A Cortical Network for Directed Attention and Unilateral Neglect

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Unilateral neglect reflects a disturbance in the spatial distribution of directed attention. A review of unilateral neglect syndromes in monkeys and humans suggests that four cerebral regions provide an integrated network for the modulation of directed attention within extrapersonal space. Each component region has a unique functional role that reflects its profile of anatomical connectivity, and each gives rise to a different clinical type of unilateral neglect when damaged. A posterior parietal component provides an internal sensory map and perhaps also a mechanism for modifying the extent of synaptic space devoted to specific portions of the external world; a limbic component in the cingulate gyrus regulates the spatial distribution of motivational valence; a frontal component coordinates the motor programs for exploration, scanning, reaching, and fixating; and a reticular component provides the underlying level of arousal and vigilance. This hypothetical network requires at least three complementary and interacting representations of extrapersonal space: a sensory representation in posterior parietal cortex, a schema for distributing exploratory movements in frontal cortex, and a motivational map in the cingulate cortex. Lesions in only one component of this network yield partial unilateral neglect syndromes, while those that encompass all the components result in profound deficits that transcend the mass effect of the larger lesion. This network approach to the localization of complex functions offers an alternative to more extreme approaches, some of which stress an exclusive concentration of function within individual centers in the brain and others which advocate a more uniform (equipotential or holistic) distribution.

In human beings, unilateral neglect syndromes are more frequent and severe after lesions in the right hemisphere. Also, right hemisphere mechanisms appear more effective in the execution of attentional tasks. Furthermore, the attentional functions of the right hemisphere span both hemispaces, while the left hemisphere seems to contain the neural apparatus mostly for contralateral attention. This evidence indicates that the right hemisphere of dextrals has a functional specialization for the distribution of directed attention within extrapersonal space.

One manifestation of unilateral injury to the human parietal lobe is neglect for events that occur within the contralateral half of extrapersonal space. In severe cases, patients may behave almost as if that half of the universe had abruptly ceased to exist. Thus, one patient may shave, groom, and dress only one side of the body; another may fail to eat food placed on one side of the tray; while still another may omit to read half of each sentence written on a page. In cases of lesser severity, the neglect may not be as obvious during spontaneous behavior but can be elicited in the form of unilateral extinction during bilateral simultaneous stimulation. Since primary sensory or motor deficits are not necessary for the emergence of this syndrome, at least one plausible interpretation has been to assume that the unilateral neglect reflects an underlying attentional deficit for segments of extrapersonal space [14, 21].

The investigation of neglect syndromes in human beings has remained subject to the customary uncertainties inherent in clinicopathological correlations. However, recent physiological and anatomical experiments on the posterior parietal areas of the macaque monkey have provided a wealth of new information, much of which appears directly relevant to an understanding of the mechanisms of neglect and perhaps also of directed attention. This article reviews this evidence from the vantage point of a specific cerebral network that functions to coordinate the different stages of directed attention in macaque monkeys and in humans. An additional purpose is to inquire whether this network could influence

the classification of unilateral neglect syndromes in a fashion that can reconcile the apparently divergent views which have sought to explain the process of unilateral neglect as well as the organization of selective attention.

Experiments in Macaque Monkeys

Physiological Basis of Unilateral Neglect

Contralateral attention hemianopia and sensory extinction can be elicited following unilateral but extensive posterior parietal ablations in macaque monkeys [23, 52]. A physiological substrate for this phenomenon emerged in the course of single-cell recordings in the inferior parietal lobule of awake and behaving monkeys. In these experiments, neurons with response contingencies relevant to attentional processes were encountered predominantly in the dorsal portion of the inferior parietal lobule, a region that corresponds to area PG of von Bonin and Bailey [13]. Neurons in this area increase their activity when the animal reaches toward a desirable object such as food, while equivalent but passive limb displacements do not elicit a similar response [61, 97]. Other neurons react most vigorously when the eyes fixate or track a motivationally relevant object; the high rate of response continues until the animal is rewarded by a drop of sweet liquid but then declines abruptly, even in the absence of any gaze shift [82]. Still other neurons increase their rate of discharge prior to the onset of visually evoked saccades toward meaningful events within certain portions of the visual field but not in conjunction with identical spontaneous saccades [82]. In additional experiments, monkeys were taught to maintain central fixation while spots of light appeared in the peripheral fields. Under some conditions, detection of subsequent dimming of the peripheral spot was rewarded, while under other conditions identically placed stimuli had no such behavioral relevance. Even in the absence of any associated eye movements, the response of PG neurons to the onset of such peripherally placed spots of light was found to be more vigorous when reward was made contingent on accurate detection of subsequent dimming [18]. These experiments suggest that area PG in the monkey contains neurons that respond not only to the presence of a stimulus but also to its current motivational value and to the likelihood of its becoming the immediate target of visual or manual grasp.* It is therefore reasonable to

expect that unilateral ablations that include area PG will result in a state of neglect for the contralateral hemispace since the animal will have lost a neural apparatus for registering the impact of motivationally relevant events and for making them the target of subsequent behavior.

Anatomical Basis of Unilateral Neglect

Recent experiments based on axonal transport of tracer substances show that neural connections of area PG, and especially those of its dorsolateral part, provide a pattern of connectivity that is consistent with the physiological properties noted in the preceding section [31, 66, 90, 123]. Although area PG is composed of three subdivisions (intrasulcal, medial, and dorsolateral), the following comments focus on *dorsolateral PG* since this subdivision contains many of the attention-related neurons just described and since it is the most accessible to behavioral and anatomical experiments.

The large number of neural projections which have been shown to reach dorsolateral PG gives the impression of such indiscriminate heterogeneity that the functional contribution of an individual connection may appear irrelevant or impenetrable. However, each of these connections can be placed into one of only four distinct categories such as "sensory association," "limbic," "reticular," and "motor" [90]. This classification highlights the neural convergence of limbic with sensory information, a convergence that may underlie the physiologically demonstrated ability of neurons in this area to recognize motivational clues in sensory events. The group of reticular inputs may provide a means for modulating the regional level of arousal, while the motor output may guide the exploratory and orienting behavior necessary for scanning the environment.

The sensory association afferents reach dorsolateral PG only after undergoing extensive processing in other parts of the cortex (Fig 1). This cortical elaboration of sensory information occurs in orderly succession within specific subtypes of association cortex. Thus, the initial cortical relay for the three major sensory modalities occurs within discrete koniocortical fields in the supratemporal plane (auditory), occipital lobe (visual), and postcentral gyrus (somatosensory). These primary sensory areas send massive connections, either directly or through an intervening relay, to surrounding association areas: auditory cortex to the superior temporal gyrus, visual cortex to peristriate and inferotemporal cortex, and

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*Whereas Mountcastle [96] and Lynch [81] conclude that these neurons have a command function for hand and eye movements within extrapersonal space, Robinson et al [106] emphasize their sensory properties, arguing that the change in firing rate that precedes an eye movement reflects enhancement of a sensory response rather than a command signal to perform a saccade. However, both groups agree that neurons in area PG associate complex

visual and somatosensory information with the internal drive state, and that an increase in the activity of these units may reflect the psychological state of attention that the stimulus elicits on the basis of its motivational importance.
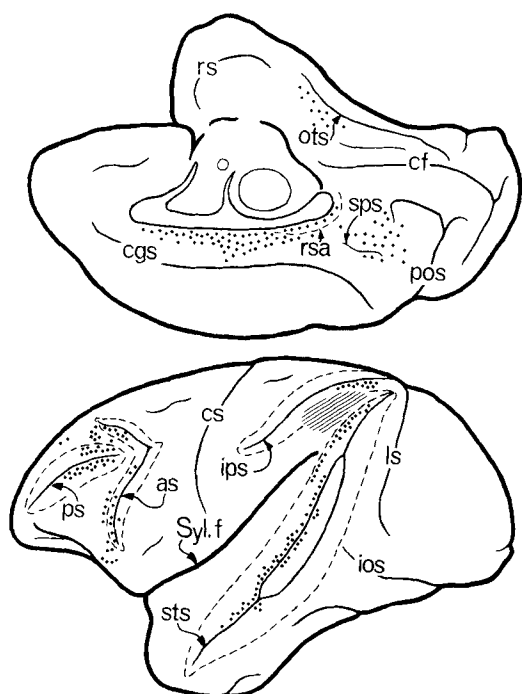
Fig 1. The selective distribution of neurons that send connections into dorsolateral PG in the rhesus monkey. The inferior parietal lobule is bound by the intraparietal sulcus (ips), sylvian fissure (Syl. f), and superior temporal sulcus (sts). Dorsolateral PG occupies the dorsal half of the inferior parietal lobule. The cortex along the dorsal half of the caudal bank in the intraparietal sulcus represents the intrasulcal part of PG, while the region bound by the subparietal sulcus (sps) and the parietooccipital sulcus (pos) contains the medial part of PG. The hatched area in this animal (area virtually confined to dorsolateral PG) was injected with the enzyme horseradish peroxidase. This tracer is transported retrograde to the perikarya of neurons that send axons into the injected area. The distribution of these neurons is indicated by diamonds on the medial and lateral surfaces of the brain. The area between the dashed and solid lines represents the cortex lining sulcal banks. (as = arcuate sulcus; cf = calcarine fissure; cgs = cingulate sulcus; cs = central sulcus; ios = inferior occipital sulcus; ls = lunate sulcus; ots = occipitotemporal sulcus; ps = principal sulcus; rs = rhinal sulcus; rsa = retrosplenial area.) (From Mesulam et al [90], Brain Res 136:393–414, 1977.)

somatosensory cortex to the superior parietal lobule [64, 99]. Each of these association regions (and perhaps others) constitutes a unimodal association area since its neural input, the behavioral deficits that follow its removal, and the response contingencies of its component neurons are predominantly confined to the one relevant modality. The next stage in processing sensory information occurs when connections from more than one type of unimodal cortex converge (or reside in close proximity) within cortical areas that can be designated as polymodal. Periarcuate cortex and the banks of the superior temporal sulcus constitute two of the better-known polymodal areas

in the brain of the rhesus monkey [20, 116]. Individual neurons in this type of cortex respond to input in more than one modality, while behavioral consequences of lesions reflect difficulties in detecting multimodal aspects of stimuli [8, 10, 125].

Neuroanatomical experiments led to the somewhat unexpected conclusion that dorsolateral PG receives exceedingly few projections either from primary sensory cortex or from traditional unimodal associated areas. Instead, this part of PG receives the great majority of its cortical sensory association input from polymodal areas [90]. Thus, just as there is at least one obligatory unimodal relay between primary sensory cortex and polymodal areas, there is generally at least one obligatory relay (mostly in polymodal areas) between unimodal cortex and dorsolateral PG [90]. It appears, therefore, that sensory information cannot have access to dorsolateral PG until it is extensively processed in unimodal and then in polymodal cortex. This ensures that dorsolateral PG is in a position to contain an exceedingly elaborate sensory representation of extrapersonal space, a condition that appears desirable for the function of an area involved in distribution of attention.*

Unit recordings indicate the presence of widespread visual responses in dorsolateral PG [97, 106, 135]. The pattern of cortical and subcortical connections is consistent with this pattern of responses. For example, three major sources of projections into dorsolateral PG, area TF in the parahippocampal gyrus, the caudal bank of the intraparietal sulcus, and the medial pulvinar nucleus, have massive connections with unimodal visual association areas and undoubtedly act as relays for visual information [90, 115, 117, 124]. Nevertheless, each of these connections still follows the general principle that there is at least one synapse interposed between traditional unimodal areas and dorsolateral PG. On the other hand, the lateroposterior and intralaminar thalamic nuclei, which have lesser connections with dorsolateral PG, do receive substantial inputs from the superficial (visual) layers of the superior colliculus [7] and may act as more direct relays for visual information. Indeed, a low degree of stimulus specificity and large receptive fields are response properties shared by units in dorsolateral PG and by those in the superficial layers of the superior colliculus but not by components of the geniculocalcarine system [47, 135]. It is interesting to note,

*In a previous publication the term supramodal was suggested as a generic name for this type of cortex [90]. Our preliminary observations in the frontal lobes indicate that this profile of sensory connections may be unique to dorsolateral PG. For example, several areas we studied in prefrontal cortex had a substantial unimodal input [2]. With the possible exception of paralimbic areas, dorsolateral PG may thus contain the most extensively processed sensory input.

however, that the medial pulvinar nucleus, which is the major source of thalamic input into dorsolateral PG, receives very few, if any, direct projections from the superficial layers of the superior colliculus [7]. Instead, the medial pulvinar nucleus is probably involved mostly in relaying highly integrated polysensory information (albeit with a bias for the visual modality) into dorsolateral PG. The predominant type of thalamic input therefore parallels the predominant type of cortical input reaching dorsolateral PG from sensory association areas.

The elaborate nature of this sensory input assumes special relevance when it is considered that the limbic projections from the cingulate gyrus are directed predominantly to the dorsolateral part of area PG rather than to its intrasulcal subdivision, which receives the less extensively processed unimodal inputs [90, 100]. In addition to cingulate input, dorsolateral PG also receives additional limbic connections, probably cholinergic, from the substantia innominata and also from the lateral hypothalamic area in the basal forebrain [89]. These limbic connections and their convergence with extensively processed sensory afferents may play a fundamental role in assigning motivational valence to complex events that occur within extrapersonal space. While the basal forebrain may be concerned with a limited set of basic reinforcements such as food or drink [107], the cingulate cortex may subserve the more complex aspects of reinforcement and their modification by learning. Indeed, it was observed that the discharge rate of neurons in area PG did not simply reflect the aversive or desirable properties of food-related stimuli [108]. Thus, it seems that the coding of motivational relevance at the level of dorsolateral PG reflects greater complexity and specificity. Moreover, while the basal forebrain projects widely to many neocortical areas [30, 68, 91], the cingulate cortex has a far more selective efferent field [100]. On the basis of this selectivity, it is reasonable to expect that the cinguloparietal connection is all the more important in shaping the functional specialization of dorsolateral PG.

A third contingent of inputs into dorsolateral PG originates in intralaminar thalamic nuclei, in the nucleus locus coeruleus, and in the brainstem raphe nuclei [90]. I have chosen to combine these projections into a category of reticular inputs. At least in the cat, stimulation of intralaminar thalamic nuclei can elicit cortical recruiting or desynchronization [130], while the nuclei of the locus coeruleus and midline raphe mediate the different phases of sleep [65]. These reticular projections may thus modulate regional cortical activity according to the prevailing level of arousal. Since the effectiveness of attention and the level of arousal are clearly interrelated [58],

this group of inputs may be of considerable functional relevance.*

The *efferent* projections of area PG are reciprocally directed to most of the afferent sources already listed here [64, 99]. Of special interest for directed attention are the projections to the frontal eye fields (area 8) and to the superior colliculus [2, 64, 72, 99, 102]. Neurophysiological and behavioral experiments indicate that these areas are crucial for the modulation of head and eye movements. For example, stimulation of each of the two regions elicits contraversive head and eye movements [38, 104, 105]. Unit recordings indicate that the deep layers of the superior colliculus contain neurons active in initiating eye movements [111, 112, 132]. The presence of similar neurons in the frontal eye fields has been questioned [12, 94]. However, there are units in the caudal portion of the frontal eye fields that do show a burst of activity just before a saccade directed to a stimulus in the appropriate part of the visual field. The burst does not occur if the animal merely attends to the stimulus but fails to make a saccade toward it [45]. Furthermore, the receptive fields of these neurons predict the direction of movement that follows their microstimulation [46]. Combined lesions of frontal eye fields and of the superior colliculus result in profound impairment of saccadic eye movements even though destruction of either site alone causes only subtle deficits [95, 113, 133]. Thus, the frontal eye fields and superior colliculus appear to have parallel but complementary and pivotal roles in modulating ocular movements.† The frontal eye fields and surrounding areas may also be involved in limb movements since complex manual tasks are also impaired following lesions that include this area [27, 49, 93, 122]. Thus, the output of dorsolateral PG to the frontal eye fields and to the superior colliculus may coordinate the motor sequences necessary for foveating, scanning, exploring, fixating, and manipulating motivationally relevant events within extrapersonal space.

While none of the projection classes just described is confined to dorsolateral PG, the individual characteristics of each of the four categories and their convergence in this region constitute a unique profile of connectivity that is consistent with functional specialization in the process of directed attention (Fig 2).

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*Dorsolateral PG also receives inputs from the claustrum [90]. The claustrum presently defies classification into any single functional category and may have sensory association, limbic, and reticular influences on dorsolateral PG.

†The motor output from the frontal eye fields appears to be mostly nonpyramidal. Thus, there are efferents to the striatum, subthalamic nucleus, and superior colliculus but relatively few to premotor or motor cortex [70, 71, 99].
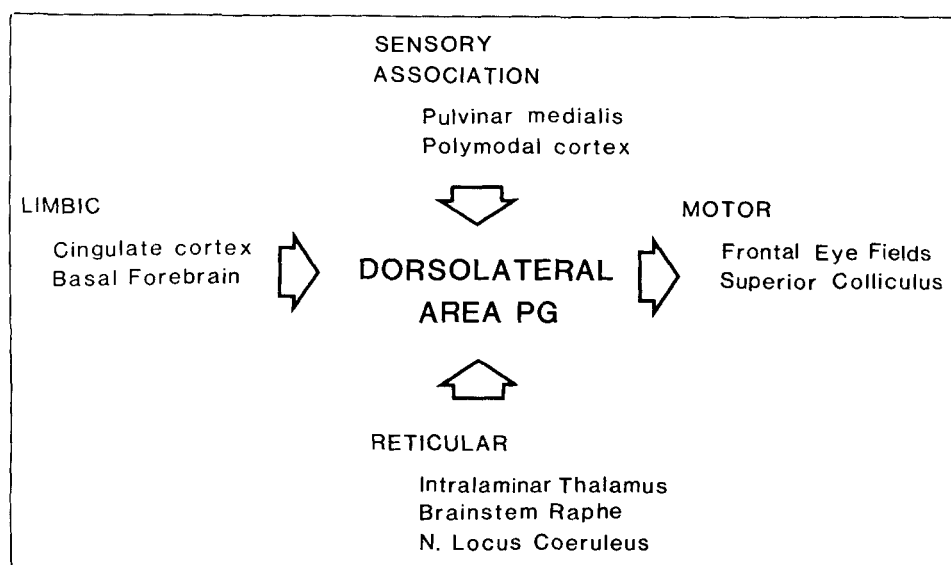
SENSORY
ASSOCIATION

Pulvinar medialis
Polymodal cortex

LIMBIC   MOTOR

Cingulate cortex   Frontal Eye Fields
Basal Forebrain   DORSOLATERAL   Superior Colliculus
                          AREA PG

RETICULAR

Intralaminar Thalamus
Brainstem Raphe
N. Locus Coeruleus

Fig 2. The organization of input and output that is relevant to directed attention.

Unilateral Neglect Syndromes

The two cortical areas that provide pivotal connections for dorsolateral PG, cingulate cortex and the frontal eye fields, are reciprocally connected with each other as well as with dorsolateral PG [2, 64, 90, 99, 100]. Furthermore, reticular input from a similar set of thalamic and brainstem structures reaches not only PG but also cingulate cortex and the frontal eye fields [2, 126]. This intimate coupling among the four regions that are relevant to directed attention raises the possibility that lesions not only in PG but also in cingulate cortex, in the frontal eye fields, and even in reticular structures may disrupt the process of directed attention. Lesions in each individual site of this interconnected network could then be expected to yield a specific clinical picture that reflects the anatomical specialization of the relevant area (Fig 3).

PARIETAL NEGLECT. With respect to directed attention, its sensory connectivity suggests that dorsolateral PG and surrounding areas may provide a stage of *afferent integration* whereby the extrapersonal space becomes transformed into a sensory representational template. The rules for this transformation are not clear. It is reasonable to assume that all three major sensory modalities as well as both sides of space are represented within the dorsolateral PG of each hemisphere. However, there appears to be a bias for the visual modality and for the contralateral hemispace, especially for its peripheral aspects [135]. Furthermore, it is tempting to speculate that the encoding in dorsolateral PG transcends a composite reproduction of actual sensory events and that it

contains additional mechanisms for providing an interaction between space and relevance. It is conceivable that area PG contains a fluid template where the transformation of external events into synaptic activity reflects not only the physical properties of the stimulus field but also the distribution of relevance within segments of extrapersonal space. Thus, for a monkey restrained to its chair, a desirable object located beyond an arm's distance is likely to be of far less relevance than an identical object similarly positioned in the visual field but which is also reachable. Indeed, neurons in the dorsolateral PG of awake but restrained animals showed a marked attenuation of response when a motivationally relevant object was moved beyond reach [97]. It appears, then, that under these conditions events inside a sphere with a radius approximately equal to an outstretched arm have a preferential impact value. It is conceivable that relatively more synaptic space is devoted to this segment of the world than would have been the case in the absence of restraints.

Unilateral damage in dorsolateral PG may permanently bias this internal representation in favor of the hemispace ipsilateral to the lesion. In contrast to lesions in primary or unimodal sensory cortex, PG lesions may allow sensory stimuli in any modality and from all parts of extrapersonal space to be analyzed with customary acuity as long as meaningful events occur on one side of space at a time. However, when both hemispaces contain potentially meaningful events of equivalent value, as in the paradigm of bilateral simultaneous stimulation, the contralateral event fades into relative neglect since its synaptic representation within the context of the entire extrapersonal space is markedly attenuated in comparison to the competing events in the ipsilateral hemispace.
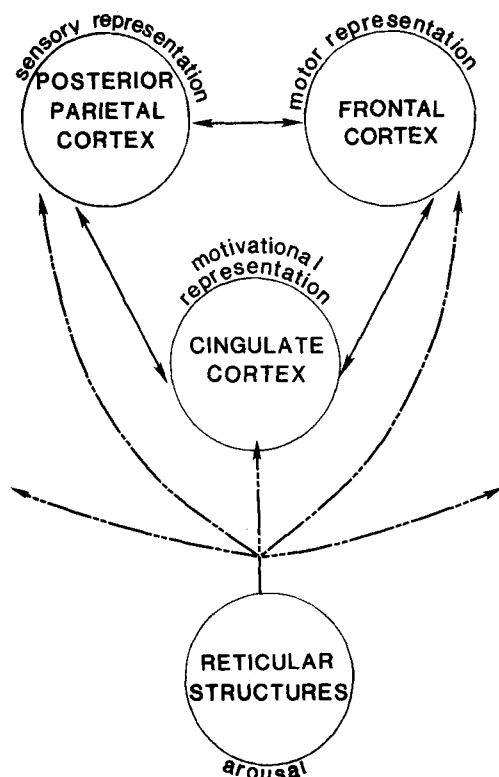
Fig 3. The components of a neural network involved in modulating directed attention.

This hypothesis is consistent with two sets of experimental observations. First, Heilman et al [52] found that rhesus monkeys with unilateral posterior parietal lesions (including area PG) show neglect (extinction) of a contralateral stimulus, predominantly under conditions of bilateral simultaneous stimulation. However, identical stimuli elicited adequate responses when presented unilaterally. Since the authors stressed the absence of primary motor or sensory impairment, the unilateral neglect in these experiments may well have reflected a disturbance in the distribution of attention subsequent to distortion in the inner representation of extrapersonal space. In another set of experiments, by Lamotte and Acuña [73], manual reaching toward a visual target was impaired following unilateral posterior parietal lesions that included PG. The misreaching consisted of deviation toward the side of the lesion with either limb, even when the target was in the ipsilateral hemispace. It is conceivable that the internal representation of space had become skewed in favor of the ipsilateral side and that the motor program for reaching merely reflected this bias, in a fashion somewhat analogous to the behavior of humans subjected to prismatic distortion of visual space.*

*Humans rapidly adapt to prismatic distortion, perhaps with the assistance of the neural mechanisms in parts of the brain homolo-

FRONTAL NEGLECT. The frontal eye fields (area 8) and surrounding regions may provide a stage of *efferent integration* for the initiation or inhibition of motor mechanisms involved in exploratory or attentive behavior. Unilateral neglect following damage to the frontal eye fields has been known for almost a century [9, 67, 76, 131]. Depending on details of the individual experiment, the neglect encompasses auditory, visual, and tactile stimuli and manifests itself as failure of orienting and reaching toward the contralateral space. Since the animals show no evidence of hemiparesis or conventional sensory loss [67], this phenomenon may be attributed to a distortion in the distribution of attention behavior within extrapersonal space. In contrast to the posterior parietal syndrome, in which bilateral simultaneous stimulation is most effective in eliciting inattention, even unilateral stimulation can be neglected following frontal lesions so that spontaneous behavior displays ongoing contralateral neglect [9, 67].

The predominance of motor over sensory factors in frontal neglect was specifically demonstrated by Watson et al [129]. Macaque monkeys were trained to respond to unilateral tactile stimulation with the contralateral limb. Following unilateral lesions centered around the frontal eye fields, the spontaneous behavior of these animals displayed contralateral neglect even in the absence of hemiparesis. During subsequent retesting in the experimental paradigm, errors were more common when the response was generated by the limb contralateral to the ablation (sensory stimulus being directed to the intact hemisphere). A more accurate performance was obtained when the response was generated by the ipsilateral limb (sensory stimulus directed to the ablated side). These experiments indicate that the unilateral neglect which emerges after frontal lesions reflects a disturbance of motor output rather than of sensory input. Just as PG lesions result in neglect not because of a field cut but because of bias in the internal representation of the sensory space, frontal eye field lesions seem to cause neglect not because of hemiparesis but because of a disinclination to perform motor operations aimed at the contralateral hemispace. Thus, even limbs ipsilateral to the lesion are ineffective in orienting toward meaningful objects in the neglected hemispace [9, 67].

The frontal eye fields and surrounding cortical areas may contain an inner representation of motor programs for the distribution of exploratory sequences within extrapersonal space. In contrast to parietal neglect, which is most active when attention

gous to dorsolateral PG in the monkey. One would predict that such adaptation is far more difficult in patients with unilateral posterior parietal lesions.

needs to be simultaneously distributed across both hemispaces, frontal neglect may reach maximal expression when the task requires systematic and sequential scanning of the environment.

CINGULATE NEGLECT. The cingulate cortex may provide a locus for *limbic integration* within the network depicted in Figure 3. This area may play a pivotal role in assigning motivational relevance to sensory events according to past experience as well as to present needs. Consequently, events with special motivational meaning can acquire greater impact value, and perhaps a more extensive representation in PG, so that they will be more likely to activate and engage the frontal mechanism for orienting, reaching, and fixating. Thus, a hungry animal may spend a disproportionately long time exploring the area around the door through which the trainer is expected to enter during feeding time. It is conceivable that information concerning the state of hunger and traces related to previous feedings become integrated in the cingulate area. This may cause increased activity in PG neurons representing that portion of space as well as in the corresponding neurons of the frontal eye fields. The net result may be to direct attention preferentially to that part of extrapersonal space. The anatomical basis for this functional property may well be found in the extensive connections of the cingulate region not only with such limbic structures as the hippocampal formation, presubiculum, and amygdala but also with polymodal sensory association areas [100, 109, 126]. Thus, cingulate cortex may participate in directed attention by regulating the spatial distribution of expectation and by assigning impact value to motivationally relevant events. The cingulate area may therefore constitute a third type of parallel and complementary representation of extrapersonal space in a manner that is primarily sensitive to motivational impact.

Unilateral cingulate stimulation in the cat does elicit searching head and eye movements directed at the contralateral space as well as concomitant cessation of all other ongoing activity [63]. Furthermore, Watson et al [127] demonstrated the emergence of contralateral neglect in rhesus monkeys subjected to unilateral lesions in the region of the cingulate. However, the behavioral characterization of this type of neglect requires further delineation.*

*In the rat, unilateral damage to ascending dopaminergic connections elicits contralateral neglect [39, 79, 84]. One target of these projections is the nucleus accumbens. That nucleus provides a major source of neural input to the substantial innominata, which is in turn one of the two sources of limbic input into dorsolateral PG [89]. Furthermore, there seem to be direct corticopetal dopaminergic connections to cingulate cortex, at least in the rat [35]. Thus, the unilateral neglect secondary to interruption of dopaminergic pathways may reflect involvement of the limbic component in the network shown in Figure 3.

RETICULAR NEGLECT. The importance of the reticular formation to arousal and of arousal to attention is a concept that needs no introduction [58]. In the most trivial instance, bilateral lesions within the reticular formation lead to irreversible depression of consciousness that is inconsistent with the operations of selective attention. More selective lesions may also disrupt the distribution of attention. In the rat, for instance, interruption of the ascending noradrenergic bundle from the nucleus locus coeruleus interferes with attentional processes [85, 86]. In the monkey, unilateral lesions in intralaminar nuclei or in the mesencephalic reticular formation result in unilateral neglect [128, 129]. It is conceivable that these lesions interfere with general activation of the relevant cortical regions in the frontal eye fields, dorsolateral PG, and cingulate gyrus by reticular inputs (see Fig 3).

Action and Perception
While the role of dorsolateral PG in directed attention appears to be mostly sensory and that of the frontal eye fields mostly motor, the distinction is by no means absolute. Thus, area PG appears to have some motor properties, and the frontal eye fields have functional aspects that may be characterized as sensory [10, 36, 40, 73, 75, 76, 81, 82, 94, 96, 97, 134]. Therefore, unilateral neglect syndromes are unlikely to be exclusively sensory or motor; rather, they are a mixture of both. This duality becomes more intelligible in light of a recent essay by Droogleever-Fortuyn [32], who challenges the traditional view that sensory input is the primary building block of experience. Instead, he proposes that sense organs are comparable to "feelers of tentacles" used to scan the world in order to update an inner representational map. Thus, perceiving is as much a motor phenomenon as it is sensory, and this is nowhere more understandable than in the process of selective attention.

While these parietal, frontal, cingulate, and reticular components undoubtedly hold pivotal roles in the distribution of directed attention, I do not wish to imply that they account for *all* operations relevant to sensory attention. Indeed, Hubel et al [60] have demonstrated that some neurons even in the primary auditory cortex of cats increase their response to sound when the animal appears to direct attention to its source. In striate cortex and even in the lateral geniculate nucleus, the response to visual stimuli can be enhanced by experimental manipulations which increase the general level of neural activation [4, 44]. Furthermore, in the rhesus monkey, lesions of primary somatosensory cortex may lead to sensory extinction, while unimodal visual areas in inferotemporal cortex appear necessary for inhibiting the impact of irrelevant visual stimuli and for identifying

those that are meaningful [34, 50, 120]. However, the role of these areas in attention is probably more limited, being confined to single sensory modalities. It is reasonable to assume that the attention-related responses in these areas predominantly reflect the overall distribution of attention as determined by the network shown in Figure 3. I do not wish to suggest that the regions depicted in Figure 3 are exclusively concerned with functions related to the distribution of attention. For example, the frontal eye fields also appear to play a major role in multimodal sensory integration [125], while dorsolateral PG is essential for complex visuomotor activity [103]. This characteristic functional heterogeneity in areas that are components of an integrated cerebral network will receive further comment.

Human Syndromes

Injuries that result from head trauma, neoplasm, or stroke rarely respect architectonic or topographic landmarks that guide experiments in animals. Moreover, homologies between cortical areas of human beings and other primates are not always clear, and the pattern of intercortical connections that characterizes the human brain is incompletely understood.* It is therefore difficult to compare the details of cerebral organization in different primate species with that of the human. Nevertheless, several independent lines of evidence support the conclusion that the four subtypes of unilateral neglect described in the macaque monkey can also be identified in human patients, suggesting that a cerebral network with a similar organization may be responsible for the coordination of directed attention within extrapersonal space. Since most human unilateral neglect cases reported in the literature consist of patients who have right hemisphere lesions and neglect the left hemispace, the subsequent discussion addresses left-sided neglect exclusively. The assumption that this difference in frequency implies right hemisphere specialization for directed attention will then be analyzed in the light of pertinent evidence.

Parietal Neglect

Severe unilateral neglect in humans is almost automatically attributed to parietal lobe involvement.

*According to Brodmann [16, 17], the human inferior parietal lobule consists of areas 39 and 40. Brodmann did not find equivalent achitectonic regions in the monkey. Instead, he designated the inferior parietal lobule in the monkey as area 7. Since area 7 in human beings is situated along the rostral bank of the intraparietal sulcus, this would be the area in the human homologous to the monkey's inferior parietal lobule. According to this scheme, then, the monkey brain contains no architectonic analogue to the human inferior parietal lobule. However, von Economo's [33] work in human beings and that of von Bonin and Bailey [13] in monkeys indicate that the inferior parietal lobules in the two species are far more analogous in that they both consist of areas PG and PF.

Indeed, the earlier case reports of this syndrome described patients with lesions in the posterior parts of the right hemisphere [14, 87, 101]. While the parietal lobe was often incriminated as the principal site of damage, localization was hampered because each of the patients in these reports had suffered either multilobar infarcts, head injury, or intracerebral neoplasm. Subsequently, Hécaen et al [51] described the emergence of unilateral neglect in patients subjected to cortical excision of the right inferior parietal lobule (mostly area PG and PF) for control of epilepsy. This localization acquired greater certitude with the help of case reports describing unilateral neglect after infarctions in the area of the intraparietal sulcus and inferior parietal lobule in individuals without a history of prior neurological impairment [22, 23, 54].

Contrary to widespread opinion, the unilateral neglect following an infarction limited to the posterior parietal area is not always severe, and mere observation of spontaneous behavior may fail to reveal consistent deficits. Indeed, bilateral simultaneous stimulation may become necessary for eliciting neglect in the form of extinction while responses to unilateral stimulation may show no abnormality. In more severe cases, however, the tendency to extinction may be so powerful that the mere presence of ambient visual input on the side ipsilateral to the lesion elicits neglect for the contralateral hemispace so that even unilateral stimulation appears to be ignored during bedside examination. In such cases, I have found that presenting brief flashes of light in a darkened room will reveal extinction to be the underlying mechanism of the neglect. Since neither limitation of head and eye movements nor primary sensory loss is a necessary condition, the neglect can be attributed to an attention deficit within the hemispace contralateral to the lesion. Although several authors have already demonstrated that primary sensory loss is not the cause for the neglect [19, 42, 54], one case deserves comment for emphasis. A 74-year-old right-handed man was admitted with a gradually progressive neurological deficit caused by a glioma that included the posterior parietal cortex in the right hemisphere. He showed left-sided extinction to tactile, visual, and olfactory stimuli. Since primary olfactory pathways are not crossed, the olfactory extinction should have occurred on the right rather than on the left if primary sensory loss, however subtle, had been responsible for the neglect.

Although the relevant neural connectivity in humans is less well known than that in the monkey brain, it is likely that parts of the posterior parietal cortex of the human brain have connections similar to those of dorsolateral PG in the rhesus monkey (see Figs 1–3). It is reasonable to assume that this

region contains an elaborate sensory template of the external world, perhaps obtained through a process similar to the one for which Denny-Brown et al [24] coined the term *morphosynthesis*. Through mechanisms similar to the ones postulated to exist in the monkey, unilateral damage in this region may induce distortion in this representation so that events in the contralateral hemispace lose their relative impact on awareness, thus leading to the phenomenon of extinction.

The role of inner representation in the genesis of parietal neglect has been championed by, among others, Bisiach et al [11]. In their experiments, patients with right hemisphere damage (all of whom had independent evidence of left-sided neglect and most of whom had lesions involving the posterior parietal cortex) were presented with pairs of geometric shapes and asked to judge if the two stimuli in each pair were identical or different. The subjects viewed the stimuli not in their entirety but through a centrally placed slit under which the objects were passed at a constant rate, one at a time. Thus, the subject had to reconstruct the entire object in mind and store it in memory for subsequent comparison with the next object in the pair. The results indicated that the patients were less accurate in detecting differences on the left side of the objects, whether the objects moved leftward or rightward under the slit. Since sensory input during the experiment was centrally situated, the outcome cannot be attributed to neglect of actual events in the extrapersonal space; rather, it was the result of neglect of the inner representation per se, even though the constituent sensory information had originated in the nonneglected parts of the external world [11].

A rather unusual case from our files provides additional support for this position. A right-handed chronic alcohol abuser was admitted with an embolic infarction that included the posterior parts of the right hemisphere. He had severe neglect of the left hemispace. Several days after admission he developed delirium tremens and entered into heated arguments with hallucinated individuals in his room. The hallucinations appeared only on his right, never on his left. It is as if the internal representation of the left hemisphere was so rarefied that it could not even harbor ghosts.

Frontal Neglect
A region in the human frontal lobe has been designated as the frontal eye fields because its stimulation elicits contralateral deviation of the eyes while its destruction leads to transient paralysis of gaze toward the side opposite to the lesion [41]. Unilateral neglect in humans does arise as a consequence of tumors or infarcts in frontal cortex [55,

119]. It is conceivable that the neglect in these patients reflects involvement of the frontal eye fields and immediately surrounding areas. Analysis of frontal neglect in the monkey suggests that these patients should experience greatest difficulty in tasks that depend on exploring, searching, or manipulating objects in the contralateral hemispace. In fact, deficits of active visual scanning have been described with lesions of the frontal lobe [80]. Patients with frontal neglect would therefore be expected to show unilateral neglect in copying figures, route finding, letter cancellation, and even reading, since these tasks require systematic and sequential scanning of the external space. Frontal neglect would also be more likely to result in spontaneous inattention, whereas parietal neglect would be more likely to cause extinction. It is unlikely, however, that either of these two subtypes will be seen in isolation, not only because lesions are rarely that specific but also because effective scanning is likely to require a reliable internal representation, whereas the accuracy of the internal representation probably depends on adequate scanning.

Experiments by DeRenzi et al [25] and by Heilman and Valenstein [56] have demonstrated that one major component of unilateral neglect consists of hypokinesia for exploration and manipulation within the contralateral hemispace. I would suggest that this motor aspect of unilateral neglect reflects involvement of the frontal component in the network that subserves attention (see Fig 3). Just as the sensory aspect of parietal neglect is not the outcome of a multimodal field cut, I believe the motor aspect of frontal neglect does not reflect hemiparesis of limb, head, and eye movements, but rather an underlying disinclination to move within and toward the neglected hemispace, whatever the specific muscle groups required for such activity may be.* Indeed, there is reason to believe that some aspects of motor output in the intact person are also organized according to the hemispace within which the movement occurs. Anzola et al [1] required subjects to make a decision concerning which hand to use in a choice reaction-time experiment depending on the position of a visual stimulus. The experiment was performed with and without hand crossing, and the results showed that the faster hand in the crossed condition was not the one anatomically ipsilateral to the stimulus but the one situated in the same hemispace with the stimulus. Thus, under special condi-

*Bard [3] in 1904 had already suggested that the contraversive head and eye deviation seen in many patients with unilateral lesions reflects not so much motor weakness as diminution in the impact of events emanating from the contralateral hemispace. While Bard did not mention localization, the findings in many of his case studies suggested frontal lesions.

tions requiring concentrated attention to a task, the neural organization of motor output may reflect the part of the extrapersonal space where the movement will be discharged and not exclusively the muscle groups that will be activated.

A relevant case is that of a right-handed man admitted with a stroke in the right hemisphere. He showed left-sided neglect, especially during tasks of visual scanning and figure copying. While no documentation of the lesion site was available, a mild left hemiparesis in the absence of primary sensory loss suggested a frontal localization. During testing he was blindfolded and asked to detect and retrieve, by manual exploration, an object placed on either side of him on the surface of his bed. When the object was placed on his left side, manual exploration with either hand was haphazard and erratic so that failures and delays of retrieval were common. However, performance was virtually intact, even with the mildly hemiparetic left hand, when the object was on his right.

Whereas the salient manifestations of parietal neglect may well be sensory and those of frontal neglect motor, the dichotomy is unlikely to be absolute. Thus, patients with parietal neglect may also show reluctance to project the contralateral limb into the neglected hemispace, while those with frontal neglect may show such diminished reaction to contralateral visual stimuli that the presence of a hemianopia may be suspected in the acute phase. The universality of such sensory-motor duality in attentional mechanisms has been addressed in the preceding discussion.

Cingulate Neglect
Evidence for cingulate neglect in human beings is indirect and speculative. However, one of the patients with unilateral neglect reported by Heilman and Valenstein [55] had a medially situated frontal infarction that could have involved predominantly the cingulate cortex. On the basis of the corresponding connectivity in the monkey, neglect arising from cingulate lesions in humans may reflect a loss in the perception of biological importance associated with events in the contralateral hemispace. If so, the distribution of expectancy for *potential* events and also the attribution of motivational relevance to *actual* stimuli would be impaired on the side contralateral to the lesion. Consequently, the contralateral hemispace would attract less scanning and fixation. The net outcome of these factors may culminate in unilateral neglect. While no specific localization was suggested, the contribution of motivational variables was first stressed by Denny-Brown et al [24], who described one aspect of unilateral neglect as a "diminution in biological

stimulus value in the left exteroceptive field." It seems reasonable to attribute this aspect of unilateral neglect to disruption of the limbic component in the network depicted in Figure 3.

Reticular Neglect
It is generally accepted that the overall process of attention refers to at least two different operations [88]. One of these is *tonic* in character and regulates the threshold that a stimulus must exceed before gaining access to consciousness; the second is *phasic* and selects, from among the many stimuli which exceed this threshold, those which will occupy the center of awareness. The parietal, frontal, and cingulate mechanisms already discussed reveal one way in which selective (phasic) attention is coordinated within extrapersonal space. On the other hand, the tonic process of attention is intimately related to the level of vigilance and depends on the integrity of the reticular formation. Thus, focal mesencephalic infarcts that interfere with the reticular formation and its ascending connections result in severe disturbances of vigilance and arousal [15, 114]. In the monkey, the reticular input to the cortical areas implicated in the regulation of selective attention originates in the intralaminar thalamic nuclei, the nucleus locus coeruleus, and the midline raphe nuclei (see Figs 2, 3). Similar connections may exist in the human brain, and it is conceivable that unilateral lesions in these structures may elicit neglect for the contralateral hemispace.

Compound Neglect Syndromes
In naturally occuring lesions that come to clinical attention, damage is rarely confined to one of the four components in Figure 3 so that the patient may simultaneously manifest many aspects of unilateral neglect. The same patient may show marked extinction, a distorted inner representation of external space, failure to scan the contralateral hemispace, devaluation of its biological significance, and even diminution of overall arousal and vigilance. In some cases it appears as if the contralateral side of space has ceased to exist in the patient's consciousness not only with respect to actual sensory stimuli but also as far as potential events are concerned. The deficit is not one of seeing, hearing, feeling, or moving but one of looking, listening, touching, and exploring. The neglect encompasses extrapersonal space, body surface, and even intrapsychic representations. These severe manifestations of unilateral neglect could not be expected to arise from lesions confined to posterior parietal cortex and indicate the involvement of additional components in the network that subserves directed attention.

Agreement with Other Theories of Unilateral Neglect

The preceding account suggests that four distinct contributions to the overall organization of directed attention may be identified in human beings as well as in the monkey. It is likely that lesions which do not directly involve one of these four regions but which interrupt their interconnections may disrupt the effective coordination of directed attention through a mechanism of disconnection. Thus, despite their apparent disagreements concerning the cause of unilateral neglect, the theories of amorphosynthesis [24], extinction [6], disconnection [43], representational distortion [11], hypoarousal [53], and hemispatial hypokinesia [56] each appears valid depending on the anatomical locus of the principal lesion, while none is, by itself, sufficient to explain the entire phenomenon.
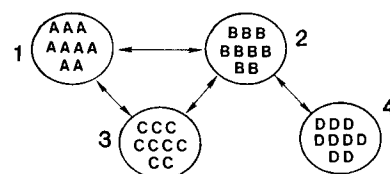
Network Approach to Cerebral Localization

Directed attention to extrapersonal space appears to be a compound function based on concerted interaction among at least three major cortical areas. Additional functional specializations characterize each of these areas [22, 51]. For example, anosognosia, dressing apraxia, and construction apraxia are additional major deficits that emerge after right parietal damage. The coordination of one complex function such as directed sensory attention by the interaction of several distinct regions, none of which is exclusively devoted to that function, suggests an approach to functional localization in terms of integrated networks. This network approach offers an alternative to more established views on localization.

To describe it in oversimplified terms, the centrist approach to localization [37] implies that certain complex functions may be integrated by specific cortical areas which are exclusively devoted to that function (Fig 4A). While a similar or identical function may also be represented in additional (supplementary) areas, the principle of functional homogeneity applies to these regions as well. Clinical manifestations of lesions are attributed to the destruction of such centers and of their interconnections. There is the expectation that a propitious case will be discovered in which the clinical deficit is confined to the relevant complex function so that the site of the lesion can help delineate the "center" for that function. By contrast, the concept of cerebral equipotentiality [74] minimizes the role of centers and assumes an organization of brain whereby each complex function is, at least potentially, represented widely in cortex even though slight local variations in the concentration of specific functions may be present (Fig 4D).
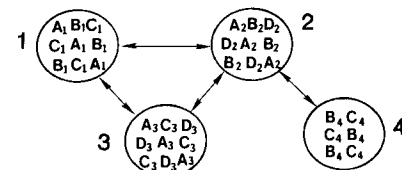
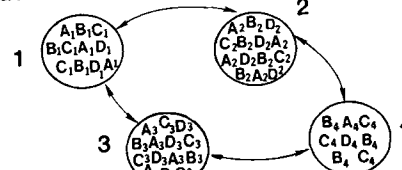The network approach suggested in this paper (Fig
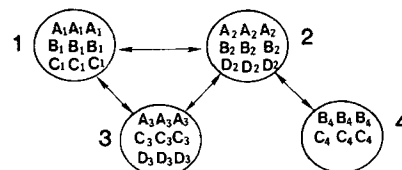
Fig 4. Four approaches to the cortical localization of complex function. B represents a version of the network approach based on the organization of function along discrete cortical columns [48, 96].

4B, C) constitutes an intermediate position between these two views. Thus, a complex function such as A in Figure 4B is considered in terms of several component processes, A_1, A_2, and A_3, each of which has a distinct localization in sites 1, 2, and 3, respectively. The component sites are intimately interconnected and constitute an integrated network subserving that particular complex function. Each of the sites has a unique set of additional functional specializations, some of which are components of intersecting but distinct networks. For example, function B is confined to sites 1, 2, and 4, a network that partially overlaps with that for function A (Fig 4B).

For the sake of illustration, it could be assumed that function A in Figure 4B is directed attention. A_1, A_2, and A_3 would correspond to the component functions of scanning, sensory representation, and motivational mapping. Sites 1, 2, 3, and 4 represent the frontal eye fields (site 1), area PG (site 2), the cingulate gyrus (site 3), and the cortex of the superior

temporal sulcus (site 4).* Let functions A, B, and D in site 2 (area PG) correspond to directed attention, dressing apraxia, and anosognosia. According to the network approach, the deficits at the highest level of perceptual integration that occur in unilateral neglect, dressing apraxia and anosognosia, become attributed to involvement of area PG (site 2). In the case of directed attention, the relevant neural transformation in area PG is the formation of a template for extrapersonal space, as already discussed; in the case of dressing apraxia and anosognosia, the relevance of area PG may be based on the neural encoding of a body scheme in the same area. The additional affective component of anosognosia (function D) may then reflect the relationship of site 2 (area PG) with site 3 (cingulate gyrus), while the components of dressing apraxia (function B), which indicate difficulties with visual-somesthetic integration, may reflect the interactions of site 2 (area PG) with site 4 (superior temporal gyrus).

This network approach suggests several general principles applicable to the clinicopathological correlation of complex functions: (1) components of a single complex function are represented within distinct but interconnected sites which collectively constitute an integrated network for that function; (2) individual cortical areas contain the neural substrate for components of several complex functions and may therefore belong to several partially overlapping networks; (3) lesions confined to a single cortical region are likely to result in multiple deficits; (4) severe and lasting impairments of an individual complex function usually require the simultaneous involvement of several components in the relevant network; and (5) the same complex function may be impaired as a consequence of a lesion in one of several cortical areas, each of which is a component of an integrated network for that function.

It is likely that different approaches to localization may have validity depending on the function under consideration. Thus, visual acuity within segments of the visual fields is organized in striate cortex according to the centrist point of view. In contrast, generalized attributes such as intelligence, creativity, or personality may well follow the equipotentiality model of organization. On the other hand, functions such as directed attention, language, and memory may be organized according to the network approach.

Corticalization of Attention Functions
In the cat, unilateral ablations of the superior colliculus elicit marked contralateral neglect [121], whereas equivalent lesions in the monkey merely

yield subtle delays of contralateral saccades but no evidence of neglect [133]. In the cat, prefrontal ablations do not elicit the contralateral neglect seen in monkeys or humans. Furthermore, the unilateral neglect that follows frontal or parietal lesions is mild and brief in the monkey when compared to that which follows upon analogous lesions in humans. Markowitsch et al [83] have been unable to find substantial connections between posterior parietal lobe and prefrontal cortex in the cat, a projection which is well developed in the rhesus monkey and, undoubtedly, in humans. The corticalization of directed attention may therefore depend upon the development of the relevant cortical connections.

Hemispheric Asymmetry in the Organization of Directed Attention
Most of the cases of unilateral neglect reported in the literature deal with lesions in the right hemisphere. Indeed, it can be shown that left-sided neglect after right hemisphere lesions is more common, more severe, and more lasting than right-sided neglect following lesions in the left hemisphere [19, 25, 42, 98].

Other evidence also implies that the intact right hemisphere is more active and efficient than the left in attentional tasks. Evoked responses to visual and somatosensory stimuli are generally of greater amplitude in the right hemisphere [110]. Furthermore, Dimond [28, 29] tested each hemisphere in a group of split-brain patients and showed that right hemisphere performance was superior in tasks of vigilance. In normal subjects, simple reaction times to ipsilateral visual stimuli are faster with the left hand [1].

Additional experiments show that the attentional function of the right hemisphere is not confined to the contralateral hemispace but may involve the entire extrapersonal space. Active touch exploration with fingers of either hand, for example, elicits specific evoked electrogenesis preferentially in the right hemisphere of intact humans [26]. Similarly, left parietal electroencephalographic leads showed desynchronization mostly after right-sided stimuli, while those over the right parietal area recorded equivalent desynchronization whether stimulation was contralateral or ipsilateral [57]. In another setting, in which patients with unilateral lesions were asked to perform a simple reaction-time task with the hand ipsilateral to the lesion, those with nondominant hemisphere lesions (overwhelmingly right) showed significantly more delays than those with lesions in the dominant (left) hemisphere [59]. Finally, in some cases of prefrontal or posterior parietal infarction in the right hemisphere, the attentional deficit was bilateral and led to the emergence of a confusional state [92].

*The cortex that lines the banks of the superior temporal sulcus, at least in the monkey, is a polymodal area known to have reciprocal connections with area PG [64, 90, 99, 116].

These observations suggest that the right hemisphere of dextrals has a predominant and specialized function in the distribution of attention. This conclusion has often been challenged on the basis of work by Battersby et al [5], who reported a failure to substantiate statistically significant group differences even though 12 out of their 41 patients with right hemisphere lesions showed neglect as opposed to 3 out of 24 testable cases with left hemisphere lesions. The authors argued that even these results reflected a bias in favor of larger lesions in the right hemisphere since equally large lesions in the left hemisphere result in severe aphasias that make patients untestable. They concluded that unilateral neglect may be equally common after lesions in either hemisphere and that primary sensory loss may be an important factor in the genesis of neglect.

Both of these points have been addressed in the course of experiments by Chain et al [19], who measured the distribution of attention by quantitating the amount of time spent looking at each sector of a projected picture. Aphasic patients were not excluded since no verbal responses were required. The results showed that the frequency of contralateral neglect was not significantly different with lesions of the right hemisphere compared to left hemisphere lesions. However, strong qualitative differences emerged. Many patients with a unilateral lesion in the right hemisphere spent virtually all of the 15-second viewing period looking at the far right side of the picture and avoided its left extreme aspect. In contrast, the neglect of patients with left hemisphere lesions was mostly confined to spending a longer time in the left paramedian region, merely exaggerating a tendency shown by subjects without hemispheric lesions. Some patients with lesions in the left hemisphere showed visual neglect of the right side mostly during the first 5 seconds of viewing, whereas those with right hemisphere lesions continued to neglect the left side throughout the entire 15 seconds. Finally, it was shown that the degree of hemianopia was not correlated with the magnitude of neglect. Thus, while there is no doubt that unilateral neglect occurs after damage to the left hemisphere [5, 21, 77], its extent and severity are far less than the neglect resulting from lesions in the right hemisphere.

These observations support a specialized role for the right hemisphere in directed attention, and a simple model may be proposed to explain this functional asymmetry. The model is based on three assumptions: (1) the intact right hemisphere may contain the neural apparatus for attending to both sides of space although the preponderant tendency is for attending to the contralateral (left) hemispace; (2) the left hemisphere is almost exclusively concerned with attending to the contralateral right hemispace; and

(3) more synaptic space is devoted to attentional functions in the right hemisphere than in the left, so that most attentional tasks involving either hemispace will generate greater activity of the right hemisphere. According to this model, unilateral lesions of the left hemisphere are unlikely to yield neglect since the intact right hemisphere may take over the task of attending to the right side. By contrast, in the absence of similar compensatory mechanisms in the left hemisphere, right hemisphere lesions will result in marked unilateral neglect. Furthermore, in some patients in whom even ipsilateral attention is predominantly modulated by the right hemisphere, universal neglect (a confusional state) will emerge after a lesion confined to the right hemisphere. This model is consistent with the right hemisphere superiority in vigilance tasks in split-brain patients [28, 29] as well as with the slight tendency of normal persons to pay more attention to the left side [1, 19].

In a review article, Kimura [69] pointed out that the magnitude of left hemispheric superiority for language and related tasks is far greater than the magnitude of right hemisphere superiority in nonlinguistic tasks. This observation is consistent with the supposition that, at some point in primate evolution, each hemisphere shared higher cortical functions more symmetrically. However, with the emergence of language skills, synaptic space in the left hemisphere formerly devoted to other functions was redirected for linguistic abilities. Conceivably, nonlinguistic functions acquired a relative hemispheric specialization in the right hemisphere because the synaptic space for analogous functions in the contralateral hemisphere became devoted to language functions, a view consistent with a proposal by LeDoux et al [78]. Thus, there are great interhemispheric asymmetries in favor of the left hemisphere for language-related functions since these emerged as a left-sided synaptic specialization without having depended on the participation of contralateral neural elements. On the other hand, the differences are not as absolute for nonlinguistic tasks since residues of synaptic space devoted to these functions may still remain in the left hemisphere.

Relevance to Other Aspects of Attention

"Everyone knows what attention is," wrote William James in 1890. "It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others, and it is a condition which has a real opposite in the confused, dazed, scatterbrained state . . ." [62].

The effective execution of attention requires a

flexible interplay among intense concentration, inhibition of distractibility, and the ability to shift the center of awareness from one focus to another according to inner needs, past experience, and external reality. The object of attention is not always a sensory event in extrapersonal space but also can include trains of thought or even sequences of skilled movements. In this paper my comments are limited to the factors that influence the spatial distribution of sensory attention within extrapersonal space. Even this portion of attentional functions appears to require the integrated action of a complex network. How much more intricate must be the neural network that also encompasses the additional aspects of attention. One can only agree with Sherrington [118] that "the climax of mental integration would seem to be attention," and with Ferrier [38] that "in proportion to the development of the faculty of attention are the intellectual and reflective powers manifested."

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