. The results of several such experiments with different subjects indicated clearly that there was in fact essentially "no delay" for the subjective sensory experience induced by the skin pulse. That is, the skin pulse-sensation was reported to occur "first" even when this pulse was delivered at a time as little as 100 msec ± before the end of the minimum cortical T.D.; when the pulse was delivered at or near the end of the cortical T.D., the two sensations were reported to appear synchronously.

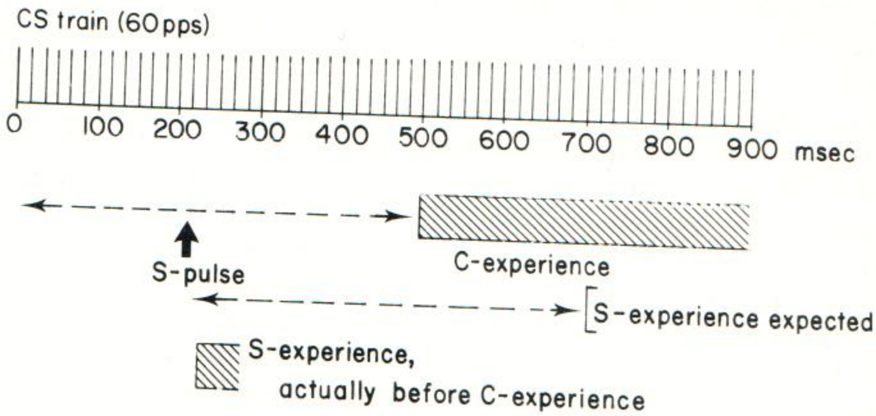

Fig. 3. Subjective timing of sensory experience for a skin pulse relative to that for stimulus train at S I cortex. Diagram shows cortical stimulus train at liminal intensity, producing a sensory (C-) experience no earlier than the utilization T.D. of 500 msec (see Fig. 1). With a near-threshold single pulse to skin (S- pulse) delivered 200 msec after onset of CS train, subjective sensory experience of it (S-experience) was expected to occur after the "C-experience" (if a similar period of cerebral activations was required). Actually, S-experience was reported to precede C-experience. (From Libet et al.[7])

The absence of any substantial delay for the subjective experience of the skin pulse appeared to falsify our general hypothesis; but, strictly speaking, the hypothesis had dealt with a delay in neuronal <u>adequacy</u> rather than in subjective timing. Continuing tentatively with the assumption that the timing of neuronal adequacy for both the peripheral and cortical stimuli have similar delays, a modified working hypothesis was developed that might explain the discrepancy between the timings of the <u>subjective</u> experiences for the two stimuli.

<u>Modified hypothesis: Subjective referral in time, retroactive to primary evoked response</u>. In the modified hypothesis there are two new features which apply to peripheral sensory inputs: (1) The early or "primary" evoked response of S I cortex, to the afferent volley delivered by the fast, specific lemniscal projection system, is postulated to serve as "time-marker"; and (2), there is an automatic subjective referral of the conscious experience backwards in time to this time-marker, after the delayed neuronal adequacy has been achieved. With such an arrangement this sensory experience would appear subjectively to occur with no significant delay from the

arrival of the fast projection volley. It should be recalled that the primary evoked response at S I begins about 10-25 msec, depending on the bodily location, after delivery of a single pulse peripheral stimulus (e.g., Fig. 2); also, that a near liminal stimulus train applied to the pial surface of S I cortex does not elicit a response resembling the primary evoked potential, presumably because it does not initially excite the ascending projection fibers (from ventrobasal thalamus) which are responsible for this response[4,5]. Fortunately, it was possible to subject these newly added postulates to experimental tests that could potentially falsify or contradict them.

<u>Subjective timing for thalamic vs. cortical stimulus trains</u>. One type of test is based on the unique conditions associated with a stimulus applied in a cerebral but subcortical level of the specific projection pathway. As noted above, a stimulus applied to LM or n.VPL requires the same kinds of minimum train durations as one applied to S I cortex, in order to elicit a conscious sensory experience. However, unlike S I cortex, each volley in LM or n.VPL should generate a primary evoked response in S I cortex (e.g., Fig. 2); this primary response should supply the same putative timing signal as does the single skin pulse. Consequently, the modified hypothesis would lead to a startling prediction: The subjective timing of a sensory experience elicited by a stimulus train in LM or n.VPL should be essentially similar to that for a skin pulse (i.e., as if there were no perceptible delay from the onset of the LM train); this should occur in spite of the experimental fact that the stimulus to LM or n.VPL does not become adequate until its train duration has achieved a substantial value of up to about 500 msec, depending on the intensity employed.

A diagram of the experimental paradigm for these tests with pairs of temporally-coupled stimuli is shown in Fig. 4. For the cerebral stimulus train at 60 pps, whether cortical (S I) or subcortical (LM or n.VPL), the intensity (peak current per pulse) was adjusted, for practical experimental reasons, so that a minimum train duration of about 200 msec was required in order to elicit any conscious sensory response. When a peripheral stimulus pulse (P) to the skin is delivered synchronously with the <u>start</u> of the stimulus train to S I cortex (C), we would expect the subject to report that the skin-elicited sensation appears before the cortically-induced one, as in previous experiments (see section I above). On the other hand, a similarly synchronous delivery for a skin stimulus relative to onset of a stimulus train in n.VPL or in LM should result in an apparent synchrony for the subjective onset of both conscious sensations,

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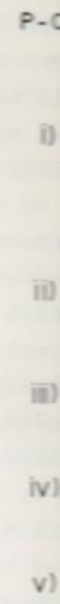

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according to the modified hypothesis (Fig. 4). Related predictions can be made for cases of other timings of the skin stimulus relative to the onset of cortical and thalamic stimulus trains.

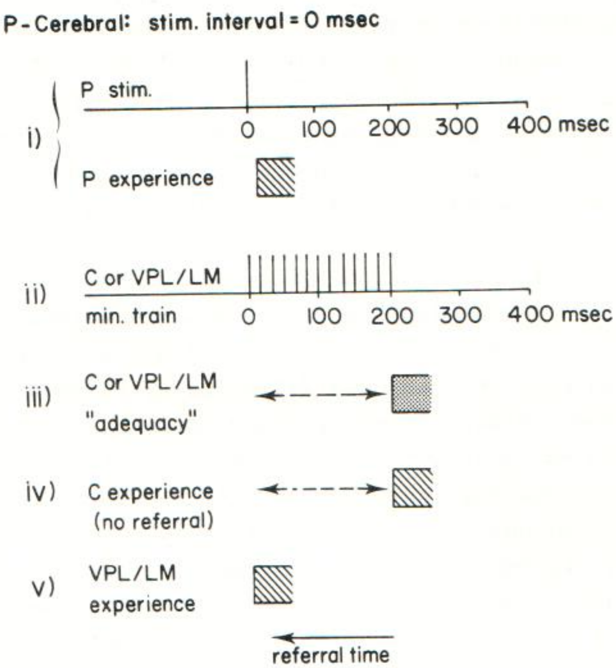

Fig. 4. Timing relationships of reported subjective experiences, for peripheral vs. cerebral stimuli, as predicted by the modified hypothesis. Each pair of stimuli consists of a peripheral pulse (P) and a cerebral train of pulses. The cerebral stimulus train may be either at S I cortex (C) or in n.VPL (or LM). Therefore, timing relationships may be compared for two types of pairs: (a) P paired with S I cortex (C); and (b) P paired with n.VPL/LM. In this set the time interval, between (i) P stimulus and (ii) the onset of a cerebral train (C or VPL/LM) = 0. P usually consisted of a single pulse to skin of the hand, on the side of body opposite to that in which a referred sensation was elicited by the cerebral stimulus. The cerebral stimulus was a train of pulses, 60 pps, with peak current I adjusted so that a minimum train duration of about 200 msec was required in order to produce a conscious sensory experience; this meant that "neuronal adequacy" for either C or for VPL/LM could not be achieved before 200 msec had elapsed (as in iii). The subjective timing of the experience of C stimulus should be delayed for a similar time (iv); but the postulated subjective referral retroactively, to a time associated with the primary evoked cortical response elicited by the afferent specific projection volley, should place the experience of both P and of VPL/LM earlier, as shown in (i) and (v). (From Libet et al.[7])

The experimental results of the studies carried out support the modified hypothesis. (The full experimental study will be reported elsewhere[7].) For each subject, the subjective timing orders were determined not only for test pairings of a peripheral and cerebral stimulus, but also for test pairs in which both stimuli were peripheral. With either type of test pairing, three or more different time intervals between the two stimuli in each pair were employed. Almost all subjects were essentially 100% "accurate" in their subjective timing orders for two peripheral stimuli delivered with intervals of ± 200 msec, but only partially accurate for ± 100 msec intervals. When a skin stimulus was paired with a stimulus train to LM/n.VPL, the relative time orders reported for the two subjective sensations tended to approximate those reported for similar intervals between two peripheral stimuli. For example, consider the tests in which the two stimuli of each pair were delivered synchronously, stimulus interval = 0. If a P pulse to right hand was delivered synchronously with another P pulse to left hand, the subject usually reported that the sensory experiences for right and left hand appeared subjectively at the same time. Similarly, as in Fig. 4, if a P pulse to right hand was delivered coincidentally with the starting of a train of stimulus pulses in right VPL (which elicits a sensation referred to the left hand, with electrode placement in a given subject), the subject usually reported that the right and left hand sensations began together. This occurred in spite of the fact that the VPL stimulus intensity was set so as to require a minimum train duration of 200 msec in order for the subject to report any conscious sensory experience for it at all. This result with VPL/LM contrasted sharply with relative time orders for skin vs. S I cortex. If a P pulse to right hand was delivered coincidentally with the start of a train of stimulus pulses (minimum of 200 msec required) to the right S I cortical area representing the left hand, the subject usually reported feeling the sensation in the right hand before the onset of that in the left hand (as diagrammed in Fig. 4).

Another type of test series of the hypothesis is in progress. It is based upon the consequences of unilateral but severe pathological destruction of the specific projection pathway at a cerebral level, i.e., upon a loss or deficiency in the source of the putative timing signal for one side of the body. The hypothesis would predict that subjective timing of a sensation produced by a peripheral stimulus to the affected side of the body would show a substantial delay relative to that for a peripheral stimulus to the normal side. Thus far, only one patient has been studied who fulfilled the pathological criteria. In tests for subjective sensory timing orders resulting from paired stimuli, one to each hand, this subject exhibited a "delay" of roughly 200-400 msec for the abnormal (left) side.

General discussion. The present proposal of a new functional role for the specific projection system, in the subjective timing of a sensory experience, would extend the already accepted role for this system in mediating subjective localization of a sensory stimulus in space. To the already familiar though still mysterious "automatic" subjective referral of sensory perceptions (bodily image, visual images, etc.) in the spatial dimension, we are now adding an "automatic" subjective referral in the temporal dimension. A number of further interesting possible implications and inferences stem from the temporal features postulated here for the conscious sensory process:

(a) A requirement for a substantial period of neuronal "activations" could act as a "filter" mechanism in keeping much ongoing sensory inputs from reaching conscious levels, if most of these only elicit shorter-lasting activations of the cortex[6].

(b) One may speculate that this requirement may have a more general significance for the mechanisms that differentiate all kinds of conscious from unconscious mental functions, not merely those in sensory responses. A controlling physiological factor in the transition between unconscious and conscious experiences generally might simply involve a shorter vs. an adequately longer duration respectively for the suitable neuronal activities[14].

(c) A delay in achieving neuronal adequacy would provide an opportunity for modifying or modulating a perception during the delay interval. Experimental examples of modulation by delayed inputs to the sensory system were already discussed above in connection with the retroactive effects of delayed conditioning stimuli to S I cortex. However, possible delayed modulators might also encompass endogenous cerebral actions. For example, psychological suppressor or censor actions, as postulated by Freud, would require that unconscious cerebral processes intervene to block or modify the production of a conscious sensory or other experience. The presently postulated delay in achieving neuronal adequacy for the experience provides an opportunity for the interaction of such physiological mechanisms, even after the arrival of the initial afferent projection message at the cortex.

(d) A substantial delay in the actual production of a conscious sensory experience, as distinguished from its subjective timing, would imply that quick behavioral responses, even when complex and purposeful, would arise unconsciously[8]. This could put limitations on the kinds of actions in which conscious free choice could be exercised.

(e) The findings relative to a retroactive subjective referral of an experience in time, appear to present us with a temporal dissociation between a subjective sensory experience on the one hand, and the adequate neuronal state that elicits or accompanies the experience on the other. (Professor Donald MacKay raised the possibility that the subjective antedating of the experience might be due to an illusory judgment by the subject when he reports the timings after a test, and not to an actual difference in subjective and neuronal timings when they occur. It could be argued that during the recall process, cerebral mechanisms might "read back" to the primary evoked response and then construe the timing of the experience to have occurred prior to the time of the actual occurrence of the original experience. Again, such a possibility cannot presently be excluded; it would, however, suffer from an inability to explain the absence of asynchrony or "jitter" among the immediate subjective experiences for a variety of synchronous sensory inputs of differing intensities, etc., if the postulated delays in neuronal adequacy are accepted.) Some possible philosophical implications of such a temporal dissociation for the mind-brain relationship can only be touched upon here; they will be developed more fully elsewhere. On the face of it, an apparent lack of synchrony between the "mental" and the "physical" would appear to provide an experimentally-based argument against "identity theory", as the latter has been formulated by Feigl, Pepper, etc.[15]. Of course, it could be argued that a dissociation or discrepancy in the temporal dimension is, in principle, no different from the well-known discrepancy in the spatial dimension (the discrepancy between the subjective referral of an image in space and the spatial pattern of the neuronal activities that "give rise to" the spatially patterned experience). Since there is presently no logical explanation of the relationship between the "mental" and the "physical" (cerebral) events[16], there are currently no necessary restrictions on the manner in which subjective experiences may relate either spatially or temporally to the neuronal activities that "underlie" them. Yet, a temporal dissociation between the mental and physical events would further stretch the concept of psychophysiological parallelism or, if one prefers[15], of co-occurrence of corresponding mental and neuronal states. It could thus have an impact on the philosophical interpretations of such parallelisms or co-occurrences when formulating alternative theories of the mind-brain relationship.

SUMMARY

Two temporal features for the cerebral processes that lead to a conscious sensory experience are proposed:

(a) A substantial delay (up to about 0.5 sec) before "neuronal adequacy is achieved.

(b) A subjective referral backwards in time, after neuronal adequacy is achieved, which antedates the experience to correspond to the time of early cortical responses to specific afferent projection signal.

Evidence for these postulated features, obtained with intracranial stimulation and recording techniques in awake and attentive human subjects, is presented. Some implications of these features for perceptual and conscious mental functions are suggested.

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