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"Space and Selective Attention"

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Space and Selective Attention

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ABSTRACT This chapter is divided into three parts. In the first part we discuss the issue of how space is represented in the brain. After reviewing a series of recent anatomical and physiological data we reach the following conclusions: (1) space representation derives from the activity of several independent brain circuits, (2) those cortical areas that code space are also involved in programming motor actions (spatial pragmatic maps), and (3) neuron mechanisms for coding space are different in the oculomotor and in the somatomotor pragmatic maps.

The second part deals with spatial attention. After dismissing the possibility that there is something like a unitary superordinate system for selective attention, we argue that there is no need to postulate for spatial attention a system anatomically separated from the systems processing data. In contrast to this theoretical position, we propose a theory of attention (*premotor theory*) whose main tenets are the following: (1) Spatial selective attention is a consequence of an activation of neurons located in the spatial pragmatic maps. (2) The activation of these neurons starts in concomitance with the preparation to perform goal-directed spatially coded movements and depends upon this preparation. (3) Different spatial pragmatic maps become active according to the task requirements. Spatial attention can originate therefore from any map that codes space. (4) In primates and in man, as a consequence of the strong development of the foveal vision and the neural apparatus for foveation, a central role in selective spatial attention is played by the oculomotor pragmatic maps.

In the last part of the chapter we present a series of new data that strongly support the premotor theory. We show that the trajectory of vertical saccades in response to an imperative (visual or acoustic) stimulus deviates according to the location of subject's attention on different positions along a horizontal line. We argue that if spatial attention were independent of motor programming, there would be no reason why a vertical saccade should be influenced by where the subject's attention was allocated.

9.1 INTRODUCTION

In psychology, as in other sciences, the scientific concepts derive from a prescientific description of the observed phenomena and an initial, often naive attempt to interpret them. It is easy to understand why an object may fall when it is pushed. It is hard, however, even to imagine that an object may fall when nobody touches it. In spite of this, force, as a scientific concept, does not imply the physical proximity between what is acting and what is acted upon. The two concepts we will deal with in this chapter—selective attention and space—belong to the category of concepts in which the subjective intuition does not coincide with and is, in fact, contradicted by experimental evidence.

The broadest possible definition of selective attention is one that links, without any further assumption, attention with selection. To attend is to select for further processing. Our subjective perception of attention is of something unitary—an internal device that we can use when the circumstances require it. Our intuition is therefore that in the brain there must be a center or a circuit devoted to attention. It has to be a single entity, and it has to possess all those properties that selective attention subjectively has.

The same is true for space. We live in space. Although the definition of space is not easy (Can there be a space without objects? Granted that extension is a property of the objects, can it be attributed also to space that is not an object?), the idea of space as something real, fixed, and unitary is compelling. We live in a kind of large box in which objects are located. Some are close to us and some are far, but they are all contained in the same box. Our intuition is therefore that in order to perceive space, the brain should have an area or a circuit that is able to reconstruct the box. This area (responsible for space perception) is used for judging distances, for describing a scene, for reaching an object, or for walking. It is so obvious that it must be so.

Recent neurophysiological and neuropsychological data appear, however, to contradict these intuitive notions of space and attention. In this chapter we review these data and attempt to provide a theoretical framework to explain them. The main theses of this theoretical attempt are the following:

1. Conscious space perception results from the activity of several cortical and subcortical areas, each with its own neural space representation. By neural space representation, we mean the coding of the external world in a system of nonretinal coordinates.
2. The cortical areas, in which space is represented, are also involved in programming motor actions related to specific sets of effectors.
3. Spatially selective attentional processes are embedded within these areas. They depend on the motor programming carried out in the same areas rather than on an anatomically separate, superordinate control system.
4. In primates, the development of foveal vision and mechanisms necessary for foveation gives a particular prominence for spatial attention to areas that code space for programming oculomotion.

9.2 SPACE REPRESENTATION

Visual Cortical Areas and Space Representation

The visual cortical system of primates is formed by a mosaic of heavily interconnected areas in which two broad streams of visual centers, arising from the primary visual cortex, can be recognized: a ventral stream largely projecting to the inferior temporal lobe and a dorsal stream that terminates in the inferior parietal lobule (Ungerleider and Mishkin 1982; Felleman and Van-Essen 1991).

The ventral stream is responsible for the analysis of the qualities of an object. It enables the visual system to categorize visual inputs as visual objects, regardless of the visual conditions in which the objects are presented. The dorsal stream is responsible for space computation. It transforms retinal representations into spatial descriptions and transmits these descriptions to the frontal lobe for immediate and delayed action.

Two issues concerning the functional organization of the dorsal stream are crucial for understanding space perception. The first issue concerns the notion of a unitary, multipurpose brain structure (area or circuit) that mediates space perception. Is this notion consistent with the organization of the dorsal stream and, in particular, of the inferior parietal lobule? The second issue is whether the dorsal stream codes primarily space. The alternative possibility is that the dorsal stream codes action. Space is represented inasmuch as it must be computed in order to act.

Space Representation in the Parietal and Frontal Lobes

The inferior parietal lobule is constituted of several distinct anatomical (Brodmann 1925; Von Bonin and Bailey 1947; Pandya and Seltzer 1982) and functional areas (Hyvarinen 1982; Goldman-Rakic 1988; Andersen et al. 1990). Recent studies, carried out on monkeys, showed that each of these areas has specific connections with premotor, oculomotor, and prefrontal areas (Pandya and Kuypers 1969; Petrides and Pandya 1984; Godschalk et al. 1984; Matelli et al. 1986; Cavada and Goldman-Rakic 1989; Andersen et al. 1990). Among the various frontoparietal circuits, three circuits have been extensively studied: lateral intraparietal area (LIP)—area 8, PF (area 7b)—premotor F4, and “manipulation” anterior intraparietal (AIP) area—premotor F5.

The LIP—area 8 circuit contains three main classes of neurons: neurons responding to visual stimuli (visual neurons), neurons firing in association with eye movements (movement neurons), and neurons with both visual- and movement-related activity (visuomovement cells) (Bruce and Goldberg 1985; Bruce 1988; Andersen and Gnadt 1989; Goldberg and Segraves 1989; Barash et al. 1991a, 1991b). Visual neurons respond vigorously to stationary light stimuli. Their receptive fields are large, varying from a few degrees to an entire quadrant of the visual field. Movement neurons fire in relation to ocular saccades, most of them discharging before the saccade onset. Of these, the vast majority become active only during goal-directed movements. Visuomovement neurons have both visual and saccade-related activity. Visual receptive field and “motor” fields are in register.

The neural machinery of the PF-F4 circuit reveals a functional organization analogous to that of the saccade circuit. As in the LIP—area 8 circuit, neurons in areas PF-F4 can be subdivided into three main classes: sensory neurons, movement neurons, and sensory-movement neurons. The majority of the cells belong to the last category (Leinonen et al. 1979; Gentilucci et al. 1983; Gentilucci et al. 1988). Sensory and sensory-movement neurons respond to

tactile stimuli or to tactile and visual stimuli (Leinonen et al. 1979; Gentilucci et al. 1983, 1988; Graziano and Gross 1992; Graziano and Gross, n.d.). Their visual properties, however, are markedly different from those of neurons in the LIP–area 8 circuit. In contrast to the latter neurons, they typically do not respond to stimuli located far from the animal. Their receptive fields are restricted to the space around the animal's face or body (peripersonal space). The extension in depth of individual receptive fields is not fixed. In many neurons, the fields expand when the stimulus velocity increases (Fadiga et al. 1992). Movement cells become active during proximal arm movements (especially reaching), as well as during oro-facial and axial movements. Sensory-movement neurons exhibit both sensory and movement-related activity. The primary function of this circuit appears to be that of transforming visual information into signal for reaching and other arm and body movements.

It is clear from this description that the parietofrontal circuits code space not *per se* but in function of the motor requirements. Thus, in the arm reaching circuit, the peripersonal space is essentially coded. Peripersonal space coincides with the motor space of the arms. Far space, important for exploration and for motor activities such as walking but not for reaching, is not represented. It is important to note also that sensory-movement neurons in both the oculomotor and arm reaching circuits code position of the stimulus and a specific motor command. This command is a command for either an eye movement or an arm movement. Therefore, the neurophysiological evidence does not appear to support the idea that the same spatial information is used for programming both saccade and arm movements. The spatial information necessary for these acts appears to be segregated.

Space Coding at the Single Neuron Level

Recent data on the neural mechanisms responsible for space coding provide further evidence against the idea that space perception is mediated by a single multipurpose area. The neurons located in the LIP–area 8 circuit show retinotopic receptive fields (Andersen and Gnatdt 1989; Goldberg and Segraves 1989). Space coding results here indirectly from a computation performed by these neurons. There are two competing theories on how this may occur. According to one of them, space representation is achieved by retinotopic neurons whose response intensity is modulated (in contrast to that of neurons in the earlier visual stations) by the eye position in the orbita (Andersen, Essick, and Siegel 1985). These neurons would integrate retinal signals about the visual target with extraretinal signals about eye position. By using this double information, the LIP–area 8 circuit would be able to compute the position of the targets in space and direct the gaze toward them.

Another way in which the oculomotor system can achieve a spatial frame of reference is suggested by Goldberg and Bruce (1990): when there is a dissonance between the retinal vector of a stimulus and the movement vector of the saccade necessary to acquire it, a change occurs in the topographical location of the retinal receptive field. This remapping, possibly based on a

vector subtraction, should be responsible for the correct acquisition of a target (Duhamel, Colby, and Goldberg 1992).

In contrast to the indirect space coding of the oculomotor circuit, the PF-F4 area circuit codes space explicitly at the single neuron level. The large majority of neurons in F4 have receptive fields anchored to the body. When the monkey moves the gaze and fixates a new target, the receptive field does not change position, as it should if the field were coded in retinal coordinates (Gentilucci et al. 1983; Fogassi et al. 1992). This way of coding space fits well the motor requirements of the PF-F4 circuit. It would be a computational burden to update the eye position continuously for a circuit whose goal is to organize arm and other body part movements, regardless of eye location. In contrast, such an updating should not give particular trouble to a circuit specifically devoted to eye movements. Regardless of the reasons for the different coding, what interests us more here is that not only the space circuits for eye and arm movement are anatomically segregated, but they also use different mechanisms for space coding.

From this brief review of the neuronal properties of the frontoparietal circuits the following conclusions emerge: (1) computation of space is performed in different cortical circuits, in parallel; (2) space representation is linked to movement organization; and (3) mechanisms for representing space are different in different circuits and most likely are related to and depend on the motor requirements of the effectors controlled by a given circuit. The question left is whether the inferior parietal lobe, which appears to have a nodal position between the posterior visual retinotopic areas and the frontal motor centers, should be considered spatial, the traditional view (Critchley 1953; Hyvarinen 1982; Ungerleider and Mishkin 1982; Grüsser and Landis 1991), or whether a more appropriate description of its function is in terms of visual information coding for action.

Space versus Action

The study of arm movements during prehension showed that this action consists of two main components, reaching and grasping. In order to generate these movements effectively, the nervous system has to solve a series of computational problems, which differ for reaching and grasping. Reaching requires the localization of objects in space with respect to the body. This implies the formation of a stable frame of reference independent of eye position and the encoding of visual information in body-centered coordinates. By contrast, grasping deals with intrinsic qualities of the objects. The coordinate system in which grasping movements are generated relates to the object and the hand. The knowledge of the position of the object in the external space is irrelevant (Arbib 1981; Jeannerod 1988).

The properties of neurons forming the PF-F4 circuit fit well the computational requirements for reaching movements. Those neurons compute the extrinsic spatial relations between the target object and the body and transform it into a pattern of proximal movements (Gentilucci and Rizzolatti 1990).

The properties of PF-F4 neurons are therefore consistent with both the idea that the parietal lobe is for space representation and the idea that this lobe is related to action.

Recent data show that the visuomotor integration of grasping is also carried out in the parietal lobe, and precisely in a circuit that involves the parietal AIP (Sakata and Musunoki 1992) and the premotor area F5 (Rizzolatti et al. 1988). Parietal neurons specifically related to grasping ("manipulation neurons"; Mountcastle et al. 1975) fall into three classes:

1. Motor dominant neurons, which are similarly activated during grasping movement executed in light and darkness. A large number of neurons of this class fire exclusively during particular types of grasping movements.
2. Visual dominant neurons, which are not active when grasping is made in the dark.
3. Visual-and-motor neurons, which are less active in the dark than in the light.

Many neurons of the last two classes respond to the sight of objects in the absence of hand movements (Taira et al. 1991).

Neurons of area F5 are also selective for different types of grip. Some of them fire at the object presentation in the absence of any movement. The visual discharge is evoked only if the object size is congruent with the coded grip (Rizzolatti et al. 1988). Areas AIP and F5 appear, therefore, to code the intrinsic visual characteristics of the objects and to transform them into the appropriate distal movements.

The interest of these findings for the understanding of the parietal lobe functions lies in the fact that manipulation neurons do not compute space. The stimulus processing they perform is for many aspects similar to that performed by the neurons in the visual ventral stream and in the temporal lobe in particular. As those neurons, they describe objects. The description, they carry on, however, is not for object recognition but for the organization of the appropriate object-related hand movements. This pragmatic function is shared with the adjacent circuits that organize reaching and oculomotion. It appears therefore that the notion that the dorsal stream-inferior parietal lobe is the brain region related to space representation is only partially true. A more comprehensive interpretation is that this region codes the visual information for the organization of actions. The areas of this region provide a series of pragmatic representations of the visual world as opposed to the semantic representations of the temporal lobe.

A similar interpretation of the functional organization of parietal lobe has been recently advanced by Goodale and Milner and their co-workers (Goodale et al. 1991; Milner et al. 1991) on the basis of their neuropsychological findings. They analyzed in great detail the visual behavior of a patient with a severe visual agnosia following carbon monoxide poisoning. The patient was unable to perceive the size, shape, and orientation of visual objects, yet she showed accurate reaching and grasping of those same objects whose qualities she was unable to perceive. When she was presented, for

example, with a pair of rectangular blocks of the same or different dimensions, she was unable to indicate whether they were the same or different. Yet when she was asked to reach and grasp the block, the aperture between her index finger and thumb was systematically related to size of the object in a manner not dissimilar from that of normal subjects. The authors concluded that the distinction between object vision and spatial vision cannot account for the described dissociation and convincingly argued that the main role of the inferior parietal lobule is to provide visual information required for acting on objects (Goodale and Milner 1992).

Conclusions

In summary, the neurophysiological and neuropsychological studies of the parietofrontal circuits indicate that the scenario of space perception is radically different from that of a simple spatial box. There is no evidence of a spatial map on which the "light" of attention could act. Furthermore, even the idea of a brain region specifically devoted to space is under dispute. The inferior parietal lobe, rather than being a spatial lobe, appears to be the cortical region where visual information is coded for different types of actions, some of them requiring spatial information.

One may argue that if the organization of the cortical parietofrontal circuits appears to contradict the notion of a multipurpose space map, nevertheless, such a map could exist elsewhere—for example, in the subcortical structures. The hippocampus, the basal ganglia, and the cerebellum are all centers that use spatial information and one (or more) of them could code space using rules different from those of spatial cortical maps. Even if this were so, however, the principle on the basis of space representation should not change radically. Evidence from a large number of clinical and experimental studies shows that damage to the parietal lobe and the related frontal areas produces severe space perception deficits (Critchley 1953; De Renzi 1982; Ungerleider and Mishkin 1982). Among them, particularly dramatic is the neglect syndrome, a syndrome in which part of space representation (Bisiach and Vallar 1988; Rizzolatti and Berti 1990, 1993) is "truncated" (De Renzi 1982). Thus, the existence of a hypothetical subcortical multipurpose center would not contradict our conclusions.

It is important to note that lesions of the parietofrontal circuits coding space produce perceptual deficits that are much more severe and diffuse than those one may expect from the physiological properties of the damaged circuits. Stimuli in the affected space sector are ignored and not responded to, not only when the required responses depend on the activity of the damaged circuits but also when they depend on circuits that are spared by the lesion. For example, following a unilateral lesion of the frontal eye fields, monkeys are unable to detect and respond manually to visual stimuli presented to the space contralateral to the lesion, in spite of the fact that the circuits responsible for the visual control of arm movements are intact (Latto and Cowey 1971).

Similarly, monkeys with restricted lesions to the premotor areas do not react emotionally to threatening stimuli, although there are plenty of intact circuits that may convey visual information to the emotional centers (Rizzolatti, Matelli, and Pavesi 1983). These findings indicate that conscious space representation depends on the concomitant activity of a multiplicity of cortical (and subcortical) centers. Although it is by no means clear how this multiple system is coordinated, there is little doubt that the unity of space perception is not due to the activity of a unitary space map but results from the coordinated activity of several highly specialized sensorimotor circuits. An interesting consequence of this type of organization is that it predicts implicit processing of information coming from the space sector contralateral to the lesion in neglect patients. Recent experiments confirmed this prediction (Volpe, Ledoux, and Gazzaniga 1979; Marshall and Halligan 1988; Berti et al. 1992; Berti and Rizzolatti 1992). Visual information, although not consciously perceived, can be processed in the spared circuits and its effect revealed with specific tests. For a discussion of this issue see chapter 2 of this book.

We now turn to how the activity of these spatial centers is related to selective spatial attention. Selective attention in the semantic maps is outside the scope of this chapter and will be not dealt with here.¹

9.3 SPATIAL ATTENTION

Selective Attention: One superordinate system, many superordinate systems, or intrinsic mechanisms within the pragmatic and semantic representations?

Although attention can be conceptualized as an outcome that characterizes the behavioral state of the organism, the term, as used by most current theories of attention, indicates some hypothetical agency that can be directed or focused on an entity (Johnston and Dark 1986; Allport 1993). Introspectively, this mechanism is unitary, and this unity has been implicitly accepted by most attention theorists.

Evidence accumulated in the past ten years shows that this idea is untenable. The literature on this issue has been reviewed elsewhere (Rizzolatti, Gentilucci, and Matelli 1985; Rizzolatti and Gallese 1988; Posner and Petersen 1990; Allport 1989, 1993) and will be not dealt with here in details. We will summarize only the results of two studies that have been particularly influential in disproving the notion of a central attentional system. Both used positron emission tomography (PET) to identify the neural systems involved in selective attention. In the first study (Posner et al. 1988), changes in cerebral blood flow were examined during a series of visuo-verbal tasks (fixation of a target, passive looking at foveally presented nouns, repetition of concrete nouns, and generation of words describing the use for concrete nouns). The results showed that, besides the occipital cortical areas, which were active when the material was presented visually, the areas that were selectively

activated during the attentionally highly demanding generation task were a lateral frontal region and the anterior cingulate gyrus. These researchers concluded, "There is no evidence of activation of any parts of the posterior visual spatial attention system (for example, parietal lobe) in any of our PET language studies" (p. 1629). The parietal lobe was traditionally the favorite cortical region for localizing the attention center in the human brain.

The task of the second PET study (Corbetta et al. 1990, 1991) was to discriminate a stimulus change of shape, color, or velocity. In one condition (Selective Attention), the subjects were instructed to focus on one stimulus attribute and disregard possible changes in the other attributes. In a second condition (Divided Attention) the subjects had to detect changes in any stimulus attribute, dividing attention across stimulus attributes. The results showed that Selective Attention for a given attribute increased the metabolism of different sectors of extrastriate cortex specialized for processing the selected feature. Outside the visual areas, Divided Attention activated the frontal lobe and the cingulate cortex, while Selective Attention activated essentially sub-cortical centers. "The only region commonly activated across conditions was the left globus pallidus" (Corbetta et al. 1991, p. 2392).

These results are obviously devastating for any theory that maintains that there is an attentional unitary central system. So how can attention be conceived following these findings? Two alternatives appear to be logically possible. The first, more linked to the old unitary conception, is to postulate a few distinct attention systems related to different cognitive functions—for example, attention for space, for object attributes, or for language. This idea has in common with the previous unitary conception the tenet that the attention systems are anatomically separated from the data processing systems (semantic, pragmatic, language representations) (Posner and Petersen 1990). The other alternative is that attention mechanisms are intrinsic to pragmatic and semantic maps. Attention derives from the activity of these representations without any intervention of other hypothetical anatomical structures. As far as the spatial attention is concerned, attention is the consequence of the activity of pragmatic maps and is strictly related to motor preparation. The theory that maintains this point of view was first formulated by Rizzolatti (1983; see also Rizzolatti and Camarda 1987) on the basis of a series of neurophysiological data. This theory, usually referred to as the premotor theory of attention, was subsequently expanded by Rizzolatti, Umiltà, and Riggio (see below) and used to explain some intriguing psychological findings.

Selective Attention as an Intrinsic Mechanism

The premotor theory of attention has three main claims:

1. The mechanisms responsible for spatial attention are localized in the spatial pragmatic maps. There are no such things as selective attention circuits defined as anatomical entities separated from the spatial maps.

2. Spatial attention is a consequence of a facilitation of neurons in the spatial pragmatic maps. This facilitation depends on the preparation to perform goal-directed, spatially coded movements.

3. Different spatial pragmatic maps become active according to the task requirements. Spatial attention can be produced by any map that codes space. In humans and primates, as a consequence of the strong development of the foveal vision and the neural mechanisms for foveation, a central role in selective attention is played by those maps that code space for programming oculomotion.

In this section, we will discuss to which psychological experiments the premotor theory can apply and its limitations. In the next sections, we will present evidence for the validity of the theory in cases in which spatial attention appears to be related to oculomotion or to other types of movements.

In very general terms, the psychological studies of selective attention fall into two main broad classes: studies based on the filtering paradigm and studies based on the selective-set paradigm (Kahneman and Treisman 1984). The filter paradigm experiments are characterized by the following features: (1) the subjects are presented simultaneously with relevant and irrelevant stimuli; (2) the relevant stimuli control a relatively complex process of response selection and execution; and (3) most frequently a physical feature distinguishes relevant from irrelevant stimuli and determines the correct response. Examples of filtering paradigm can be found in the work of Broadbent (1952, 1958), Cherry (1953), and Treisman (1964), among others. The selective-set paradigm experiments are based on the expectation by the subject of a particular stimulus. As soon as the expected stimulus is detected or recognized, a speeded response has to be emitted. There are two main variants of selective-set paradigm: studies of search (Schneider and Shiffrin 1977) and studies of cost and benefits of expectations (Posner 1978). In both variants, attention is set to detect one or more potential targets.

The premotor theory of attention is strictly related to the experimental paradigm described by Posner and his co-workers (1978, 1980). In this paradigm the task is essentially spatial. Usually, it demands only a detection of an unstructured visual stimulus. The required manual response is arbitrary. It does not depend on the solution of a spatial problem. The "austerity" of the experimental conditions renders the Posner paradigm particularly suitable for an analysis in terms of psychological and physiological mechanisms and, as will be discussed later, the data obtained by employing this paradigm are well explained by the premotor theory of attention.

Can the premotor theory explain also the findings obtained using other paradigms, such as, for example, the filtering paradigm? The main claim of the premotor theory is that movement preparation facilitates the input side of the pragmatic maps involved in the task, thus improving the stimulus detection. The theory is therefore a selective-set one. The machinery involved in spatial attention, however, is not exclusively facilitatory. In several visuo-oculomotor centers (see below), the abrupt presentation of a new stimulus concomitantly to a facilitation of the neurons related to its visual field location produces

an inhibition of the remaining unstimulated neurons. This inhibition, by reducing or even blocking the information coming from visual field locations different from that where the new stimulus is presented, gives subjective relevance to this stimulus and facilitates the disengagement of the gaze (and attention) from the spatial locus that is processed at the moment of the new stimulus presentation. The mechanism acting in the case of filtering paradigm experiments could be similar in its essence to this disengagement mechanism but oriented in the reverse direction. In a visual experiment based on a filtering paradigm, fundamental for the task is the maintenance of the fixation on a certain part of a spatial scene in spite of the simultaneous occurrence of competing distracting stimuli. In such a task, the presence of oculomotor commands that impose fixation and simultaneously inhibit those sectors of the involved pragmatic maps that are related to the visual periphery should be critical. Such an oculomotor mechanism would decrease the relevance of the simultaneously incoming stimuli competing with the attended one and would allow the information contained in it to be adequately processed.

We are not aware of experiments that have formally tested these predictions. The findings of Moran and Desimone (1985), however, are indicative of the existence of a filtering mechanism similar to that postulated above. These authors recorded single neurons from two areas of the visual ventral stream, area V4 and the inferotemporal cortex, in behaving monkeys. The monkeys were trained to attend to stimuli at one location and to ignore them at another. The results showed that the responses to the unattended stimuli were dramatically reduced. One cannot infer from these data the mechanisms that subserve the filtering of the irrelevant information and where they originate. However, although other explanations of the phenomenon are possible, our proposal is that the filtering process originates in the pragmatic maps and that it is related to commands for fixation maintenance.

In contrast to Posner's paradigm, where the expectancy concerns exclusively the locus of stimulus appearance, search paradigm requires that specific stimuli be detected and identified. It is usually assumed that the detection and identification process requires the activation of units (single neurons, assembly of neurons, nodes in long-term memory) that are tuned for specific stimuli. When these units are fully activated, we perceive familiar objects, their properties, or events (Schneider and Shiffrin 1977; Johnston and Dark 1982). Stimulus expectancy, although unable to activate these units fully, renders their activation more likely (LaBerge 1975; Schneider and Shiffrin 1977). Regardless of what exactly the detection and identification units could be, according to our subdivision of the cortical areas, they should belong to the semantic areas. The issue of attentional mechanisms of these area is outside the limits of this chapter and will be not dealt here.

Premotor Theory of Spatial Attention

Active (Endogenous) Orienting of Attention Attention can be oriented actively or passively. Passive orienting describes cases in which a stimulus

attracts the individual's attention for its intrinsic properties or for the way in which it is presented. Active orienting arises from the subject and is characterized by an effort to increase the clearness of a given external stimulus (James 1890; Titchener 1966). This distinction between active and passive attention has been developed by, among others, Posner (1980), Jonides (1981), and Muller and Rabbitt (1989). Using criteria such as capacity demands, resistance to suppression, and sensitivity to expectancy, they showed that external, abruptly presented stimuli ("peripheral cues") cause "automatic" (passive) shifts of attention, whereas cues presented centrally and that have to be interpreted in order to orient attention ("central" or "cognitive" cues) cause "voluntary" (active) shifts of attention. These and other results showing differential time courses of orienting in response to peripheral and central cues (Yantis and Jonides 1984; Muller and Findlay 1988; Spencer, Lambert, and Hockey 1988; Muller and Rabbitt 1989) suggest that different mechanisms are involved in the two phenomena.

Psychological Experiments Figure 9.1 shows the visual display used in most of our experiments (Rizzolatti et al. 1987; Umiltà et al. 1991). The subject's task was to direct attention to the cued box while maintaining fixation on a central point and to press a response key as fast as possible at the occurrence of the imperative stimulus. Trials on which the imperative stimulus was shown in the cued box are referred to as valid; trials on which the stimulus was shown in a box different from the cued one are referred to as invalid; and trials on which all boxes were cued are referred to as neutral (see Posner, Snyder, and Davidson 1980). Table 9.1 illustrates the results typically obtained in these experiments.

Table 9.1

Arrangement of stimulus boxes	Type of trial				
	Valid	Invalid			
		4°s	4°o	8°o	12°o
Horizontal	212	234	255	261	265
Vertical	208	222	242	253	266
	210	228	249	257	266

Abbreviations: s, same hemifield, o, opposite hemifield (with regard to the attended location).

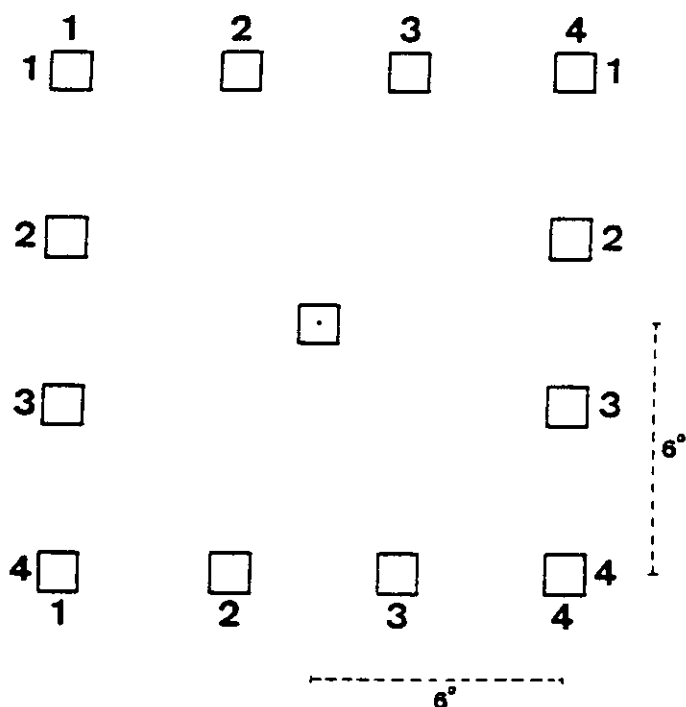


Figure 9.1 Stimulus display in the experiment by Rizzolatti et al. (1987). Four possible configurations of boxes (two horizontal and two vertical) were used. Only one configuration was shown in each experimental condition. Each configuration consisted of a central fixation box with the fixation spot inside, and four boxes, marked by an adjacent digit (1-4) for stimulus presentation.

The main findings can be summarized as follows:

1. Valid trials are faster than neutral trials and neutral trials are faster than invalid trials.
2. Invalid trials are longer than valid trials also when the imperative stimulus that triggers them is presented in the cued hemifield.
3. When the imperative stimulus is presented at the same distance from the cued location in the cued and noncued hemifield, reaction times are slower in the noncued hemifield. This effect is called the meridian effect.
4. Within the noncued hemifield, reaction times increase as a function of the distance from the cued location. This effect is referred to as the distance effect.

The premotor theory offers a satisfactory explanation of most of these findings and suggests some neurophysiological mechanisms that may underlie them. Its first assumption is that, in the described, impoverished, experimental situation, attention is linked to the oculomotor circuits. There is no need for activation of other pragmatic areas.² The second assumption is that both covert orienting of attention and motor programming (in this case programming of ocular saccades) are controlled by the same pragmatic maps. Covert orienting occurs when a behavioral situation or a verbal command prevents eye movements but leaves unchanged the oculomotor program. This pro-

gramming of saccades is responsible for the endogenous attention movement, whereas inhibition of the saccade that in natural conditions, outside the laboratory, would be the response to a peripheral cue determines the complex pattern of facilitation-inhibition typical of this condition (Posner and Cohen 1984; Maylor 1985; Maylor and Hockey 1985; Possamai 1986; Berlucchi et al. 1989; Rafal et al. 1989).

Given these premises, the sequence of the events consequent to the presentation of a cognitive cue is the following. As soon as the location of the imperative stimulus can be predicted, a motor program for a saccade toward the expected location is prepared. This program specifies the direction and the amplitude of the saccade. When the two parameters are set, two events occur. First, the location of the expected stimulus becomes salient with respect to all other locations (Bashinski and Bacharach 1980; Downing 1988; Muller and Humphreys 1991; Hawkins et al. 1990; Riggio and Kirsner, n.d.). Then the stimuli appearing in that location are responded to faster (Posner 1980). This is true both when the required response is an ocular saccade toward the target or a manual pressing of a switch.

The situation is obviously different when the imperative stimulus occurs in an unexpected position. In this case, in agreement with the original proposal by Posner (1980), the premotor theory postulates that the manual response (and other not hard-wired, arbitrary responses) can be emitted only when attention is allocated to the new point. Thus, the invalid response is delayed both because the expected location is not facilitated and because a time-consuming change in the saccade program should take place before the manual response is emitted.³

Once it is accepted that attention is subserved by the same mechanisms that program eye movements, several puzzling experimental findings become easier to explain. One of them is the intriguing meridian effect, a robust effect that is constantly observed when attention is directed by cognitive cues (Downing and Pinker 1985; Hughes and Zimba 1985; Rizzolatti et al. 1987; Shepherd and Muller 1989; Umiltà et al. 1991; Gawryszewski et al. 1992; Reuter-Lorenz and Fendrich 1992). Typically, its value is in the order of 20 to 25 ms. If one conceives of the attentional system as independent of any physiological and anatomical constraint, this result is hard to explain. Why should attention movement be delayed when attention crosses something like the horizontal meridian, of whose presence we are not aware and whose existence is known only to those acquainted with the anatomy of the eyes and the nervous system? The situation becomes different if one considers the organization of the oculomotor system.

There is good agreement that goal-directed saccades are prepared in two steps. First, a decision concerning the direction is taken (Wheless, Boynton, and Cohen 1966; Komoda et al. 1973; Becker and Jurgens 1979; Findlay 1982). As Becker and Jurgens stated, "The decision to elicit a saccade is identical with the decision about the direction of the saccades." Second, when the direction is established, the amplitude is calculated. There are two main

consequences of this formulation: changes in saccade direction require a radical modification in oculomotor program, and changes in saccade amplitude imply only a readjustment of a preexisting program. According to the premotor theory, the meridian effect results from identical causes. When the amplitude of the attention movement has to be modified without changing direction, what is needed is only an adjustment in the parameters of a set of eye movements whose general programming has already been made. In contrast, when the imperative stimulus appears in the hemifield opposite the one containing the cued location, then it is the direction of the attention that has to be modified. In this case, the process is more time-consuming because a new program, involving (if executed) a radically different set of muscles, has to be constructed. This complete program change would be the origin of the meridian effect.

Less straightforward is the prediction of what should occur when both the direction and the amplitude of the oculomotor program have to be changed. Granted that changing direction determines a large cost, the issue is whether (once direction is set) programming a large-amplitude eye movement costs more than programming a small one or whether the cost is the same regardless of the amplitude to be programmed. If the first hypothesis is correct, the distance effect would be, analogous to the meridian effect, a pure consequence of the time necessary for programming eye movements. However, the facilitation of a given sector in an oculomotor map is frequently accompanied by inhibition of other sectors. One cannot exclude, therefore, that even if the first hypothesis is correct, some inhibitory factors can intervene in the origin of the distance effect. These factors, by decreasing the responsiveness of the oculomotor maps, would impair the detection of stimuli located far from the attended location. Inhibition might be the major factor responsible for the distance effect if, as postulated by the second hypothesis, the same amount of time is required to program small and large movements (Remington and Pierce 1984).

Neurophysiological Experiments Let us see now how the premotor interpretation of the psychological findings fits with the neurophysiological evidence. A situation of stimulus expectancy similar to that determined by cognitive cues in the Posner paradigm has been studied by Wurtz, Goldberg, Hikosaka, and their associates in conditioned monkeys (for a detailed review, see Robinson and McClurkin 1989; Hikosaka and Wurtz 1989). The animals were taught two basic tasks: a fixation task, consisting of the detection of a brief dimming of a spot of light presented in front of the animal, and an eye response task, which started as a fixation task, but, after a brief time interval, the fixation point was turned off and a second spot presented peripherally. The monkey had to make a saccade to the second stimulus and detect its dimming. The stimuli were presented in blocks, in the same spatial position within a block. Thus, after the first trials, the monkey could predict the stimulus location.

Once the animals mastered the tasks, single neurons were recorded from the superior colliculus (SC) and other visual and oculomotor centers. Taking advantage of the temporary immobility of the gaze during the fixation task, the authors could map the neuron receptive fields and establish the intensity of the neuronal response to light stimuli. Subsequently, the neurons were tested during the eye response task. The same visual stimulus as in the first task was used, but now, unlike in that task, the animal expected the occurrence of the stimulus (target of the required saccadic eye movements) and could predict its location (Goldberg and Wurtz 1972; Mohler and Wurtz 1976; Wurtz and Mohler 1976).

We will review here only the results concerning the SC, which are very detailed and the easiest to interpret. The SC has a peculiar anatomical and functional position in the visual system. It receives direct projections from the retina, its neurons located in the superficial layers have clear sensory properties, it is connected, although indirectly, with motor centers controlling eye and head movements, and the neurons of the layers below the stratum opticum (intermediate and deep layers) have essentially premotor properties (Sprague, Berlucchi, and Rizzolatti 1973; Goldberg and Robinson 1978).

The experiments showed that a large proportion of SC neurons responded stronger to light stimuli during the eye response task than during the fixation task. Note that the stimuli were identical in both conditions. This response increase due to internally generated stimulus relevance was named an enhancement effect (Goldberg and Wurtz 1972). A particularly important finding was that the enhancement effect concerned the purely visual neurons of the superficial layers. This indicates that the preparation to make a saccade toward a certain space position not only facilitates the motor response toward that point but also increases the responsiveness of visual neurons related to that position.

Another finding of great interest is the temporal course of the enhancement effect. The stimuli were presented in blocks. Thus, during the first trials of the eye response task, the monkey could not predict the stimulus location, while subsequently she could. It is likely, therefore, that in the first trials, the monkey responded passively to the stimulus without preparing the ocular motor program toward the stimulus, while later she prepared it. The enhancement effect was absent in the first trials (Mohler and Wurtz 1976).

Two other results of these experiments are also relevant for the premotor theory of attention. The first is that when the saccades occurred soon after stimulus presentation, the early part of the visual response was facilitated. In contrast, when the saccades occurred late, the late part of the response was enhanced (Wurtz and Mohler 1976). The second result concerns the activity of the neurons located in the intermediate and deep SC layers. These premotor neurons become active in concomitance with saccadic eye movements, and their discharge typically precedes the saccades of about 100 ms (Schiller and Koerner 1971; Wurtz and Goldberg 1972). However, when the monkey expected a stimulus, these neurons started to discharge well in advance of

the saccade bringing the eye to the target (Mohler and Wurtz 1976). The premotor activity, therefore, prepares the eye movement toward the cued location and simultaneously activates the neurons of the superficial layers corresponding to the expected location.

The modifications in the SC excitability are modulated by a circuit formed by the cortical oculomotor areas, the caudate and the pars reticulata of the substantia nigra (SNr). The essence of this control mechanism is the following. At rest, the SNr neurons are tonically active and inhibit the SC (Hikosaka and Wurtz 1983a, 1983b). The inhibition is topographically organized. In turn, the SNr is under inhibitory control from the caudate. When a saccade has to be generated, the cortical activity excites the caudate neurons, which, in turn, inhibit the topographically related neurons in the SNr (Hikosaka, Sakamoto, and Usui 1989a, 1989b). The SC neurons are therefore disinhibited and ready to generate the appropriate saccade (Hikosaka and Wurtz 1989).

This disinhibitory mechanism may explain the excitability changes that occur in the SC during expectancy. The cortical motor program (prepared, but not implemented) disinhibits, by means of the caudate nucleus and SNr, the SC premotor neurons related to the cued space position. The increase in firing of these neurons facilitates the collicular superficial neurons, allowing a better detection of the stimuli. In addition, the readiness to respond when the expected stimulus occurs is increased.

Passive (Exogenous) Orienting of Attention In the section on active orienting of attention we started with a review of psychological data and finished with the physiological mechanisms that may underlie them. In this section we use the reverse strategy. We examine first the physiological changes determined by the presentation of stimuli endowed with attentional properties (Titchener 1966; Berlyne 1960, 1970), and we end by comparing the physiological processes with the psychological findings. As for active attention, our review of physiological data will concern essentially the SC.

The most detailed study on the modification induced by visual attentional stimuli on neuron activity was carried out by Rizzolatti and his co-workers on the SC of the cat (Rizzolatti et al. 1973, 1974). They plotted the receptive fields of SC neurons and determined for each neuron the best stimulus parameters. The neuron was then stimulated at regular intervals with the most effective stimulus (called S1). When it was clear that the response was stable, a second stimulus (S2) was abruptly presented simultaneously with S1 and moved outside the neuron's receptive field. The main finding of the experiments was that neuron responses were strongly inhibited every time the extra field stimulus was presented to the animal. This inhibitory effect was present in the great majority of collicular neurons, including those located in the superficial layers. Large S2s (e.g., 10 degrees in diameter) were typically more effective than small S2s. Black, high-contrast stimuli were more effective than low-contrast light stimuli. A similar inhibition due to an abrupt presentation of visual stimuli is present also in the cat extrastriate visual areas but not in the primary visual cortex (Rizzolatti et al. 1973).

An important variable for the inhibitory effect was the location of S2 in respect to S1. In virtually all neurons, the inhibitory effect was found to be stronger when S2 was presented in the same hemifield as S1. In contrast, the distance between S1 and S2 within the same hemifield did not appear to influence the neuron responses. The direction of movement of S2 toward, away from, or parallel to direction of S1 was immaterial for the occurrence of the inhibitory effect.

Typically Rizzolatti et al. (1973, 1974) presented S2 for a short time. In one set of experiments, however, they examined whether S2 would continue to exert an inhibitory influence over the responses to S1 after prolonged presentation (Rizzolatti et al. 1973). This point is fundamental for maintaining that the inhibitory effect is related to attention. If it is related, one should anticipate that a prolonged presentation of the stimulus would determine a progressive decrease of its effectiveness, by analogy, with what occurs in behavioral experiments, when the same stimulus is repetitively presented to the animal. In contrast, if the inhibitory effect is due to visual receptive field properties of SC neurons, one should expect no changes in the inhibitory effect intensity even after a prolonged S2 presentation. The inhibitory flanks adjacent to the excitatory part of the receptive field that some visual neurons have do not disappear with repetitive visual stimulation.

The results clearly showed that when S2 is kept in motion and S1 is periodically swept across the neuron's discharge area, the inhibitory effect disappears. The time length between the presentation of S2 and that of S1, which completely nullifies the S2 inhibitory action, ranges between 1 and 2 sec. Delays of 250 ms between the two stimuli produce a marked decrease in the inhibition strength.

The inhibitory effect is present in the monkey as well. Wurtz, Richmond, and Judge (1980) recorded single neurons from SC in conditioned monkeys and examined the effect of restricted light stimuli flashed in different parts of the visual field on the neuron's responses. They found that, as in cats, the presentation of an extra field stimulus produces a marked decrease of collicular responses. The effect of the stimulus is present when it is flashed simultaneously with S1 or precedes S1 by small intervals (about 100 ms). In good agreement with the findings in cats, stimuli presented in the hemifield opposite to that where the receptive fields is located give an inhibition much weaker than stimuli located on the same side of the vertical meridian as the receptive field.

From these data, it is clear that peripheral attentional stimuli determine a series of modifications in the SC which are absent in the case of voluntary attention. These peripheral cue effects can be summarized as follows:

1. A recruitment of premotor neurons topographically related to the stimulus location.⁴
2. A short-lasting facilitation of the superficial neurons topographically related to the stimulus location. (This facilitation should result from the activation of the premotor neurons).

3. A short-lasting inhibition of the visual responses outside the stimulated area ("inhibitory effect").
4. An inhibition of the natural orienting reaction. There is no physiological evidence for this point, but, as suggested by Tassinari et al. (1987), because of instructions, the subjects "have to generate a central command that counteracts the natural orienting reaction and vetoes the eye movement."

Psychological Experiments If the premotor theory of attention is correct, the changes in the excitability of oculomotor centers produced by the presentation of peripheral stimuli should have a counterpart in the findings of psychological experiments in which attention is summoned by these stimuli. In the case of valid trials, if the cue is not informative (that is, it does not predict the location of the imperative stimulus), the attention should remain only briefly on the cued location, since the premotor activation, due to local collicular circuits, is short-lasting. In contrast, if the cue is informative, the facilitation should be long-lasting because the local premotor activation is subsequently substituted by the cognitive facilitation determined by the central oculomotor program. In the case of invalid trials, the presence of an early inhibition ("inhibitory effect"), which is strong for stimuli ipsilateral to the cue and weak for stimuli contralateral to the cue, should favor the contralateral invalid trials. Finally, the suppression of the orienting toward the peripheral cue should produce a long-lasting bias in favor of the contralateral field (Tassinari et al. 1987).

Recently Umiltà et al. (1991) examined the effects of peripheral cues on spatial attention and compared the relationships between the cued location and the target location following presentation of cognitive and peripheral cues. The visual display was the same as in the experiment of Rizzolatti et al. (1987; see fig. 9.1). The manipulated variables were type of cue (cognitive or peripheral) and time interval between cue and imperative stimulus onset (SOA). The results obtained with peripheral cues clearly differed from those obtained with central cues. There were two main differences: (1) with peripheral cues, the meridian effect was absent with both long and short SOAs, and (2) the distance effect was present but did not show the regular increase in cost observed with central cues. Identical results were recently obtained by Reuter-Lorenz and Fendrich (1992).

These results appear to fit well with the data one would have predicted to obtain on the basis of the SC (and other oculomotor centers) modifications following presentation of passive cues. Let us start with the absence of meridian effect with long SOAs. According to the premotor theory, a peripheral cue automatically activates a collicular local motor program for a saccade in the direction of the stimulated visual field. This local program, however, must be counteracted by a central program in the opposite direction (a kind of antisaccade program) because of the previous instructions to keep the eyes still at the occurrence of the peripheral cue. The central program should cause a bias against eye movements (and attentional shifts) that share direction with the

local program and, possibly, a bias in favor of movements (and attentional shifts) in the opposite direction (Tassinari et al. 1989). As a consequence, the meridian effect should disappear, or at least decrease, because orienting within the cued hemifield is hindered, whereas orienting to the opposite hemifield is not affected or even facilitated.

The explanation of the absence of the meridian effect with short SOAs is even more straightforward. The responses of neurons in the SC (and related cortical areas) are inhibited by presentation of stimuli outside the receptive fields that capture the animal's attention. This inhibition is maximal at the time of stimulus presentation and is particularly evident on the side where the attentional stimulus is presented. This early, fast-acting inhibitory process, which increases the salience of the stimulated location, should have as a behavioral counterpart the slowing of reaction times to stimuli located in the same hemifield where the cue was presented. This is exactly what was found by Umiltà et al. (1991). With SOAs of 100 ms, the responses to invalid trials across the vertical meridian were faster than those on the same side of the vertical meridian. The difference exceeded 10 ms.

Criticisms of the Premotor Theory of Attention The link between oculomotion and attention is phenomenologically so obvious that the idea that there should be a close relation between the "movements of the body's eye" and the "movements of the mind's eye" has been advanced in the past by several authors (Crovitz and Daves 1962; Jonides 1976; Rayner, McConkie, and Ehrlich 1978; Klein 1980; Shepherd, Findlay, and Hockey 1986). The disputed point is whether (as the premotor theory states) the two phenomena are causally related. Particularly influential in refusing a causal relationship between oculomotion and attention has been an article by Klein (1980), whose purpose was to test the oculomotor hypothesis directly. In a first experiment, he examined whether a preprogrammed eye saccade facilitates the manual response to visual stimuli presented in the close proximity of the saccade target. In a second experiment, he studied whether the latency of an ocular saccade decreases after cuing a location. Although the results of the second experiment are difficult to interpret, those of the first, which are very clear, have been considered to be strong evidence against the oculomotor hypothesis.

Klein's subjects were presented with three dots, horizontally arranged, and were instructed to fixate the central one. After an interval, three types of events could occur: (1) the left or the right dot brightened, (2) an asterisk could appear over the left or the right dot, or (3) there was no change in the display. The subjects were instructed to respond manually if one of the dots brightened or to make a saccade in a prespecified direction if an asterisk appeared. According to Klein, since the subjects were told to move the eyes toward a fixed point, the detection of stimuli in that point should be facilitated, if the oculomotor hypothesis were true. The facilitation was not found and the premotor hypothesis rejected. The experiment, however, had a logical flaw.

The stimuli appeared randomly to the right or left of fixation. If in order to detect and discriminate these stimuli the subjects had to direct attention toward them, the best strategy for solving the task was to wait until the stimuli appeared and then orient attention in the direction specified by the instructions. It would have been uneconomical to prepare a motor program that in at least half of the cases should be subsequently cancelled. Subjects quite rightly waited for the stimuli, directed accordingly their attention (prepared the relevant oculomotor program, according to the premotor theory), and finally made the saccade. The experiment therefore neither proves nor disproves the premotor hypothesis.⁵

Another "disproof" of the premotor theory was recently reported by Crawford and Muller (1992). They used an experimental procedure and a display similar to that of Rizzolatti et al. (1987), the main differences being that there were six boxes instead of four. Three were on the right of the fixation point and three on the left. In one experiment, the response to the imperative stimulus was a saccade toward the illuminated box; in another, it was a simple speeded manual response. The vertical meridian effect was absent in the case of eye responses and present in the case of manual responses. Because of this incongruence between ocular and manual responses, the authors concluded that spatial attention and oculomotor preparation are mediated by different mechanisms.

The cue that Crawford and Muller (1992) used was a flash of light, that is, a peripheral cue. The meridian effect is not observed (also in the case of manual responses) with this type of cue (Shepherd and Muller 1989; Umiltà et al. 1991; Reuter-Lorenz and Fendrich 1992). Thus, the surprising finding in those experiments was the appearance of the meridian effect in a situation in which it usually does not occur. If the data are carefully analyzed, however, it is clear that in spite of the authors' claim, no meridian effect was present. The so-called meridian effect of their manual response experiment results from a mistake. In order to calculate the meridian effect, they erroneously pooled together all the invalid trials of the cued field and compared the resulting value with that obtained by pooling all the invalid trials of the uncued hemifield. However, when three boxes are placed in each hemifield, the distance between cue and imperative stimulus locations is, by necessity, greater in the uncued than in the cued hemifield. Thus, the so-called meridian effect was less surprisingly a distance effect. The meridian effect, if properly calculated, was absent (Crawford and Muller 1992, fig. 6).

The assumption that cognitive and peripheral cues determine identical attentional effects is at the basis of the criticism of premotor theory made by Egly and Bouma (1991). In their experiment, they calculated the time attention takes to cross the principal visual meridians following presentation of peripheral cues. The results showed that the distance between cue and the imperative stimulus, plus some quadrant effects, most likely related to inhibition of return, were the factors controlling the rapidity of attentional shifts. The meridian effect was not found, and, consequently, the premotor theory re-

jected. An experiment conceptually similar to that of Egly and Bourma was recently carried out by Gawryszewski et al. (1992). Cognitive cues instead of peripheral cues were used. The data confirmed the previous data by Rizzolatti et al. (1987). In addition, the results showed that the cost for reorienting attention across both the vertical and horizontal meridians is greater than the cost for crossing one meridian only.

Evidence Supporting Directly the Premotor Theory of Spatial Attention
The psychological evidence thus far discussed supporting the premotor theory of spatial attention is only indirect. It is based on analogies between attention orienting and eye movement programming. In this section, we report two new experiments that yielded direct evidence in favor of the premotor theory.

The basic experimental situation for many aspects was similar to that employed by Rizzolatti et al. (1987). There was a visual display of four boxes arranged in a horizontal row and a fixation point. In addition there was a fifth box located 6 degrees below the fixation point (fig. 9.2). Digit cues indicated in which of the four boxes the imperative stimulus (a small cross) was most likely to appear. Seventy percent of the trials were valid and thirty percent invalid. The subject's task was to look at the fixation point, to direct attention to the cued box, and to perform a saccadic eye movement toward the fifth (lower) box as fast as possible at the appearance of the imperative stimulus. The eye movements were recorded using an infrared oculometer. The head was fixed.

The response required from the subjects was very simple. If attention is independent of motor programming, there is no reason that a vertical saccade should be influenced by the fact that the subject allocates attention to one box or to another. In contrast, if directing attention implies an oculomotor program, the trajectory of the saccade should be influenced by the direction of attention because the local oculomotor program evoked by the imperative stimulus and the central oculomotor program necessary for directing spatial attention will interfere with that necessary for executing the ocular saccade. Evaluation of the deviation of saccadic trajectory was carried out in two ways:

1. Average saccade deviation (AD). The value of the X-component of the saccades was calculated from the moment of saccade initiation until the saccade reached its vectorial peak velocity, with sampling rate of 1 ms. The value of the X-component at the moment of saccade initiation was used as the reference value. The differences between the current values of the X-component and the reference value were summed and the sum of differences divided by the number of the performed summations.
2. Average velocity (AV). The average velocity of the X-component was calculated by measuring the velocity of this component from the saccade onset to the peak of vectorial velocity. Reaction time was also measured.

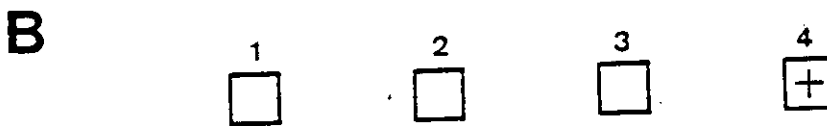
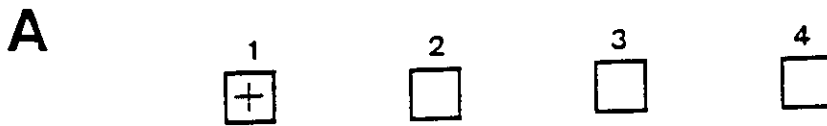


Figure 9.2 Schematic drawing of the visual display used for testing directly the premotor theory of attention together with a series of individual saccadic trajectories. *A.* Valid condition with imperative stimulus presented in box 1. *B.* Valid condition with imperative stimulus presented in box 4. Notice the horizontal deviation of the saccadic trajectories contralateral to the side of the imperative stimulus presentation. For condition *A*, the first twenty trials are presented; for condition *B*, those with the clearest deviation.

The results showed that the valid trials were faster than invalid trials (248 ms versus 268 ms). The analysis of saccade deviation and velocity was carried out using two separate ANOVAs. In both of them, the main factors were Stimulated Field (left or right), Within Field Location of Imperative Stimuli (near to or far from the vertical meridian), and Cued Field (cued or not cued). For both AD and AV, Stimulated Field was significant: AD, $F(1,8) = 14.18, p < 0.005$; AV, $F(1,8) = 7.02, p < 0.05$. Figure 9.2 clarifies this finding. When the imperative stimulus is presented to the left hemifield, the saccades deviate to the right, and, conversely, when the stimulus is presented to the right hemifield, the saccades deviate to the left. Among the two-way interactions, the only significant was Stimulated Field \times Cued Field: AD, $F(1,8) = 15.79, p < 0.005$; AV, $F(1,8) = 29.4, p < 0.001$. The reason for this interaction is as follows. Deviations away from a straight trajectory were larger when the imperative stimulus was presented to the cued field than when it was presented to the uncued field. Thus, when the imperative stimulus was presented to the left hemifield, AD and AV were more deviated to the right if the left hemifield had been previously cued than if the right hemifield had been previously cued. The opposite was true for presentations of the imperative stimulus to the right hemifield. In this case, both AD and AV were more deviated to the left if the right hemifield had been previously cued than if the left hemifield had been previously cued.

These results strongly support the premotor theory of attention. The first finding indicates that the presentation of the imperative stimulus triggers a strong tendency to orient toward it. This stimulus-driven orientation is responsible for passive spatial attention. Given the instruction to keep the eyes still, the subject has to suppress the overt orienting. This suppression command is reflected in the trajectory of the vertical saccade, which deviates to the side opposite to the stimulus presentation. The second finding indicates that when active (endogenous) spatial attention is allocated to a given hemifield, its effect is additive to that of passive attention. This is shown by the vertical saccade deviation, which is larger when the imperative stimulus is presented to the cued hemifield than when it is presented to the uncued hemifield. This increase in deviation suggests that endogenous attention activates oculomotor mechanisms as it occurs in the case of passive attention and that the activation of both mechanisms has to be suppressed for the execution of the vertical saccade.

In the experiment, the imperative stimulus was a visual signal. Thus, active and passive attentional phenomena were partially intermixed. To avoid this, a second experiment was carried out. Here, the visual display consisted of five boxes that formed a cross, with the two arms orthogonal one to another. The central box served as the fixation point. A small line, attached to the central box and pointing in different directions, indicated where the imperative stimulus would appear. In fifty percent of the trials, the imperative stimulus was a thin line, which could appear in one of the two lateral boxes or in the central box. In fifty percent of the trials, a sound was given while the subject waited for the line appearance. Half of the subjects were instructed to make a saccade

to the upper box when the line was presented and a saccade to the lower box when the sound was presented. Half of the subjects had the opposite instructions. There were no invalid trials.

The results confirmed the deviation of the vertical saccades contralateral to the cue. In the case of visual imperative stimuli, the deviation was markedly larger than in the previous experiment. This deviation increase is very likely due to the fact that the detection of the imperative stimulus was more difficult than in the former experiment. This implies that the more strongly attention is engaged, the greater is the suppressing oculomotor signal. Most important, the deviation of the vertical saccades was present with the auditory imperative stimuli. This finding provides direct evidence in favor of the premotor theory. When subjects attend to a given location, their oculomotor system is also engaged in the attended direction, in spite of eye immobility.

Attention and Arm-Related Pragmatic Maps

We began this chapter by showing that space is represented in several pragmatic maps. Some of them control oculomotion, others control movements of the arms and other body parts. Is spatial attention related always to oculomotion, as in the case of Posner paradigm, or can it result from the activity of other nonoculomotor pragmatic maps? Logically, there is nothing unique in the oculomotor system that should grant it a special status. The basic neurophysiological organization of nonoculomotor spatial maps is similar to those controlling eye movements. Thus, the preparation to reach an object (or, possibly, to walk toward a target) should improve the capacity to select a location in the same way as the preparation to make a saccade does it. The experimental evidence for this claim, however, is not particularly rich.

A finding that suggests that attention is controlled, in addition to oculomotor centers, by maps related to body movements is the symptomatology exhibited by monkeys with damage to inferior area 6 (Rizzolatti, Matelli, and Pavesi 1983). Following such a lesion, the monkeys show a contralateral neglect, which is limited to the body and the space immediately around it (personal and peripersonal neglect). They tend to ignore their contralateral arm and are unable to grasp food with the mouth when it is presented contralateral to the lesion. Eye movements are normal. When two stimuli are simultaneously presented in the peripersonal space ipsilateral to the lesion (in the normal field), in contrast to normal animals that constantly prefer the stimulus near the fixation point, the animals with neglect choose the one located most peripherally in the normal field (Rizzolatti, Gentilucci, and Matelli 1985). An attraction toward the ipsilesional stimuli is observed commonly in patients with extrapersonal neglect (Kinsbourne 1987; De Renzi et al. 1989; Ladavas, Petronio, and Umiltà 1990), and there is a general consensus that this attraction reflects a perturbation of attentional mechanisms. The fact that a similar disturbance occurs following damage to a pragmatic map for arm and head movements suggests that circuits other than those for oculomotion also subserve attention.

The importance of arm movement for spatial attention was recently documented by Tipper, Lortie, and Baylis (1992), who instructed normal subjects to depress one button of a series of nine located on a board and arranged in horizontal rows. The subject's hand was located at either the bottom or the top of the board. The arm movements toward a button were triggered by turning on a red light adjacent to the selected button. In most cases, a yellow light, also located near the buttons, was turned on simultaneously to the red light, and the interference effect produced by it was studied. The results showed that the interference depended on the arm's starting position. When the arm movement started from the board bottom, the most interfering stimuli were those located in the board's lower row, whereas when the arm was located at the top of the board, the most interfering stimuli were those of the upper row. It appears, therefore, that arm location produces an attentional field extending from the hand to the target location. A second, and extremely important finding of the experiment, was that the arm-related attentional field changed location according to which hand was used. When the subject used the right hand, the stimuli presented in the right part of the board produced a greater interference than those in the left part. In contrast, when the left hand was used, the left stimuli were more interfering. These data are in good agreement with previous observations that each arm acts better in its ipsilateral field (Prablanc et al. 1979; Fisk and Goodale 1985). Together, these data demonstrate that programming arm movements produces a spatial attentional field and that this field does not depend on oculomotion.

In summary, although the evidence that programming body movements can produce attentional shifts is not rich, the available data suggest that this may occur. The poverty of data on this issue is most likely due to fact that experimental paradigms in which spatial attention is required for successive arm or other body movements were very rarely used in both psychological and physiological experiments.

9.4 CONCLUSIONS

The aim of this chapter was to give a unitary account of spatial attention using psychological and neurophysiological data. We are aware of the difficulty of the task and that many important issues have been dealt with superficially or not at all. We hope, however, to have demonstrated that there is no need to postulate two control systems in the brain—one for spatial attention and one for action. The system that controls action is the same that controls what we call spatial attention.

NOTES

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1. The attentional searchlight hypothesis of Crick (1984) represents an attempt to explain the brain capacity to give a unitary description of a visual stimulus simultaneously processed by a large number of visual maps. It deals, therefore, with object- rather than space-related attention. The notion, however, of a synchronous activity between maps might be of interest also for space perception. Unfortunately, the Crick theory, as originally formulated, has no neurophysiological basis. There is no evidence that the inhibitory action of the reticular thalamic complex can provide a positive feedback to the dorsal thalamus. Furthermore, the reticular neuron rapid bursts of firing, which, according to Crick, should facilitate the dorsal thalamic nuclei, occur in artificial unphysiological conditions (Jahnsen and Llinas 1984) and during synchronized sleep but not during wakefulness (Mukhametov, Rizzolatti, and Tradardi 1970). The theory, albeit interesting, is devoid of any empirical support and will not be discussed further.

2. It is possible that areas controlling head orienting movements become active when the task requires attention allocation to visual stimuli distant from the fixation point. This possibility, although interesting, will be not considered here.

3. One may argue that there is no need to shift attention in order to detect a light stimuli. Evidence from neglect studies, however, indicates that damage to one of many pragmatic cortical representations is sufficient to render an individual unaware of the stimuli. When there is no full agreement in the pragmatic representations about the presence of a stimulus, the stimulus is ignored in spite of its being processed in several cortical and subcortical centers (Rizzolatti and Berti 1990). This requirement of a "unanimous consensus" before a response could be emitted lends support to Posner's idea that arbitrary (not hard-wired) responses occur only when the stimulus is within the focus of attention.

4. The evidence for a recruitment of premotor neurons after attentional stimulus presentation is as follows. First, the most effective stimuli in eliciting the inhibitory effect are dark, relatively large stimuli. Stimuli with these characteristics do not activate the neurons of the SC superficial layers better than white stimuli. However, they are much more effective than the latter in driving the premotor neurons of the deep layers (Gordon 1973). Second, there is evidence that the deep SC neurons, unlike the superficial ones, are often multimodal. They can be triggered by tactile, nociceptive, and auditory stimuli, as well as by visual stimuli (Stein 1984). These nonvisual stimuli may also produce the inhibitory effect. Third, a repetitive presentation of a visual stimulus determines a strong habituation of the deep collicular neurons, as well as marked decay in the intensity of the inhibitory effect. Habituation is weak or absent altogether in the superficial collicular neurons.

5. Recently, Klein, Kingstone, and Pontefract (1992) readdressed the issue of the relations between eye movements and orienting of attention in two experiments conceptually similar to the previous ones. In the first experiment, the auditorily presented words *left* and *right* served as cues to orient covertly toward the indicated direction. The imperative stimuli could be either the same two words or light probes occasionally presented to the right or left of fixation. The verbal imperative stimuli required a saccade in the indicated direction; the light imperative stimuli required a manual response. The results showed a large cue effect (84.5 ms) for eye responses and a small cue effect (13.5 ms) for manual responses. However, whereas the cueing effect for rightward and leftward eye movements was approximately the same, the cueing effect for the manual responses was significant only when rightward ocular movements were prepared (24 ms versus 3 ms). Of these results, the first—that is, the presence of a cue effect for manual responses—supports the premotor theory, while the last one, the asymmetry of the effects, appears to contradict it. In the second experiment, central visual cues indicated the location likely to contain the visual signal requiring a manual response. Occasionally, the verbal command "right" or "left" was presented. The subjects were required to respond with a saccade in the corresponding direction. The results showed a significant cueing effect for the manual responses but no evidence of cueing for the verbally elicited saccades.

Both experiments are rather complex and not easy to interpret. Unlike in the usual Posner's paradigm, in which the (manual) responses are identical in valid and invalid trials, in the first

experiment here, the valid saccades differed from the invalid ones for their direction. Furthermore, the detection of the verbal imperative stimulus did not require allocation of spatial attention. Thus, when the verbal imperative stimulus was invalid, the subjects had to change both their central and peripheral motor sets in order to respond correctly; this was not the case for the manual responses, which remained the same regardless of the imperative command. The huge cost of the invalid eye responses as compared with the invalid manual responses is not surprising. The two response situations are not comparable. An interesting result is the asymmetry in the advantage of cued manual responses. This result obviously needs confirmation. It is important to note, however, that when subjects engage in mental processes that are largely based on the activity of one hemisphere, they "emit a selective orienting response observable behaviorally in terms of submotor attentional (Kinsbourne 1970) and overt gaze (Kinsbourne 1972) shifts towards contralateral space" (Kinsbourne 1987). Thus, in Klein's experiments, the activation of the left hemisphere due to the expectancy of verbal command should have increased the effectiveness of the command "right" and thus produced a marked advantage in manual responses to right stimuli. In contrast, the same left hemisphere activation should have decreased the effectiveness of the command "left" and the advantage of cued manual responses to left stimuli. This is exactly what was found. The first experiment is therefore more in favor of than against the premotor theory. Considering the interpretation difficulties, however, its relevance as a test of the premotor theory is rather dubious. The same is true for the second experiment. It is hard to know a priori the effectiveness of the verbal command "right" or "left" in producing an orienting reaction. It might well be that the effectiveness is so high that it overrides any motor preparation.

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