Visibility of Brief Images:
The Dual-Process Approach

Talis Bachmann[1]

University of Portsmouth, King Henry Building, Portsmouth PO1 2DY, United Kingdom

If successive, brief visual images are exposed for recognition or for psychophysical ratings, various effects and phenomena of fast dynamics of conscious perception such as mutual masking, metacontrast, proactive enhancement of contrast, proactive speed-up of the latency of subjective visual experience, the Fröhlich Effect, the Tandem Effect, attentional facilitation by visuospatial precuing, and some others have been found. The theory proposed to deal with these phenomena proceeds from the assumption that two types of brain processes are necessary in order to consciously recognize visual stimuli: (1) fast, specific processes of encoding that allocate and reactivate the stimulus representation which is based on the activity of selected cortical neurons and (2) relatively slower processes of facilitation of the activity of this specific representation that are mediated by the excitatory modulation of the EPSPs of those selected cortical neurons by the ascending input from nonspecific thalamus. The *perceptual retouch* construct is proposed in order to characterize and analyze the interaction of (1) and (2). The neurophysiological characteristics of this bifunctional system of afference help to put forward several predictions that are found to be consistent with the empirical regularities of the above-described perceptual-attentional phenomena. These data form a body of converging evidence that is consistent with the predictions of the perceptual retouch approach. © 1997 Academic Press

1. INTRODUCTION

Many of you who read this sentence here, now, believe that the so-called nonspecific thalamus in your brains should be active in order to somehow help to be aware of the visual material provided on this page. The present author shares this belief. The idea about the activity of reticular formation and nonspecific thalamic nuclei as the correlate of awareness and conscious states in humans is quite well known and goes back to seminal works of many researchers such as Bremer (1935), Moruzzi and Magoun (1949), Magoun (1958), Lindsley (1960), Jung (1958), Jasper et al. (1958), and Gellhorn (1961). With the accrual of new facts from neurophysiology, neurology, and psychophysiology this idea has been developed further and scrutinized, without losing its general popularity (e.g., Riklan & Levita, 1969; Brazier, 1977; Hassler, 1978; Scheibel & Scheibel, 1967, 1970; Scheibel, 1981; Steriade, 1981; Bogen, 1995; Newman, 1995). But it was only in the 1980s when this idea was brought over to psychophysics and visual information processing in the form of more or less detailed explanations, models or simulations for various phenomena and research problems of conscious vision. One could mention here the timing of subjec-

491

tive tactile experiences (Libet, 1978), preconscious versus conscious perceptual processing (Dixon, 1981), visual masking and metacontrast (Bachmann, 1980, 1984, 1994), attentional binding of features into coherent perceptual objects (Crick, 1984), various phenomena of perceptual multistability and selective attention (Bachmann, 1985; LaBerge, 1995), and general information-processing (meta)theories (Baars, 1988).

Some researchers who adore the idea of nonspecific thalamic processes as being crucial in mediating conscious awareness can be characterized as the proponents of the dual-process approach (e.g., Crick, 1984; Bachmann, 1984; Baars, 1995; Bogen, 1995; Newman, 1995). The core idea that stands behind this approach has been well expressed by Kimble (1977): the specific system of cortical neuronal representations (SP) of the specific features and characteristics of the visual environmental objects that receives its afferents through the primary, classical pathways (e.g., through the lateral geniculate body that sends axons to V1 and then to further visual centers) provides the basis for the *contents* of the conscious perceptual representation (the ''what-it-is'' of the image) whereas the nonspecific reticulo-thalamic system (NSP) provides necessary background neural activity or modulations for the emergence of the *consciousness quality* of the contents of activated SP-representations to emerge. SP, no matter how well activated within this system *per se,* is necessary, but insufficient for conscious perception. Its interaction with NSP, however, seems to constitute the sufficient conditions for any perceptual object to be represented in the awareness of a healthy, awake, subject (Bachmann, 1984, 1994; Baars, 1995). Even if the sufficiency notion seems premature at the present stage of our knowledge as unfounded by firm empirical support, it seems still to be true that interaction of SP with NSP is a necessary condition for conscious perception among, perhaps, some other prerequisites (see, e.g., Crick & Koch, 1995, concerning the problems with the view that relatively low level SP-representations may be sufficient to mediate visual awareness). This requires us to regard the SP-system as a multilevel representational medium, the precise nature of interaction of which with NSP modulation remains largely hypothetical. It may well be that the modulation of the lower-level SP-neurons (e.g., in V1) by the ascending NSP pathways constitutes a necessary condition for these neurons to become a part or a prerequisite to the activation of a larger and multilevel representation that is needed for establishing visual awareness.

This approach is not without its serious problems. Some of them are methodological and philosophical (consult, e.g., Searle, 1994; the target article by Block, 1995, and its commentaries; Cogan, 1995; Dennett, 1996). For many it seems, if not impossible, then questionable to try to cross the gap between the domains of natural-scientific data that can be analyzed from the third-person perspective and the first-person perspective of the realm of subjectivity. Some other problems are more related to neuroscience and within-domain theories (e.g., Greenfield, 1994). One could mention also the falsifiability problem because of the seemingly unspecific generality of the ''thalamus-as-the-awareness-mechanism'' approach. The normal-scientific way out should be then (1) to look for the regularities and working characteristics of the real neuronal systems that constitute the NSP-system and see if some of these specifications could provide more or less detailed, falsifiable predictions for the psychophysical experiments with human observers and (2) to remain cautious by

avoiding discussion in terms of causal relations between the subsystems of our theoretical concern and keep speaking about the neural *correlates* of conscious awareness. (Or NCC, as suggested, e.g., by Crick, 1996.) This interdisciplinary and ''correlational'' approach has been taken by the present author. The main objective of this article is to introduce a metatheory for a variety of empirical visual-perceptual phenomena as explained from the dual-process point of view together with respective experimental evidence. Moreover, I would like to stress here that most of our data and theories about perceptual and attentional processes are based on conscious reports that are provided by the observers as the subjects of psychophysical experiments. It seems to be natural to see if neuroscience data about the mechanisms that seem to be necessary for creating conscious representations for perceived stimuli can be used in order to develop psychophysiological models that predict psychophysical data. Historically, this approach stems from what Fechner (1882) termed ''inner psychophysics.''

2. THE CHARACTERISTICS OF BRAIN PROCESSES NECESSARY FOR CONSCIOUS PERCEPTION

Visual images are processed in a cascade of ascending, afferent pathways that traverse through the lateral geniculate body and project to primary (occipital) and further cortical centers that are organized in modular manner. This SP-system is set to encode a wide variety of specific characteristics and features of the image. Definite specialized subsystems are tuned to specific features of the image in parallel (they perform the function of analysis of the image into its elementary subcomponents and higher-order, integrated, complex components or characteristics). The relevant literature has documented selectively tuned neural systems for SP-characteristics such as orientation, color, form, texture, spatial frequency, etc. (Zeki, 1978; van Essen, 1979; Livingstone & Hubel, 1988; Kandel, Schwartz, & Jessell, 1991; Churchland & Sejnowski, 1992). We have many reasons to believe that this system of analysing units in SP is necessary and sufficient for fulfilling the functions of more or less exhaustive encoding of any visual image *A* into its specific cortical representation $R(A)$ without the need to create cognitively transparent, conscious representations. Recent data by Leopold and Logothetis (1996) and Logothetis, Leopold, and Sheinberg (1996) who used the paradigm of binocular rivalry and findings of He, Cavanagh, and Intriligator (1996) who used selective orientation-specific adaptation only support this standpoint. Preconscious encoding in SP can be extremely precise and fine-tuned despite the lack of cognitive transparency. As it was said above, if the specific sensory-perceptual data have to become consciously experienced in the form of perceptual images it is necessary that ascending activation from the NSP participate in elaborating the respective afferent information that are processed in SP. (Some interesting possibilities to hypothesize about the neural correlates of visual awareness as mediated by NSP in its interaction with SP exist: selectively channeled modulations of the activity of cortical neurons through the gating system of *nucleus reticularis thalami*—Scheibel, 1981; Crick, 1984; synchronous activity of the cortical representational neurons under the effects from NSP and/or by building up cortico-thalamic feedback loops—Crick and Koch, 1990; Crick, 1984; Llinás and Ribary,

1993; activity of the intralaminar nuclei of the thalamus—Bogen, 1995; activity of a special, limited group of cortical ''consciousness neurons'' in the intermediate layers of the cortical columns—Koch and Crick, 1991.)

Of course, a logical problem may emerge here. How can it be that *non*specific system is crucial in fine-tuning the *specific* perceptual representations for consciousness. At the metaphorical level of description there seems to be no problem if constructs like ''searchlight'' (Crick, 1984) or ''retouch'' (Bachmann, 1984) are used in order to describe the interaction of SP and NSP. For a beam of searchlight it is just the same anyway if a rounded or square-shaped object falls within its focus. The same source of light energy that in itself is *un*specified with regard to the form of its object is employed in a *directionally specified* manner. Its resources are used for making certain object selected and more conspicuous, whatever its characteristics. Like a beam of coherent light is invariant with regard to the hologram, the source and distribution of the rays of the searchlight are invariant with regard to the form of the object it illuminates. But in terms of the *result* of this interaction a quite specific image of reflections will be highlighted together with its immediate surroundings. At the level of discussion that uses the vocabulary of cognitive representations the solution to the puzzle may be related to the distinction between the *contents* of the representations on the one hand (as based on the principle of encoding by the *specific locus* among the alternative representational loci and/or by the *configurational organization* of the elementary features into integrated perceptual objects) and the *level of relative activation* of specific representational units that is controlled by a general-purpose activator, on the other hand. (The clear possibility to accept the initial non-specificity of the processes of activation that vary the degree to which certain cognitive units are active and thus enable or do not enable to exceed the threshold for consciousness of whatever perceptual material is represented, was pointed out, for example, by Bachmann, 1984, and in the Dennett and Kinsbourne, 1992.) Physiologically spoken, the nonspecificity of the modulator that modulates the activity of specific cortical neurons can be regarded logically sound a possibility given that we find that the same functional subsystem (e.g., reticular-thalamic NSP) is being used for modulation of the activity of various specific cortical neuronal units. Convergent and divergent links between the neurons at various CNS levels and enormous amount of synaptic links within and between the systems enable this principle to be actually implemented. A principally important requirement though is that receptive fields of the NSP-neurons are larger and considerably less form-specific than the receptive fields of the SP-neurons and that the former should in principle overlap with the latter. Is it so in reality? And do objective characteristics and behavioral results of the physiological interaction of SP and NSP allow us to accept the proposed conceptualization?

Ascending afferents of both systems, SP and NSP converge on the same set of cortical neurons. NSP provides primarily presynaptic excitatory influence that helps to modulate the activity of the specific representational neurons that are activated by SP processes and that signal the presence of the defining features of the stimulus image. A stimulus that is presented to the observer not only causes specific processes of encoding in SP but also evokes the activity of NSP via the collaterals from ascending subcortical pathways of SP. Thus a bifunctional map of afference is built

up (see, e.g., Keidel, 1971; Brazier, 1977). Synaptic interaction of SP and NSP at the cortical level is not something rare: according to Akimoto and Creutzfeldt (cf Brooks & Jung, 1973), two-thirds of the cortical neurons possess converging afferents from both, SP and NSP. The latter provides mainly facilitatory effect (facilitatory modulating effects of NSP on SP have been described, e.g., by Livingstone & Hubel, 1980; Scheibel & Scheibel, 1967, 1970; Brazier, 1977; Singer, 1979; Purpura, 1970; Steriade, 1981).

Works of Bremer (1935), Magoun (1958), Jung (1958), Livingstone and Hubel (1980), Moruzzi and Magoun (1949), Riklan and Levita (1969), Doty (1970), Somjen (1972), Brooks and Jung (1973), Singer (1979), Worden et al. (1975), Libet (1978), Smirnov et al. (1978), Mesulam (1985), Newman (1995), and many others allow me to draw the following description of the effects and characteristics of NSP. (In part 2.1 let me list the evidence why NSP is related to providing conscious state as such in the first place. In part 2.2 the typical effects of NSP on SP functioning will be described. In part 2.3 the comparative characteristics of NSP system vis-à-vis SP system will be presented.)

2.1. NSP and the States and Phenomena of Consciousness

1. Alternation of sleep and wakefulness (i.e., the states of not being conscious or being consciously aware of the environmental stimuli) depends on NSP. For example, intralaminar thalamocortical neurons increase their firing rate about 10 s before EEG desynchronization in natural transitions from slow-wave sleep to waking or active sleep (Steriade, 1981b). Genuine manifestations of sleep occur necessarily after deafferentation in the thalamocortical systems. During paradoxical sleep some remnants of conscious awareness in the form of dreams can be registered. It is no surprise that thalamocortical sources of activation send their excitatory signals up to cortex immediately before the paradoxical sleep episodes (Steriade, Sakai, & Jouvet, 1984). Inversely, deafferented reticular nucleus of the NSP-thalamus generates spindle rhythmicity that is characteristic to sleep (Steriade et al., 1987). The states that provide the capacity for subjective perceptual experience are functionally related to the activity of the NSP system.

2. Another possibility to observe information processing functions with subjects being unconscious can be obtained by general anesthesia. Barbiturate anesthesia, for example, leads to slowing down and synchronization of EEG oscillations somewhat similar to normal slow wave sleep states, but without making the primary sensory pathways dysfunctional. If NSP of the anesthetized experimental animals is electrically stimulated, however, then desynchronization of the EEG occurs and the pattern of activity that is typical to the awake brain is displayed (Bremer, 1935; Moruzzi & Magoun, 1949; Brazier, 1977). Recent investigations (Munk et al., 1996) have found that in parallel with typical EEG desynchronization, NSP-activation leads also to intracortical modulation of the neuronal activity in SP so that these neurons start to fire synchronously in the gamma frequency range (above 30 Hz). This is the range that has been found to correlate with conscious perception of visual features as integrated into coherent objects.

3. Injuries and tumors localized in NSP often cause absence of consciousness in

patients (e.g., Riklan & Levita, 1969; Penfield, 1975; Bogen, 1995; Newman, 1995b). What is noteworthy in the context of our present discussion, is that in many cases the primary afferents that project via subcortical parts of SP onto cortical projection of SP have remained intact. The combined activity of both, SP and NSP provides direct perceptual awareness of definite environmental objects.

4. Another instance of pathology that includes absence of direct awareness is visuo-spatial hemineglect. Subjects are functionally blind to a selective (e.g., left side) portion of their visual field. In addition to possible cortical determinants, this phe-nomenon can emerge from selective destruction of subparts of NSP (Mesulam, 1985; Bogen, 1995; LaBerge, 1995). Although primary input to cortical SP centers that are tuned to receive signals from the neglected field has remained intact, subjects are not aware of respective stimuli.

5. If NSP serves the function to modulate the activity of selected SP-system neu-rons so as to mediate awareness of the sensory signals that are carried by these neu-rons, then it should be possible to ''recruit'' certain SP-units by the NSP input even without the presence of normally adequate trigger stimuli in the receptive field of these SP-units. Indeed, artificial stimulation of the nuclei in NSP-thalamus of human patients has been shown to be capable of eliciting ''phosphenes'' or artificial sensa-tions (e.g., Gellhorn, 1961; Smirnov, Muchnik, & Shandurina, 1978; Tasker, Or-gan, & Hawrylyshyn, 1980). Clarity of respective experiences has been found to depend directly on the nature of NSP-stimulation, and spatially selective projection of these pseudoimages into visual environment has been another interesting result (Smirnov, 1974).

6. Besides qualitative and spatial characteristics of visual experiences there is an-other potentially interesting dimension as well, that of time. Already some earlier works on NSP systems, although using indirect measurements instead of direct psy-chophysical evaluations, did show that stimulation of NSP systems can lead to speed-up of human reaction time to sensory stimuli (Lindsley, 1960). Later on, using more direct psychophysical procedures Benjamin Libet did demonstrate that stratification of the moments of appearance of sensations on the subjective time axis depends on NSP-activation of SP-representations, and not only on SP-afference *per se* (e.g., Li-bet, 1978). Just the timing of thalamic stimulation was the best means to predict the moments of appearance of sensation, including antedating of the sensation onto an earlier time moment, if NSP-stimulation was experimentally prepared well ahead in time in comparison with normal or control conditions.

7. If NSP has a special role in mediating (visual) awareness, then we should expect it to be sensitive to the effects of psychopharmacological treatment that is used for general anesthesia. The facts support our conceptualisation: while the activity of the neurons of SP and fast primary cortical SP-responses show high resistance to the effects of certain general anesthetics, then NSP, on the contrary, can be considered as the principal target of the anesthetic procedures (Brazier, 1977; Menshutkin, Su-vorova, & Balonov, 1981). This picture is consistent with data from Doty et al. (1973), who found that in anesthetized monkeys diencephalic stimulation of NSP did not cause the effect of facilitation of SP-processes, whereas in alert monkeys this effect was obtained (with peak latency equal to about 70–120 ms). Consistent with this picture are the effects of caffeine, amphetamine, and their derivatives. These

substances can effectively arouse subjects and increase vividness and subjective ''clarity'' of sensory experiences. They are known to have especially strong facilitative effects on thalamic nuclei in NSP (Menshutkin, Suvorova & Balonov, 1981).

2.2 The Effects of NSP on SP Functioning

1. There is a high correlation between (a) the activity of cortical projections of the SP-pathways from the retina through LGN to cortex and (b) the activity of the afferent neurons in the thalamic NSP (Purpura, 1970; Scheibel & Scheibel, 1970; Brooks & Jung, 1973). The two systems work hand in hand. If the activity of cortical SP-neurons of the projection areas in monkey brain is registered in total darkness (i.e., in the absence of external visual input to SP), nevertheless clear state-dependent fluctuations of this activity can be observed. It is logical to hypothesise about the strong NSP-dependence of that activity (cf. Doty, 1970). NSP-input that originates from subcortical sites and projects onto cortical SP-neurons modulates the activity of the latter.

2. It has been shown also that the number of active visual cortical neurons in response to retinal afferents increases as a result of NSP-stimulation (Jasper et al., 1958; Brooks & Jung, 1973; Worden, Swazey, & Adelman, 1975; Singer, 1979). NSP must increase the responsibility of cortical SP neurons to their normal afferent signals and increase thus signal-to-noise ratio of the neural activities that carry specific information about stimulus objects.

3. If SP and NSP are simultaneously interactive, increase in the cortical area within which the neurons respond to retinal afferents can be observed (Jasper et al., 1958; Brooks & Jung, 1973). This refers to the more exhaustive (more ''fully descriptive?'') processing of input data by SP under the influence from NSP.

4. It has been found that spatial organization of the active visuocortical receptive fields is temporally unstable, especially during the arousal responses (Doty, 1970; Brooks & Jung, 1973; Brazier, 1977). During sleep or EEG-synchronization the stability significantly increases. The most stable responses appertain to the early components and the variability characterizes the late components of the evoked responses. The main visual relay nucleus that feeds the cortical SP-system—the lateral geniculate body—displayed also very stable responses. If we remember that SP acts faster than NSP (which takes longer to send the main shipment of modulatory activity to cortex), and acknowledge the fact that LGN responses did not show variability, then we can conclude that this variability should be primarily the result of NSP modulation and/or top-down influences.

2.3. The Principal Functional Characteristics of NSP and SP

A solid body of thorough neurophysiological and -anatomical studies exists that enables us to reach at several basic conclusions about the comparative functional properties of the visual SP systems and NSP systems (Doty, 1970; Purpura, 1970; Scheibel & Scheibel, 1970; Brooks & Jung, 1973; Brazier, 1977; Steriade, 1981; Steriade, Jones & Llinás, 1990; Boden, 1995; Newman, 1995). From the point of view of the perceptual retouch model that will be introduced later, these characteristics bear

the crucial role in helping to put forward specific predictions for psychophysical experiments.

1. Temporal resolution of the NSP-system is poorer than that of SP. The typical delay by which the main portion of ascending neural activity reaches cortical representational neurons is by about 40–90 ms slower in NSP as compared to SP. This necessarily leads to the assumptions that (a) conscious awareness of visual stimuli develops microgenetically and lags behind the processing of the specific signals that provide the material for the perceptual image, and (b) preceding brief visual stimuli are capable of exerting definite awareness-related effects on the processing of succeeding brief stimuli.

2. Spatial resolution of the receptive fields of SP is much better than that of NSP. This may be caused by the fact that while SP-afferents presuppose mainly non-branching axonal projections then axons from NSP-thalamus to cortex are richly branching, thus projecting also to the neighbouring SP-neurons. This means also that two alternative visual stimulus images, say, S1 and S2 with nonidentical receptive fields can be in principle serviced by the common modulating unit from NSP. The analogy with the searchlight metaphor is obvious here. The beam of light illuminates not only the exact configuration of an object, but also its immediate surroundings. Some additional studies have offered us data that are consistent with this notion. If a stimulus is gradually moved away from the center of the receptive field then the responses of the SP-system sooner or later disappear at the same time if the NSP-responses remain invariant (Gouras & Padmos, cited according to Bridgeman, 1980; Gusel'nikov, 1976).

3. The facilitatory effects of NSP-modulation are often universal in the sense that resultant increase in firing frequency of cortical SP-neurons can spread to almost all classes of neural units—e.g., to those that respond to diffuse light, motion, combination of hue and motion, etc. The NSP-modulation is universal and nonspecific with regard to formal characteristics of the stimulus image that are represented by the neural signals in SP, however can be spatially selective (no matter that with much poorer spatial resolution than SP). In other words, whatever the specific characteristics of the stimulus that is encoded by SP-units, are, the presynaptic NSP-input from nonspecific subcortical centers just amplifies the activity of these neurons. In terms of universality and *source* of activation the modulation is nonspecific. In terms of the *contents* of the information carried by respective SP-neurons that were modulated, the enhanced activity is, of course, specific. (A simple metaphor used earlier in this article was that of a beam of searchlihght, which originates from seminal studies of Helmholtz, 1866, Wundt, 1903, Eriksen and Collins, 1969, Posner et al., 1978, on visuospatial attention and which was hypothesised by Crick, 1984, to be based on nonspecific thalamic processes. The searchlight, i.e., covert attention that is semi-independent of overt eye movements, can enhance visibility of whatever object may fall within its focus and this focus can spread onto a wider area than it is covered exactly by the object itself.)

Taken together, the basic effects of NSP modulation on the SP-activity can be subsumed under the effect of *enhancing the signal-to-noise ratio* of the activity of a selected part of specific cortical neurons that carry the information that appertain to certain stimulus/object representation.

In several earlier studies I have proposed a special psychophysiological construct or operational concept in order to specify the process that seems to be necessary and decisive in creating conscious quality for perceptual representations of the stimuli (Bachmann, 1984, 1985, 1994). The term *perceptual retouch* (PR) denotes the originally nonspecific process of allotting conscious quality to a restricted number of perceptual representations among those that have been or are being formed or reactivated preconsciously on the basis of the processes of SP. By the virtue of juxtaposing a nonspecific process with specific preconscious representations we obtain (1) specific qualities and categorizability of the resultant perceptual experiences (images) and (2) possibility to speak about the nonspecific *degree* of conscious conspicuity of these experiences (the effect of the ''contrast of conscious experience'' that can be psychophysically evaluated invariantly with regard to specific sensory characteristics). In a sense, PR is a concept of interlevel specification that is postulated to enable to transcend from neurophysiological level of theoretical analysis onto psychophysical level of analysis. Instead of pointing to the causal relationships between neural and mental events, it is specified as a descriptive construct that helps to bridge the gap between biological and mental levels of explanation on the premise of strong interlevel correlation of events which can be tested by behavioral psychophysi(ologi)-cal methods. If we stem from this perspective, then it should not be forbidden to find empirical cases where the ratings of brightness contrast of certain stimuli can be orthogonal to, e.g., subjective ratings of the emphasis an object exerts on awareness. (The terms of priority, conspicuity, or pervasiveness of subjective experience could be applied as well.)

The following excerpt from Dennett and Kinsbourne (1992) should help to clarify how one can envisage the unspecific effects of the hypothetical PR processes. ''Couldn't consciousness be a matter not of arrival at a point but rather a matter of a representation exceeding some threshold activation . . . ? . . . an element of content becomes conscious at some time *t*, **not by entering** (my emphasis—T.B.) some functionally defined and anatomically located system, but by changing state right where it is: by acquiring some property or by having the intensity of one of its properties boosted above some critical level. The idea that content becomes conscious not by entering a subsystem, but by the brain's undergoing a state change . . . has much to recommend it'' (p. 199. op.cit.). The subsystem, primarily responsible for the state change, could be called NSP. (The last sentence certainly does not belong to Dennett.)

Let us postulate that the necessary requirement for any representation $R(A)$ to become ''retouched'' up to cognitively transparent, consciousness-related status $B/R(A)$ (as a correlate of experiencing the stimulus-image A in perceptual awareness) consists in modulation of the activity of the units in SP that stand for R(A) by the processes of NSP so that, as a result, the subject is able to report the presence of A and directly describe its qualities. The two operational criteria being, first, veridicality of response and second certainty about ''seeing,'' ''hearing,'' and ''sensing'' the qualities under concern. Common experimental means of reporting about the stimuli are voluntary identification or recognition responses or production of certain estimates on psychophysical scales. In addition to the veridicality and certainty of responses the lawful, nonrandom dependence of the psychophysical estimates about the objective characteristics of the stimuli turns out to be especially important operational means to test

if PR *of this particular perceptual characteristic* has been effective. (If one is to agree with Block's distinction between phenomenal consciousness and access consciousness then the PR theory concentrates more on what relates to the phenomenal aspect—cf. Block, 1995.)

3. THE PERCEPTUAL RETOUCH FRAMEWORK

According to Crick and Koch (1990) there are two forms of visual awareness, among which the very fast form (that one perhaps related to iconic memory/visible persistence) is considered to be difficult to study. The current *zeitgeist* to concentrate on studying the fast oscillatory activity of cortical representational neurons as the correlate of attentional binding of visual features into a coherent, consciousness-represented, visual object (e.g., Singer, 1996) dictates that certain minimum time of stimulus exposure in order to ''enter'' the time window that is sufficient for at least few cycles of 40Hz activity is necessary. However it is just the real-time dynamics of very fast form of visual awareness that has been chosen as the subject matter of the studies reported here. Just the first dozens of milliseconds that pass after the exposure to brief visual stimulus-images has been our main concern. Consider meta-contrast, for example. It has been repeatedly shown that it can be sufficient to vary the stimulus onset asynchrony (SOA) between the target stimulus and the masking stimulus, say, from 30 to 50 ms in order to lead to the dramatic change in the subject's ability to consciously perceive the target (Breitmeyer, 1984; Bachmann, 1994). In order not to enter the otherwise interesting discussion about the validity of the oscillation theory in explaining conscious visibility of visual stimuli, let me just assume the following. Given that the oscillation theory could obtain more empirically proven, firm status, then what we might be dealing with when we use experimental paradigms of interaction of extremely brief visual stimuli within a short time window (specified by SOAs in the range of 0–100 ms) could be just the initiation of the first cycle(s) of oscillation and/or causing phase shift in oscillations (comp. Paré and Llinás, 1995) and this may be sufficient in order to establish visibility of a brief visual stimulus, the representational neurons for $R(A)$ of what have been caused to fire.

If the re-entrant, feedback-type of interaction between cortical SP and thalamic NSP should indeed constitute the basic premise for awareness to be granted (cf., e.g., the general comment on this by Newman, 1995a), then from the retouch-theory point of view we may speculate that the first afferent package of presynaptic modulations from NSP onto selected SP-units put together the initial neural event that initiates respective reverberations that lead to establishing conscious representation(s). But even if the ideas of oscillation and reverberation as the bases of consciousness will not stand the test of time, there are much more traditional ways to interpret the decisive effects of NSP on visual awareness. For example, we can hypothesize that sufficient activity of prefrontal response coding and strategic planning systems are the *sine qua non* for consciousness and that a stimulus can ''enter'' consciousness only insofar as the firing frequency of its representational neurons in SP exceeds certain critical limen so as to feed respective response units or systems. Whereas SP-afference as such may be insufficient for supraliminal firing frequency, then additional NSP-modulation becomes decisive in creating a neural active representation that is
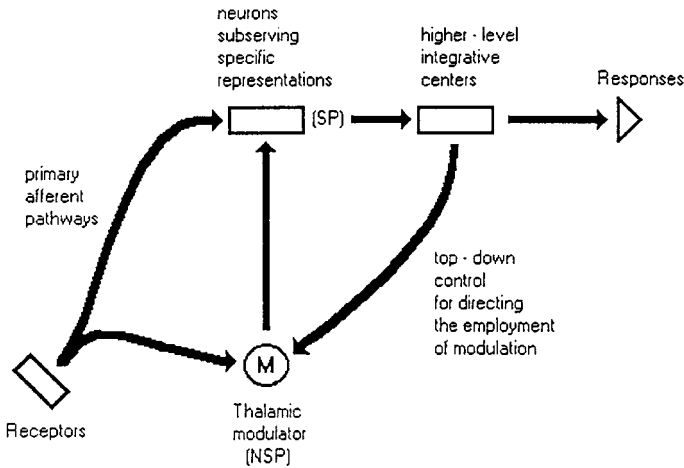
FIG. 1. The general architecture of the networks that perform the functions of NSP-modulation of specific visual representational modules (adapted from Bachmann, 1989b).

related to consciousness of its contents insofar as it necessarily becomes to be mediated by frontal processes. (For a more expanded discussion of the possible role of anterior cortical systems and arguments in favor of multiple levels of activity above V1 that is necessary for awareness consult, e.g., Crick & Koch, 1995.)

Let me now describe a simple neural net that embodies the functions and processes we should deal with in analysing SP/NSP interaction as the correlate of visual awareness in the context of PR theory (Fig. 1, adapted from Bachmann, 1989b). Although in reality the SP-NSP interaction in the context of creating consciousness-related representations would require millions of neurons to be activated in quite intricate patterns of activation over and within various levels of functionsl systems, let us, for the simplicity of argument, postulate that it is valid to use activities of single conceptual neurons that resemble the activities typical to the multitude of the real ones and that the activity of a single conceptual neuron lawfully characterises the activity of a pool of real neurons within a definite subsystem in modeling this interaction.

After passing the receptor level, the signals that were evoked by the visual stimulus travel along the classical, primary pathways within the subcortical part of SP and afterwards reach cortical specific neurons. This is a fast process; the latency that it takes to evoke initial activities of cortical neurons in SP can be measured in the order of about 8–30 ms post-stimulus and the ascending fibers of SP have faster conduction properties than those of NSP; the same regularity characterizes also respective synaptic transduction (Ingvar & Hunter, 1955; Buser & Borenstein, 1957; Magoun, 1958; Purpura, 1970; Somjen, 1972; Brooks & Jung, 1973; Gusel'nikov, 1976; Rolls & Tovee, 1994). In parallel with this route there are collateral pathways that form a by-pass from receptors through NSP-modulators to cortex. Presynaptic modulatory input from NSP converges at the same pool of cortical SP-neurons (at soma and/or apical dendrites of specific cortical nerve cells). It is not forbidden to hypothesize that considerable part of this convergence takes place at the large pyramidal cells in
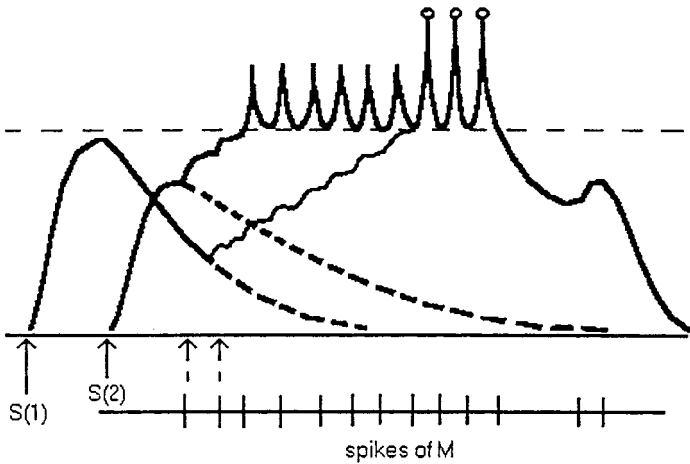
Fig. 2. Hypothetical excitatory postsynaptic potentials of the neurons that represent specific character-istics of two successive, brief, visual stimuli, modulated by the presynaptic inputs from the ascending pathways of the nonspecific thalamus.

the fifth layer that have been considered by Crick and Koch as the cells decisive in providing conscious experience, even if this could require some further processing at later stages above V1.

The typical response of a cortical SP-neuron (as a member of the representational module) to the exposure of its specific trigger features takes the form of excitatory postsynaptic potential (EPSP). The EPSP is characterised by the fast rise time and relatively slower, exponential decay. (See Fig. 2 that includes typical EPSPs.) If the level of EPSP reaches critical value, the neuron starts firing and sends signals to higher cortical centers and/or feedback signals to subcortical centers. The typical effect of the ascending excitatory axons that presynaptically converge on SP-neurons and originate from NSP thalamus (e.g., from the subcortical sites that are modulated by *nucleus reticularis thalami*, or from intralaminar nuclei) onto the dendrites or soma of the cortical cell is to quantally modulate the EPSP closer towards the level that is necessary for the neuron to start firing. Thus the level of EPSP, both as a result of the primary, specific afference and of the secondary, modulatory influence determines several outcomes that are important for the perceptual retouch theory. (1) The *latency* with which the neuron starts firing and therefore integrates its activity with higher-level perceptual processes depends on the level of EPSP (which in turn depends also on how quickly presynaptic modulatory impulses arrive and how many of them are applied within a critical time-window so as to prevent decaying of EPSP back to initial level before a succeeding depolarizing input arrives). (2) The cumula-tive frequency of firing which specifies the overall activity of a given neuron among the activities of other, competing neurons. Consequently, the *signal-to-noise* ratio for the signals that carry information about the respective stimulus-image or its features is dependent on EPSP level, including that part which is caused by presynaptic modula-

tory input. We postulate that if the level of EPSP remains below the critical limen for firing, then information that is carried by that respective neuron is not directly represented in conscious representation *B/R(A)*.

A single presynaptic impulse from the presynaptic neuron is usually insufficient in order to rise the level of EPSP up to the firing level. Typically the effect of a single quantal change amounts to about 1–5% of the level that is necessary for the neuron to start firing (Churchland & Sejnowski, 1992). If this fact is combined with the regularity by which EPSP begins to decay back to the premodulation level of the membraine potential immediately after the previous discharge and does this quite fast, then it is clear that more often than not independent SP-processes *per se* are not enough to cause neurons to participate in higher-level integrations and in the processes that are responsible for forming conscious representations. This again refers to the importance of the combined and sufficiently intense activity of both, SP and NSP systems in founding the basis for conscious awareness of the stimuli that are specifically encoded with the help of SP.

The space-time dynamics of conscious perception—the dynamics of perceptual retouch—of brief visual images that are exposed in a rapid exposure regimen can be predicted if we use a relatively simple neural net that includes few necessary representational SP-neurons (that simulate the functions of a perhaps much larger neuronal pool in SP) and a common thalamic NSP-modulator for these units.

Suppose for each stimulus image S there is a cortical SP node D(S) that is tuned to S and responds to it if S is exposed in its receptive field. Thus for S1 and S2 we have, respectively, D(S1) and D(S2). D(S) respond to S by a typical generalized EPSP. The latency for the initiation of this neural response is considered to equal, say, 10–20 ms. There is also a thalamic NSP-modulator M that receives collaterals from the ascending SP-pathways that feed D(S) upward. M shares receptive field with D(S). Given that stimuli S1 and S2 fall within the receptive field of an invariant NSP-modulator M(S), both of the respective specific encoding nodes, D(S1) and D(S2) can be modulated by the common M. The nonspecific thalamic modulator M sends its facilitatory ascending impulses to cortical D with the latency of about 40-90 ms. The receptive field of M is considerably larger than that of D and unspecific to formal characteristics of S.

Certain features of the PR model stand out as the key features. (1) Slower latency of the main portion of the ascending NSP-modulation by M to reach cortical SP-nodes D as compared to the latency with which EPSPs of D are evoked by the SP-processes. This difference in effective time consists in some 30–70 ms. (2) More coarse spatial resolution of the receptive fields of M as compared to receptive fields of D. (3) Spatially selective mode of the direction of NSP-modulation from M to D. This type of directed modulation (cf. also Scheibel, 1981, and Crick, 1984) presupposes that D and M share receptive fields in terms of the location from where stimuli are exposed in behavioral space. Features 1–3 of the model as taken together make it possible that an invariant system of modulation, M, is capable of servicing alternative D(S1) and D(S2) that carry, respectively, the signals from the visual images S1 and S2 that are mutually different in space-time. This mutual difference may include more or less slight differences in location and size, differences in form, color, etc. The main requirement that guarantees that the activity of specific representations of

alternative stimuli, S1 and S2, can be modulated by an invariant M within the elementary act of perceptual processing is the use of exposure regimens that enable that stimulus-images are exposed for brief durations each and in rapid succession. This is necessary in order to ''enter'' into the time-window where we find SP- and NSP-processes temporally still dissociated. From the dual-process point of view we can now state that the slower subprocess within the domain of NSP modulation ($B/R(A)$) that is necessary for creating or mediating conscious quality for some specific representation $R(A)$ (which is embodied and exemplified in the primary activity of cortical SP) and that was evoked by a first stimulus S1 may show up its effects on the relative activity of the representation that stands for perceiving another stimulus S2. In practice this means that we have to use stimuli with durations equal to no more than about a dozen milliseconds and time intervals between the stimuli within the window of 0–150 ms.

By using this approach we will be able to analyze the conscious perception in its emergence, in microdevelopment.

If two brief, successive stimulus images S1 and S2 are exposed to the observer within a common receptive field of M and with the time interval that is less than the standard SP plus NSP process normally takes, then we should expect that S2 will be a favoured stimulus in comparison with S1 in conscious perception. This prediction is put forward because the main share of the temprally trailing NSP-modulation from M that is necessary for creating visible (conscious) qualities of the sensory information contained in stimuli and that was evoked by S1 will be effective only after certain delay, at the moment when ''fresh'' SP-signals of S2 arrive and the ''older'' signals of a very brief, preceding stimulus S1 have been considerably decayed already. In Fig. 2 this is expressed by the larger cumulative frequency of the spikes produced by the neuron that participates in encoding S2 in comparison with the cumulative firing frequency of S1-neuron. The signal-to-noise ratio for S2-related information is higher and this information gets advantage in terms of ''feeding'' conscious representation. This is the result of the fact that excitatory presynaptic modulation from NSP that was evoked by S1 is temporally trailing behind the specific cortical input of S1 itself, but coinciding on time axis with the arrival of the optimised S2-related information (see Fig. 2 where EPSP for S2-related specific process is higher than EPSP for the previously initiated, already decayed, S1-related specific process). That is what makes S2 special for conscious awareness.

The other feature of this interaction is that the neuron that stands for S2 starts firing earlier than it would have started, given that S2 would have been exposed without the preceding S1. The firing latency of the neuron that stands for S1 exemplifies this, because S1 is not precedented by another stimulus. All this predicts also the relative speed-up of the subjective moment of conscious perception of S2, given that S2 is exposed after the preceding, proactively employed S1. The basic predictions of the PR theory are thus related to the proactive facilitation effects with brief, rapidly alternated visual stimuli.

If Libet's conjecture about the minimum duration of brain activity that is necessary for conscious awareness of a stimulus to emerge, is correct (and absolute time values are not a principal question here—one could hypothesise that in vision the process is shorter), then that could be another reason why just S2 is so special for conscious-

ness, given successive, brief, transient stimuli (see, e.g., Libet, 1993). Namely, the cumulative firing frequency of a S2-related neuron is higher and respective impulse train longer in comparison with those of S1-related neuron.

4. EXPERIMENTAL STUDIES VIS-À-VIS THEORETICAL PREDICTIONS

4.1. The Cases of Mutual Masking and Metacontrast

The subject is presented with two mutually different, but spatially overlapping (mutual masking) or closely or immediately adjacent (metacontrast) visual forms—S1 and S2, both for about 10 ms. The SOA between the exposures of these stimuli is systematically varied between 0 ms and about 150–200 ms. Our theory predicts that with very short SOAs of less than 20–30 ms SP-representations for S1 and S2 are activated almost simultaneously and before the NSP-process from M has had enough time to exert substantial modulatory effect on respective D(S1) and D(S2). When this excitatory modulation arrives, respective EPSP levels are somewhat decayed, but at the comparable levels, because neither of them has any considerable time shift with regard to the other. Modulation results in certain package of impulses that both neurons send out, and cumulative firing frequencies of these packages are comparable. As a result, the observer will consciously experience the common, integrated visual image of both, S1 and S2. In this compound image neither of the stimuli dominate in terms of their visibility. In the case of mutual masking where alternative stimuli, S1 and S2 overlap in space the result will be integrative masking, because it can not be easy to discriminate one stimulus from the other on the basis of this compound image. In Fig. 3 this is expressed in the variant ''B'' where with the shortest SOA value recognition functions for S1 and S2 are compatible, but far from the very good level of recognition.

In the case of metacontrast where stimuli do not overlap in space and thus do not obscure each other when integrated, the target stimulus (S1) is well visible at short SOAs as a spatially adjacent complement to the mask (cf. variant ''A'' in Fig. 3).

With intermediate SOAs (e.g., 40–90 ms) S2 will be dominating in conscious perception over S1, although S2 has been exposed only *after* the exposure of S1. This counterintuitive result can be explained as follows: the modulatory process from M of NSP-thalamus that is postulated to be necessary for creating conscious quality for the stimulus representations and that was evoked by the signals from the preceding S1 begins to elaborate on EPSPs of D(S1) and D(S2) at the moment when the EPSP of D(S1) has been decayed much more considerably than that of D(S2). As a consequence, the firing of the latter will provide higher signal-to-noise ratio for the neural processes that encode and represent S2 (see again Fig. 2). In the case of mutual masking this leads to the strong predominance of S2 recognition and substantial deprivation of the S1 from the clear conscious representation with intermediate SOAs (see S1 and S2 recognition levels with SOAs of 50 and 80 ms on Fig. 3). In the case of metacontrast tasks where subjects have to rate the clarity of the test (S1) or identify it, intermediate intervals provide the lowest ratings or worst identification performance for S1 (SOAs of 50 ms and 80 ms, variant ''A,'' in Fig. 3). With large SOAs over 150 ms two independent, noninteractive *B/R(A)*-processes (i.e., the equivalent
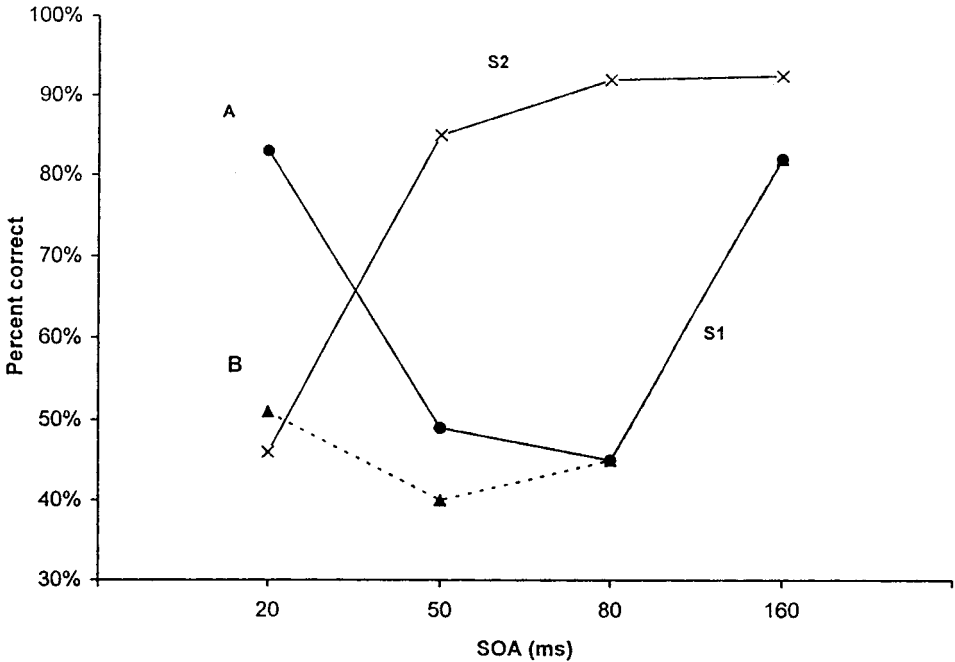
FIG. 3. Typical functions of perception effectiveness for the brief visual stimuli that are exposed in rapid succession. In mutual masking equal, however obscured visibility of S1 and S2 at short SOA can be noticed (B); this grows over to robust prevalence of S2 over S1 with intermediate SOAs and ends up with highly effective and equal visibility of both stimuli at longer SOA values. In metacontrast, where S1 as the target stimulus has to be rated for its visibility (contrast) or identified, the typical U-shaped function is obtained (A). In mutual masking the visibility function for S1 that resembles A can also be found, given that the intensity of S1 exceeds that of S2—in these circumstances S1 signal-to-noise ratio in the integrated image will be better than that of S2 (adapted from Bachmann, 1989b).

of modulation of SP-processes by NSP) are executed for two independent stimuli and both stimuli are clearly visible at different moments of subjective time.

The above-described regularities of mutual masking and metacontrast have been obtained in a number of experimental studies (e.g., Werner, 1935; Bachmann & Allik, 1976; Michaels & Turvey, 1979; Hellige et al., 1979; Bachmann, 1994; for reviews see Breitmeyer, 1984; and Bachmann, 1994).

Understandably enough, there are few possibilities to directly manipulate the activity of NSP in humans in order to test respective effects on the dynamics of visibility. In an earlier study I have had the opportunity to use Parkinsonian patients who were treated with chronically implanted microelectrodes in the Neurology Department of the Institute of Experimental Medicine of the Russian Academy of Medical Sciences. The method of artificial stable functional links practiced in the hospital of the above institute (cf., e.g., Smirnov & Resnikova, 1985) consisted in part in electrostimulation of the selected NSP-structures of the patients with brief bursts of 20 Hz current which resulted in the activation and optimisation of their state. (The electrodes were implanted in *globus pallidus, nucleus ventrolateralis, centrum medianum, nucleus retic-*
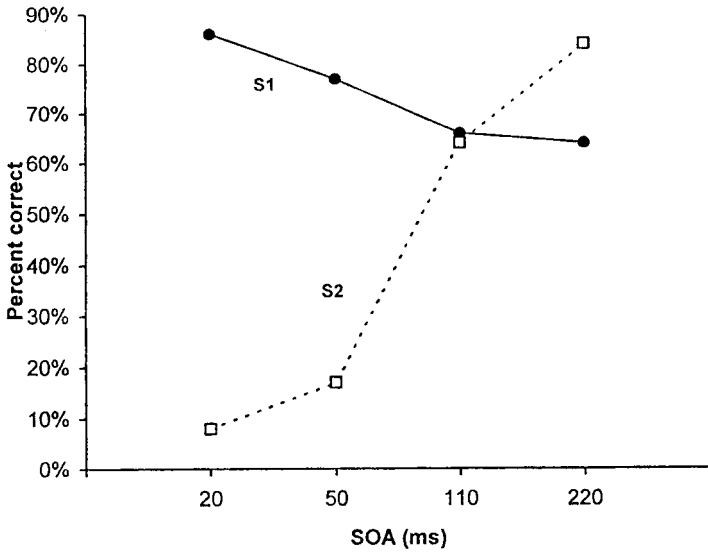
FIG. 4. Unusual mutual masking functions in Parkinson's disease patients whose nonspecific thalamus has been preliminarily activated by the chronically implanted electrodes (adapted from Bachmann, 1989b).

ularis, and some other structures of anterior, lateral, and dorsomedial thalamus.) Subjects participated in the mutual masking experiment immediately after the activating stimulation (Bachmann, 1994). In Fig. 4 we see the results of this experiment. A qualitatively unusual picture with strong S1 dominance in perception has emerged: we do not find the typical pattern of relative S1 and S2 efficiencies where S2 should have been clearly dominating in subjective reports. We can interpret this result either as a consequence of the effects of dopaminergic and/or cholinergic system deficiency or as a direct result of the NSP-stimulation. In the latter case it should provide additional support for the PR theory because unusually efficient and fast perception of S1 should be expected, given the preliminary and strong presynaptic activation from NSP.

Recently we have completed a similar experiment with ''typical'' Parkinsonian patients who were not treated by intracranial electrode stimulation (Bachmann et al., 1996). Typical mutual masking functions with S2 dominance and suppression of S1 visibility at intermediate SOAs were found similar to those in Fig. 3. Thus direct facilitatory activation of NSP seems to be capable of qualitatively changing the psychophysical masking functions in the direction that goes hand in hand with the PR theory.

4.2. The Case of Proactive Contrast Enhancement

The effect of the preceding, brief, spatially overlapping S1 on the contrast ratings of S2 as a function of SOA have also been studied (Bachmann, 1988). The average estimates in the single S2 exposure condition were taken as the baseline (''zero'' level) contrast. The theory of PR predicts that at intermediate SOAs S2 contrast should be
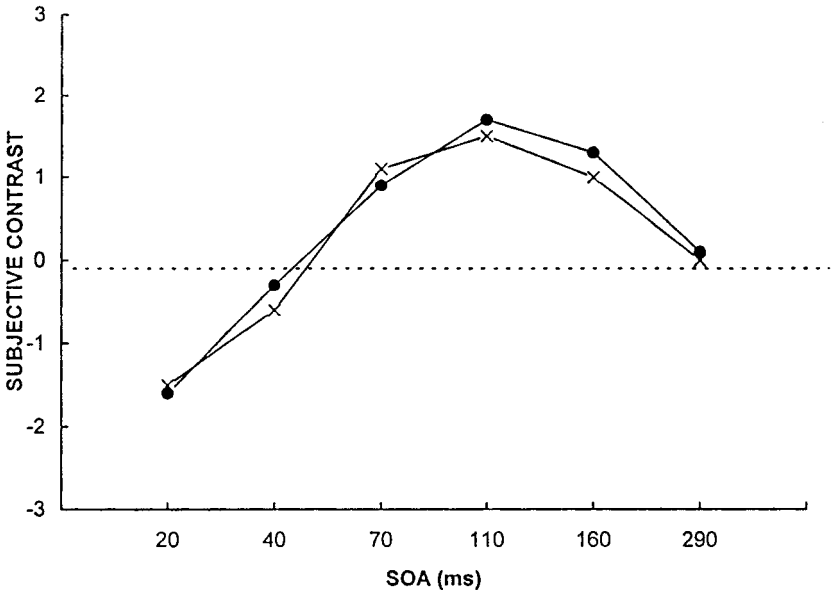
FIG. 5. Subjective contrast ratings of a brief visual stimulus, S2, as a function of SOA between the preceding, brief, S1, and S2. Intermediate SOAs lead to the proactive contrast enhancement effect (level 0 on the ordinate refers to the control condition estimates with single S2) (adapted from Bachmann, 1989b).

enhanced relative to its single-stimulus control condition level: with intermediate SOAs the nonspecific modulatory impulses that were evoked by S1 reach presynaptic sites of S2 neurons in SP when their EPSP level is just maximised and thus the cumulative frequency of firing of these neurons will be much higher than it would have been in the conditions where modulatory impulses had to be evoked by the single S2 itself. In the latter case the EPSP level should have been already decayed considerably when the presynaptic modulatory impulses arrive. On Fig. 5 basic results of that study are depicted. They are consistent with the theoretical prediction. This empirical outcome can be modelled by relative amounts of postsynaptic spikes (see Fig. 2). If a stimulus is exposed without the preliminary modulation-inducing stimulus (the S1) then our example depicts only three spikes (marked by small circles at the top of respective spikes); if the preliminary stimulus has prepared presynaptic modulation for the succeeding one, then the number of spikes amounts to nine. According to the theory, the more discharges we have in respective representational neuron in SP, the higher the subjective conspicuity of the respective stimulus in conscious perceptual image.

Some well-known regularities that characterize temporal modulation transfer functions in contrast sensitivity research (e.g., Watson, 1986) can also be explained by the PR model. For example, the unit impulse response profile that stands as the cornerstone in contemporary theorizing about the psychophysical sensitivity functions for periodically flashed visual stimuli can be derived from the temporal shift aspect

of NSP afference versus SP afference in the PR model. Let us suppose that the unit impulse construct has its correlate in the relative level of activities of the modulated SP-neurons. And let us stimulate the visual system by brief, successive light impulses. Then modulation or detection sensitivities should be highest if flicker periodicities or two-pulse SOAs have the value which is equal to the average time difference between the cortical latencies of arrival of SP afference and of the NSP modulation. In other words, the values of the constants for the psychophysical impulse responses that predict best temporal sensitivity can perhaps be derived from the time values with which the arrival to the cortex of the awareness-related NSP-modulation is shifted away from the arrival to the cortex of the primary SP-responses, given photometric conditions and the conditions of the state of the subject.

4.3. The Cases of Temporal Order Judgments and Reaction Time Measurement

The same theoretical rationale helps to predict that if a stimulus S2 is exposed after the preceding stimulus S1 within optimum SOA, then the relative moment of S2 appearance in conscious awareness (the moment of establishing its visibility) will be shifted onto an earlier moment of time as compared to the conditions where S2 is exposed alone. This speed-up effect is expected because S1 should prepare the NSP modulation ahead in time so that the SP-neurons for S2 (i.e., that stand for D[S2]) that implement S2 representation start firing sooner than they would have done without the prime. It takes now less presynaptic inputs to modulate the EPSP up to the level of firing. In Fig. 2 one can see how much earlier the neuron for S2 starts firing in comparison with the neuron for S1 that had no prime before it. Experimental tests of this theoretical prediction include the procedures that require subjects either to estimate the relative moments of subjective appearance of a visual test stimulus with regard to a sensory reference event (e.g., an auditory click) or to produce speeded reactions to test stimuli with reaction time (RT) being the principal dependent measure. The temporal order judgment (TOJ) has been successful in demonstrating proactive facilitation in the studies by Neumann (1982), Bachmann (1989), and Neumann, Esselmann, and Klotz (1993). The facilitatory effect of the preceding prime (S1) on the RT to the succeeding test stimulus (S2) was obtained by Bachmann (1994) and Klotz and Wolff (1995). In these studies S1 and S2 were either spatially overlapping or adjacent, as required by the model of the interactive system of SP and NSP in terms of their receptive field characteristics.

4.4. Some Other Subjective Space–Time Effects

4.4.1. The Fröhlich effect. If a laterally moving visual stimulus appears from behind the opaque screen, then it will be first visible not at the objective spatial position where it first appeared (i.e., not at the edge of the occluding screen), but as somewhat shifted in space toward the direction of motion (Fröhlich, 1923; Müsseler & Aschersleben, 1997). The theory of PR is consistent with this effect. The precise spatial coordinates (a characteristic of the SP system) of a moving stimulus that abruptly appeared a moment ago undergo a change during the time delay that it takes for NSP-impulses from M to reach respective SP-units. The hypothetical consciousness-related modulation mediates the first moment of visibility so as to cause the stimulus

to appear in awareness beginning with the condition where the characteristic of local-ization in physical space for the stimulus representation in SP specifies a locus that is advanced in space, in the direction away from the edge.

4.4.2. The tandem effect. The best account of the Tandem Effect is provided by Müsseler and Neumann (1992). If a pair of small vertical bars—a ''tandem'' with inter-bar horizontal distance *d*—that is moving laterally behind the opaque screen appears in the aperture (the diameter of which is specified as $D < d$) and then disap-pears again behind the other edge of the aperture, then—in perfect agreement with the Newtonian physics—it is impossible that both stimuli occupy positions in the aperture simultaneously. The first bar, S1, enters aperture, moves across it and disap-pears, and only then the other bar, S2 appears from behind the edge. However given optimum speed of motion and optimum interstimulus spatial distance both stimuli can be seen at once in the window. This effect consists in both, compression of subjective space and compression of subjective time. The Tandem Effect can be explained on the basis of (1) visual persistence of the S1 information so that S1 will be still visible in the window when S2 becomes visible and/or (2) PR theory that presumes the formally equivalent two-process account of SP-encoding plus NSP-modulation. The bar that enters the aperture as S1 opens the modulatory process so that it takes some time for S1 signals to be retouched for conscious representation whereas the following bar (S2) benefits from the preceding modulation analoguously to the speed-up effects that were described earlier. The conscious representation for the trailing S2 will be established *relatively* faster than respective representation for the leading S1. As a result, compression of subjective space-time takes place in a truly relativistic manner. In conscious representation the element S2 of the Tandem will be seen as shifted a bit more toward the S1 because the delay that is necessary for its experiencing will be shorter and the observer is faster in noticing the advanced spatial position of S2. This means that with S1 we live relatively more ''in the past'' in our subjective reality and with S2 relatively less. Which one of these two accounts is adequate, if any, should be found out in special psychophysi(ologi)cal experiments.

4.4.3. Facilitation by precueing in visuospatial selective attention. The standard method for studying selective spatial attention was introduced by Eriksen and Collins (1969). They inverted the partial report technique of Averbach and Coriell (1961) and instead of presenting the selective cue *after* the display of stimulus alternatives, they presented it in advance. The role of the spatially selective precue is to designate the spatial position where covert attention has to be directed within the succeeding stimulus field. It has been repeatedly shown that a spatially selective peripheral pre-cue, if exposed before the target display within the optimum SOA (usually within 60–150 ms), facilitates target processing (e.g., Eriksen & Hoffman, 1974; Eriksen & St.James, 1986; Possamaï, 1986; Warner, Juola, & Koshino, 1990; Tepin & Dark, 1992; Umiltà et al., 1995—all with RT as the dependent measure, and Müller & Findlay, 1988; Nakayama & Mackeben, 1989; Lyon, 1990; Chastain, 1992; Cheal, Lyon, & Gottlob, 1994—all with percent correct or sensitivity as the dependent mea-sures). Facilitation of the covert visual attention manifests itself in speeding up the RT to target(s), in increasing the sensitivity to target(s), and in increasing efficiency of detection, recognition or identification of the target(s). The explanation of the spatial-attentional facilitation from the dual-process, perceptual retouch perspective

is equivalent to what was proposed earlier for explaining proactive facilitation in RT and in subjective contrast. Due to the spatially directed nature of NSP-modulation from M and to the slower latency of nonspecific processes, and also due to the sharing of receptive fields between D(S1), D(S2), and M, the selective precue (S1) initiates facilitatory modulation that in the given circumstances leads to optimization of the PR for the target (S2) just with intermediate and above-intermediate SOAs between the precue and the target. The optimum time intervals of attentional facilitation by physical precues that have been found to have the values in the range of 60–150 ms satisfy our model. If we subtract the time value of the latency that it takes to preconsciously allocate and activate a stimulus representation in D(S) on the basis of SP-processes (e.g., 30 ms) from, say, 100 ms as the optimum cue lead time, then what we get—70 ms—nicely satisfies the time value of the typical differences between the latencies with which main portions of ascending signals from NSP and SP reach cortex.

4.5. Speculations about Binocular Rivalry and Stroboscopic Motion

If two formally incompatible visual images are presented to the observer so that S1 stimulates one retina and S2 the retina of the other eye, then rivalry of the respective alternative subjective images will be experienced: either S1 or S2 is visible, but not both of them at once (Levelt, 1968; Walker, 1978; Wolfe, 1986; Leopold & Logothetis, 1996). It has been argued that although conscious visibility of the images alternates, specific information of the currently suppressed image is still processed and represented (Dixon, 1981; Varela & Singer, 1987; Sekuler & Blake, 1985; Leopold & Logothetis, 1996). It seems appealing to apply the PR theory in order to explain the phenomenon of rivalry. We would like to speculate that if SP-processes for the competing stimuli can proceed on in parallel and specific input constantly arrives to cortical SP-centers for S1 and S2, then NSP-modulation from M that is necessary for rendering conscious quality to specific representations should alternate between two competing specific excitatory constellations. We would propose the hypothesis that rivalry starts beginning with the cortical analysis in SP that has revealed the perceptual suggestion for the ecologically invalid circumstance—the presence of two mutually different objects at once in the same spatial slot. Evolution has not prepared visual system for this impossible event; two eyes have developed for perceiving interocularly congruent scenes or objects (although with the possibility to allow some disparities, e.g., in stereopsis). A neurophysiological equivalent for this situation can be found in a hypothetical competition between two incompatible variants of corticothalamic reverberant neuronal ensembles that represent mutually incompatible images. As a solution to this paradox, NSP-modulation is applied to alternative constellations of SP-neurons on a time-sharing basis. According to this hypothesis one should expect that if competing images are exposed dichoptically for a very brief duration so that the exposure terminates before the higher-level analysis has succeeded in revealing mutual incompatibility between the two SP-representations and/or reverberant circuits have not been established yet, then there will not be time for alternation. In the studies by Goldstein (1970), Anderson, Bechtoldt, and Dunlap (1978); and Wolfe (1983) exactly this result has been obtained: if two compet-

ing stimuli are brief enough (shorter than, say, 100 ms), a phenomenon of the so-called abnormal fusion appears. Two stimuli amalgamate into the composite like in the monoptic or binocular conditions of mutual masking with very short SOAs.

It is quite realistic to suppose that although the receptive fields of NSP neurons are considerably larger that those of SP-neurons (the latter helping to encode specific form and qualities of a stimulus), nevertheless there should be some limit to this. This should reveal itself for example in limitations to the spatial areas that are dominant or suppressed in binocular rivalry. Experimental evidence supports this regularity: ''Nor is binocular rivalry a competition between the two eyes as a whole. . . . In most examples of rivalry with large stimuli, what is seen over time looks something like the sequence . . . Each region of the retinal image in one eye seems to fight with the corresponding region in the other eye . . . Regions expand, contract and vanish in a seemingly systematic fashion'' (Wolfe, 1996, p. 587).

In dealing with the phenomenon of stroboscopic motion it is quite seductive to put forward the following hypothesis: The impression of motion between S1 and S2 what we experience in our perceptual awareness (although just two stationary stimuli are successively flashed) is mediated by nonspecific modulation of those SP-neurons that stand for actually absent, but perceptually suggested stimuli which should occupy intermediate positions in space between S1 and S2. Similarity of time-course functions of apparent motion and metacontrast and some other similar space-time phenomena point towards this possibility. Another indirect suggestion comes from the studies that show close interdependencies between motion analysing specific systems and the attentional system (e.g., Sekuler, 1995; Stelmach, Herdman & McNeil, 1994; Yantis & Gibson, 1994). Attention can considerably modulate what and how we consciously perceive in otherwise invariant motion-inducing displays.

5. CONCLUSIONS

The main objective of the present article was to introduce the dual-process, perceptual retouch theory as a metatheory for a family of visual phenomena that emerge if successive, brief stimuli are exposed and their relative visibilities and timing of subjective experiences are measured in psychophysical experiments. In the tradition of the ''inner psychophysics'' (Fechner, 1882) we have proceeded from the knowledge about the natural-scientific data and parameters that characterize the functioning of the neuronal systems for specific representation vis-à-vis the system of nonspecific activation that modulates the activity of the former. Surprisingly many different effects and phenomena are consistent with the theoretical predictions put forward in the present approach. Therefore I would like to see the integrative power of the retouch theory as the principal justification for its development.

ACKNOWLEDGMENTS

REFERENCES

Anderson, J. D., Bechtoldt, H. P., & Dunlap, G. L. (1978). Binocular integration in line rivalry. *Bulletin of the Psychonomic Society,* **11,** 399–402.

Averbach, E., & Coriell, A. S. (1961). Short-term memory in vision. *Bell System Technical Journal,* **40,** 309–328.

Baars, B. (1988). *A cognitive theory of consciousness.* New York: Cambridge Univ. Press.

Baars, B. (1995). Tutorial commentary: Surprisingly small subcortical structures are needed for the *state* of waking consciousness, while cortical projection areas seem to provide perceptual *contents* of consciousness. *Consciousness & Cognition,* **4,** 159–162.

Bachmann, T. (1980). Genesis of a subjective image. *Acta et Commentationes Universitatis Tartuensis,* **522,** 102–126.

Bachmann, T. (1984). The process of perceptual retouch: nonspecific afferent activation dynamics in explaining visual masking. *Perception & Psychophysics,* **35,** 69–84.

Bachmann, T. (1985). The process of perceptual retouch. (in Russian.) *Acta et Commentationes Universitatis Tartuensis,* **722,** 23–60.

Bachmann, T. (1988). Time course of the subjective contrast enhancement for a second stimulus in successively paired above-threshold transient forms: perceptual retouch instead of forward masking. *Vision Research,* **28,** 1255–1261.

Bachmann, T. (1989a). Microgenesis as traced by the transient paired-forms paradigm. *Acta Psychologica,* **70,** 3–17.

Bachmann, T. (1989b). *Psychophysiological bases of visual masking* (in Russian). Tartu: Tartu University Press.

Bachmann, T. (1994). *Psychophysiology of visual masking. The fine structure of conscious experience.* Commack, NY: Nova Science Publishers, Inc.

Bachmann, T., & Allik, J. (1976). Integration and interruption in the masking of form by form. *Perception,* **5,** 79–97.

Bachmann, T., Asser, T., Sarv, M., Taba, P., Lausvee, E., Póder, E., Kahusk, N., & Reitsnik, T. (1996). *The speed of elementary visual recognition operations in Parkinson's disease as measured by the mutual masking method.* Submitted for publication.

Block, N. (1995). On a confusion about a function of consciousness. *Behavioral and Brain Sciences,* **18,** 227–287.

Bogen, J. E. (1995). On the neurophysiology of consciousness: I. An overview. *Consciousness & Cognition,* **4,** 52–62.

Bogen, J. E. (1995). On the neurophysiology of consciousness: Part II. Constraining the semantic problem. *Consciousness & Cognition,* **4,** 137–158.

Brazier, M. A. B. (1977). *Electrical activity of the nervous system.* London: Pitman.

Breitmeyer, B. G. (1984). *Visual masking: An integrative approach.* Oxford: Clarendon.

Bremer, F. (1935). Cerveau ''isolé'' et physiologie du sommeil. *Comptes Rendues Societé Biologie,* **118,** 1235–1241.

Bridgeman, B. (1980). Temporal response characteristics of cells in monkey striate cortex measured with metacontrast masking and brightness discrimination. *Brain Research,* **196,** 347–364.

Brooks, B., & Jung, R. (1973). Neuronal physiology of the visual cortex. In R. Jung (Ed.), *Handbook of sensory physiology. Vol. VII/3: Central processing of visual information. Part B.* (pp. 325–440). New York: Springer-Verlag.

Buser, P., & Borenstein, P. (1957). Responses corticales secondaires á la stimulation sensoirelle chez le chat curarise non anesthesié. *Electroencephalography and Clinical Neurophysiology Supplement,* **6,** 89–108.

Chastain, G. (1992). Analog versus discrete shifts of attention across the visual field. *Psychological Research/Psychologische Forschung,* **54,** 175–181.

Cheal, M. L., Lyon, D. R., & Gottlob, L. R. (1994). A framework for understanding the allocation of attention in location-precued discrimination. *Quarterly Journal of Experimental Psychology, 47A,* 699–739.

Churchland, P. S., & Sejnowski, T. J. (1992). *The computational brain.* Cambridge, Mass.: M.I.T.

Cogan, A. I. (1995). Vision comes to mind. *Perception, 24,* 811–826.

Crick, F. (1984). Function of the thalamic reticular complex: The searchlight hypothesis. *Proceedings of the National Academy of Sciences USA, 81,* 4586–4590.

Crick, F. (1996). Visual perception: rivalry and consciousness. *Nature, 379,* 485–486.

Crick, F., & Koch, C. (1990). Towards a neurobiological theory of consciousness. *Seminars in Neurosciences, 2,* 263–275.

Crick, F., & Koch, C. (1995). Are we aware of neural activity in primary visual cortex? *Nature, 375,* 121–123.

Dennett, D. C. (1996). The myth of double transduction. Paper presented at *Toward a Science of Consciousness 1996. ''Tucson II''. April 8–13, Tucson, Arizona.*

Dennett, D. C., & Kinsbourne, M. (1992). Time and the observer: The where and when of consciousness in the brain. *Behavioral and Brain Sciences, 15,* 183–247.

Dixon, N. F. (1981). *Preconscious processing.* Chichester: Wiley.

Doty, R. W. (1970). Modulation of visual input by brain-stem system. In F. A.Young, & D. B. Lindsley (Eds.), *Early experience and visual information processing in perceptual and reading disorders* (pp. 143–150). Washington, DC: National Academy of Sciences.

Doty, R. W., Wilson, P. D., Bartlett, J. R., & Pecci-Saavedra, J. (1973). Mesencephalic control of lateral geniculate nucleus in primates. I. Electrophysiology. *Experimental Brain Research, 18,* 189–203.

Eriksen, C. W., & St. James, J. D. (1986). Visual attention within and around the field of focal attention: A zoom lens model. *Perception & Psychophysics, 40,* 225–240.

Eriksen, C. W., & Hoffman, J. E. (1974). Selective attention: Noise suppression or signal enhancement? *Bulletin of the Psychonomic Society, 4,* 587–589.

Eriksen, C. W., Collins, J. F. (1969). Temporal course of selective attention. *Journal of Experimental Psychology, 80,* 254–261.

Fechner, G. T. (1882). Revision der Hauptpunkte der Psychophysik: Sektion 21 (pp. 290–299). Leipzig: Breitkopf und Hertel. [Reprinted and translated in *Psychological Research, 49,* 1987, pp. 209–212.]

Fröhlich, F. W. (1923). Über die Messung der Empfindungszeit. *Zeitschrift für Sinnesphysiologie, 54,* 58–78.

Gellhorn, E. (1961). Cerebral interactions: simultaneous activation of specific and unspecific systems. In D. E. Scheer (Ed.), *Electrical stimulation of the brain* (pp. 321–328). Austin: University of Texas Press.

Goldstein, A. G. (1970). Binocular fusion and contour suppression. *Perception & Psychophysics, 7,* 28–32.

Greenfield, S. A. (1995). *Journey to the centers of the mind.* New York: Freeman.

Gusel'nikov, V. I. (1976). *Electrophysiology of the brain* (in Russian). Moscow: Vysshaya Shkola.

Hassler, R. (1978). Interaction of reticular activating system for vigilance and the truncothalamic and pallidal systems for directing awareness and attention under striatal control. In P. A. Buser, & A. Rougeul-Buser (Eds.), *Cerebral correlates of conscious experience* (pp. 111–129). Amsterdam: North-Holland.

He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature, 383,* 334–337.

Hellige, J. B., Walsh, D. A., Lawrence, V. W., & Prasse, M. (1979). Figural relationship effects and mechanisms of visual masking. *Journal of Experimental Psychology: Human Perception and Performance, 5,* 88–100.

Helmholtz, H. von (1866). *Handbuch der physiologischen Optik, Bd 3: Die Lehre von den Gesichtsfahrnehmungen.* Hamburg, Leipzig: Voss.

Ingvar, D. H., & Hunter, J. (1955). Influence of visual cortex on light impulses in the brainstem of the unanesthetized cat. *Acta Physiologica Scandinavica, 33,* 194–218.

Jasper, H. H., Proctor, L. D., Knighton, R. S., Noshay, W. C., & Costello, R. T., Eds. (1958). *Reticular formation of the brain.* Boston: Little, Brown & Co.

Jung, R. (1958). Coordination of specific and nonspecific afferent impulses at single neurons of the visual cortex. In H. H. Jasper et al. (Eds.), *Reticular formation of the brain* (pp. 423–434). Boston: Little, Brown & Co.

Kandel, E. R., Schwartz, J. H., & Jessell, T. M., Eds. (1991). *Principles of neural science.* Amsterdam: Elsevier.

Keidel, W. D. (1971). *Sinnesphysiologie. Teil I. Allgemeine sinnes-physiologie. Visuelles System.* Berlin: Springer-Verlag.

Kimble, D. A. (1977). *Psychology as a biological science.* Santa Monica: Goodyear.

Klotz, W., & Wolff, P. (1995). The effect of a masked stimulus on the response to the masking stimulus. *Psychological Research/Psychologische Forschung, 58,* 92–101.

Koch, C., & Crick, F. (1991). Understanding awareness at the neuronal level. *Behavioral and Brain Sciences, 14,* 683–685.

LaBerge, D. (1995). *Attentional processing.* Cambridge, Mass.: Harvard University Press.

Leopold, D. A., & Logothetis, N. K. (1996). Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature, 379,* 549–553.

Levelt, W. J. M. (1968). *On binocular rivalry.* The Hague: Mouton.

Libet, B. (1978). Neuronal vs. subjective timing for a conscious experience. In P. A. Buser, & A. Rougeul-Buser (Eds.), *Cerebral correlates of conscious experience* (pp. 69–82). Amsterdam: North-Holland.

Libet, B. (1993). The neural time factor in conscious and unconscious events. In J. Marsh (Ed.), *CIBA Foundation Symposium 174. Experimental and theoretical studies of consciousness* (pp. 123–146). New York: Wiley

Lindsley, D. B. (1960). Attention, consciousness, sleep and wakefulness. In H. W. Magoun, & V. E. Hall (Eds.), *Handbook of physiology. Section I.: Neurophysiology* (Vol. 3, pp. 1553–1593). Washington, DC: American Physiological Society.

Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology and perception. *Science, 240,* 740–749.

Livingstone, M. S., & Hubel, D. H. (1980). Evoked responses and spontaneous activity of cells in the visual cortex during waking and slow-wave sleep. *ARVO 1980. Supplement to Investigative Ophtalmology and Visual Science, 223.*

Llinás, R. (1996). Content and context in the thalamocortical system: the basis for cognition. Paper presented at *Toward a Science of Consciousness 1996. ''Tucson II'',* International Conference, *April 8–13, Tucson, Arizona.*

Llinás, R. R., & Ribary, U. (1993). Coherent 40-Hz oscillation characterizes dream state in humans. *Proceedings of the National Academy of Sciences USA, 90,* 2078–2081.

Logothetis, N. K., Leopold, D. A., & Sheinberg, D. L. (1996). What is rivalling during binocular rivalry? *Nature, 380,* 621–624.

Lyon, D. R. (1990). Large and rapid improvement in form discrimination accuracy following a location precue. *Acta Psychologica, 73,* 69–82.

Magoun, H. W. (1958). *The waking brain.* Springfield: C. C. Thomas.

Menshutkin, V. V., Suvorova, T. P., & Balonov, L. Ya. (1981). Models of the functional switch-out of one hemisphere and of the neuropharmacological effects on deep brain structures (in Russian). *Fiziologiya Cheloveka, 7,* 880–888.

Mesulam, M.-M. (1985) *Principles of behavioral neurology.* Philadelphia: F. A. Davis.

Michaels, C. F., & Turvey, M. T. (1979). Central sources of visual masking: Indexing structures supporting seeing at a single, brief glance. *Psychological Research, 41,* 1–61.

Moruzzi, G., & Magoun, H. W. (1949). Brain stem reticualar formation and activation of the electroen-cephalogram. *EEG and Clinical Neurophysiology,* **1,** 455–473.

Munk, M. H. J., Roelfsema, P. R., König, P., Engel, A. K., & Singer, W. (1996). Role of reticular activation in the modulation of intracortical synchronization. *Science,* **272,** 271–274.

Müller, H. J., & Findlay, J. M. (1988). The effect of visual attention on peripheral discrimination thresholds in single and multiple element displays. *Acta Psychologica,* **69,** 129–155.

Müsseler, J., & Aschersleben, G. (1997). Localizing the first position of a moving stimulus: The Fröhlich Effect and an attention-shifting explanation. *Perception & Psychophysics,* in press.

Müsseler, J., & Neumann, O. (1992). Apparent distance reduction with moving stimuli (tandem effect): Evidence for an attention-shifting model. *Psychological Research/Psychologische Forschung,* **54,** 246–266.

Nakayama, K., & Mackeben, M. (1989). Sustained and transient components of focal visual attention. *Vision Research,* **29,** 1631–1647.

Neumann, O. (1982). Experimente zum Fehrer-Raab-Effekt und das Wetterwart-Modell der visuellen Maskierung. *Ber.Nr.24/1982, Psychologische Institut der Ruhr-Universität Bochum, Arbeitseinheit Kognitionspsychologie.*

Neumann, O., Esselmann, U., & Klotz, W. (1993). Different effects of visual-spatial attention on response latency and temporal-order judgment. *Psychological Research/Psychologische Forschung,* **56,** 26–34.

Newman, J. (1995a). Thalamic contributions to attention and consciousness. *Consciousness & Cognition,* **4,** 172–193.

Newman, J. (1995b). Reticular-thalamic activation of the cortex generates conscious contents. *Behavioral and Brain Sciences,* **18,** 691–692.

Oakley, M., & Eason, R.G. (1990). Subcortical gating in the human visual system during spatial selective attention. *International Journal of Psychophysiology,* **9,** 105–120.

Paré, D., & Llinás, R. (1995). Conscious and pre-conscious processes as seen from the standpoint of sleep-waking cycle neurophysiology. *Neuropsychologia,* **33,** 1155–1168.

Penfiled, W. (1975). *The mystery of the mind: A critical study of consciousness and the human brain.* Princeton University Press.

Posner, M. I., Nissen, M. J., & Ogden, W. C. (1978). Attended and unattended processing modes: The role of set for spatial location. In H. J. Pick, & I. J. Salzman (Eds.), *Models of perception* (pp. 137–157). Hillsdale, NJ: Erlbaum.

Possamaï, C. A. (1986). Relationship between inhibition and facilitation following a visual cue. *Acta Psychologica* **61,** 243–258.

Purpura, D. P. (1970). Operations and processes in thalamic and synaptically related neural subsystems. In F. O. Schmitt (Ed.), *The neurosciences. Second study program* (pp. 458–470). New York: Rockefeller University Press.

Riklan, M., & Levita, E. (1969). *Subcortical correlates of human behavior. A psychological study of thalamic and basal ganglia surgery.* Baltimore: Williams & Wilkins.

Rolls, E. T., & Tovee, M. J. (1994). Processing speed in the cerebral cortex and the neurophysiology of visual masking. *Proceedings of the Royal Society of London, B,* **257,** 9–15.

Scheibel, A. B. (1981). The problem of selective attention: a possible structural substrate. In O.Pompeiano, & C. Ajmone Marsan (Eds.), *Brain mechanisms and perceptual awareness* (pp. 319–326). New York: Raven.

Scheibel, M. E., & Scheibel, A. B. (1967). Anatomical basis of attention mechanisms in vertebrate brains. In G. C. Quarton, T. Melnechuk, & F. O. P. Schmitt (Eds.), *The neurosciences. A study program* (pp. 577–602). New York: Rockefeller University Press.

Scheibel, M. E., & Scheibel, A. B. (1970). Elementary processes in selected thalamic and cortical subsystems—The structural substrates. In F. O. Schmitt (Ed.), *The neurosciences. Second study program* (pp. 443–457). New York: Rockefeller University Press.

Searle, J. R. (1994). The problem of consciousness. In A. Revonsuo, & M. Kamppinen (Eds.), *Consciousness in philosophy and cognitive neuroscience* (pp. 93–104). Hove: Erlbaum.

Sekuler, R. (1995). Motion perception as a partnership: Exogenous and endogenous contributions. *Current Directions in Psychological Science, 4,* 43–47.

Sekuler, R., & Blake, R. (1985). *Perception.* New York: Knopf.

Shagass, C. (1972). *Evoked brain potentials in psychiatry.* New York: Plenum.

Singer, W. (1979). Central core control of visual cortex functions. In F. O. Schmitt & F. G. Worden (Eds.), *The neurosciences. Fourth study program* (pp. 1093–1110). Cambridge, MA: M.I.T.

Singer, W. (1996). Putative functions of temporal correlations in neocortical processing. In C. Koch, & J. Davis (Eds.), *Large scale neuronal theories of the brain.* Cambridge, MA: M.I.T. Press, in press.

Smirnov, V. M. (1974). Electrical stimulation of the human brain and the functional anatomy of mind (in Russian). In N. P. Bechtereva (Ed.), *Neurophysiological mechanisms of mental activity in man.*

Smirnov, V. M., & Resnikova, T. N. (1985). [Artificial stable functional links as a method of research and treatment in the conditions of pathological state] (in Russian), *Vestnik Akademii Meditsinskikh Nauk SSSR, 9,* 18–23.

Smirnov, V. M., Muchnik, L. S., & Shandurina, A. N. (1978). The outline and the functions of the deep structures of the brain (in Russian). In A. A. Smirnov, A. R. Luria, & V. D. Nebylitsyn (Eds.), *Estestvennonauchnye osnovy psikhologii* (pp. 76–108). Moscow: Pedagogika.

Somjen, G. (1972). *Sensory coding in the mammalian nervous system.* New York: Appleton-Century-Crofts.

Stelmach, L. B., Herdman, C. M., & McNeil, K. R. (1994). Attentional modulation of visual processes in motion perception. *Journal of Experimental Psychology: Human Perception and Performance, 20,* 108–121.

Steriade, M. (1981a). Mechanisms underlying cortical activation: Neuronal organization and properties of the midbrain reticular core and intralaminar thalamic nuclei. In O. Pompeiano, & C. Ajmone Marsan (Eds.), *Brain mechanisms and perceptual awareness* (pp. 327–377). New York: Raven.

Steriade, M. (1981b). EEG desynchronisation is associated with cellular events that are prerequisites for active behavioral states. *Behavioral and Brain Sciences, 4,* 489–492.

Steriade, M., Jones, E. G., & Llinás, R. R. (1990). *Thalamic oscillations and signaling.* New York: Wiley.

Steriade, M., Sakai, K., & Jouvet, M. (1984). Bulbo-thalamic neurons related to thalamocortical activation processes during paradoxical sleep. *Experimental Brain Research, 54,* 463–475.

Tasker, R. R., Organ, L. W., & Hawrylyshyn, P. (1980). Visual phenomena evoked by electrical stimulation of the human brain stem. *Applied Neurophysiology, 43,* 89–95.

Tepin, M. B., & Dark, V. J. (1992). Do abrupt-onset peripheral cues attract attention automatically? *Quarterly Journal of Experimental Psychology, 45A,* 111–132.

Umiltà, C., Castiello, U., Fontana, M., & Vestri, A. (1995). Object-centred orienting of attention. *Visual Cognition, 2,* 165–181.

van Essen, D. C. (1979). Visual areas of the mammalian cerebral cortex. *Annual Review of Neuroscience, 2,* 227–263.

Varela, F. J., & Singer, W. (1987). Neuronal dynamics in the visual corticothalamic pathway revealed through binocular rivalry. *Experimental Brain Research, 66,* 10–20.

Walker, P. (1978). Binocular rivalry: central or peripheral selective processes. *Psychological Bulletin, 85,* 376–389.

Warner, C. B., Juola, J. F., & Koshino, H. (1990). Voluntary allocation versus automatic capture of visual attention. *Perception & Psychophysics 48,* 243–251.

Watson, A. B. (1986). Temporal sensitivity. In K. R. Boff, L. Kaufman, & J. P. Thomas (Eds.), *Handbook of perception and human performance. Vol. 1. Sensory processes and perception* (pp. 6/1–6/43). New York: Wiley.

Werner, H. (1935). Studies on contour: I. Qualitative analyses. *American Journal of Psychology,* **47,** 40–64.

Wolfe, J. M. (1983). Influence of spatial frequency, luminance, and duration on binocular rivalry and abnormal fusion of briefly presented dichoptic stimuli. *Perception,* **12,** 447–456.

Wolfe, J. M. (1986). Stereopsis and binocular rivalry. *Psychological Review,* **93,** 269–282.

Wolfe, J. M. (1996). Resolving perceptual ambiguity. *Nature,* **380,** 587–588.

Worden, F. G., Swazey, J. P., Adelman, G., Eds. (1975). *The neurosciences: Paths of discovery.* Cambridge, MA: M.I.T.

Wundt, W. (1903). *Physiologische psychologie* (5th ed.) Vol. III. Leipzig: Engelmann.

Yantis, S., & Gibson, B. S. (1994). Object continuity in apparent motion and attention. *Canadian Journal of Experimental Psychology,* **48,** 182–204.

Zeki, S. M. (1978). Uniformity and diversity of structure and function in rhesus monkey prestriate visual cortex. *Journal of Physiology,* **277,** 273–290.