Controlling attentional priority by preventing changes in oculomotor programs: a job for the premotor cortex?

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Abstract

Abruptly presented items capture attention automatically so they constitute the first items to be examined [Yantis and Jonides, Journal of Experimental Psychology: Human Perception and Performance, 1984;10:601; Jonids and Yantis, Perception and Psychophysics, 1988;43:346; Theeuwes, Perception and Psychophysics, 1992;51:599; Theeuwes, Journal of Experimental Psychology: Human Perception and Performance, 1994;20:799]. This attentional priority can be controlled in a top–down manner by directing attention towards the locus of interest [Yantis and Johnson, Journal of Experimental Psychology: Human Perception and Performance, 1990;16:812; Theeuwes. Perception and Psychophysics, 1991;49:83; Miller, Perception and Psychophysics, 1989;45:567; Folk et al., Journal of Experimental Psychology: Human Perception and Performance, 1992; 18:1030]. The premotor theory of attention [Rizzolatti et al., Neuropsychologia 1987;25:31; Rizzolatti et al., Attention and Performance XV, 1994, p. 231] assumes that the mechanism responsible for the attentional shifts is strictly linked to that responsible for eye movements, and several studies [Corbetta et al., Society of Neuroscience Abstracts 1997;23:122.12; Nobre et al., Brain 1997;120:515; Theeuwes et al., Journal of Experimental Psychology: Human Perception and Performance, 1999;25:1595] suggested that the premotor cortex plays a role in the control of attention. However, the nature of this involvement is still unclear. We have been asking a patient (RJ) with a damage of the right premotor cortex to decide whether a target had a discontinuity on its right or left side. The absolute location of the target was pre-cued. In Section 2, an interference was observed when a sudden onset occurred in the visual space, suggesting that RJ was not able to control attentional capture. The possibility to attribute this interference to an insufficient focalization of attention or a grouping effect were discarded by Sections 3 and 4, respectively. Section 5 revealed that this interference followed exclusively the onset occurring in the hemifield opposite the one containing the target (meridian effect [Rizzolatti et al., Neuropsychologia 1987;25:31]). The results suggest that the control of attentional capture may be achieved by keeping constant the parameters of the appropriate oculomotor program. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

How does the visual system pick up a target embedded among irrelevant items? Several studies [30,7] suggested that there might exist mechanisms to prioritize the selection of newly presented events within the visual field. According to these studies [30], abrupt onsets exert control over the allocation of attention in a way that they attract attention to their location [7]. However, the location containing an onset gains priority only when attention is not focused elsewhere [23–25]. Recent studies supported that when attention is optimally oriented towards the location of the forthcoming target [11,29,23], even dynamic changes occurring in the visual space cease to attract attention. Thus, there might be volitional control of attentional capture [5,10]. Therefore, the increment in reaction time as a function of the display size (the number of items presented) observed when targets and distractors differ only in their spatial arrangement [27], is no more observed.

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This top–down prioritization of the target produces a concomitant inhibition of the distractors by reducing the information coming from their spatial location. Mechanisms underlying such an inhibitory processing could be of oculomotor nature [17]. The premotor theory of attention [16] assumes that attention and oculomotion share neural substrates [9]. An important role in selective attention is played by the pragmatic maps that code space for programming eye movements. In other words, the attentional circuits defined as anatomical entities separated from the spatial maps do not exist [17]. So, when a cue predicts the location of an impending target, a motor program is prepared via activity in oculomotor areas, such as the superior colliculus (SC) [17].

The SC receives direct projections from the retina and it is indirectly connected with the cortical premotor areas controlling eye movements (e.g. the precentral circumvolution) [20], and with the posterior parietal cortex providing location signals [2,3,21]. These anatomical arrangements suggest that the SC is responsible for detection and reflexive orienting to abruptly presented visual targets [12,19,22], as well as for setting a motor program for a saccade towards the stimulus location [9,28]. In cases where saccades are intentionally generated, precentral cortical mechanisms [18] could send the necessary information to the SC so that the appropriate program could be prepared [28,8]. Finally, when observers tend to orient their attention without any saccades (covertly), the information stream may continue flowing towards the SC. However, this time the execution of the program is inhibited [17]. In several studies using functional neuroimaging [4,13,2] an activation of the precentral circumvolution during voluntary covert shifts of attention was obtained. Additionally, when attention is oriented in a reflexive manner, no involvement of the precentral circumvolution is reported [1]. These data indicate that the signal coming from the precentral circumvolution [2,1,15] carries a command for preventing reflexive saccades to the newly presented stimuli [4,2]. However, the nature and the content of this command is not precise yet.

Here, we have been testing a 29-year-old patient (RJ) with a tumor situated in the right rolandic-premotor gyrus pars opercularis, an area involved in oculomotion [14]. RJ did not present any attentional bias for a visual hemifield, but did exhibit difficulties for keeping the eyes fixed when an object moved in his visual space. We tended therefore to investigate the effects of a premotor lesion on intentional control of attentional capture. Despite variations, two main conditions were tested in all four experiments presented in this paper: distractor-onset and neutral. In the distractor-onset condition, a distracting item was abruptly presented during visual search. In the neutral condition, no onset was generated. RJ’s performance was compared to that of a normal control subject matched in age (29 years old), gender, social status and IQ (97 and 100 for RJ and his control subject respectively in the WAIS-R) (Fig. 1).

2. Experiment 1

In Experiment 1, we assessed RJ’s ability to voluntarily eliminate abruptly onset distractors in a task requiring serial search [27] by pre-cueing the absolute spatial
location of an impending target. The target was always present among structurally similar distractors and the number of items in the display varied between three and six. It is generally assumed [29] that the absolute cueing eliminates the serial processing of the display items. If there is no use of the spatial cue, the subjects will have to serially search through the display. This would result in longer manual response times when the number of items to search is bigger. Thus, two findings would give evidence that top–down control of attention priority is intact: firstly, in the neutral condition, the elimination of the spatial certainty by the regularly valid cues would result in an absence of increment in reaction time as a function of the display size [3, 5, 6]. Secondly, independently of the display size, the pre-knowledge of the target’s location would prevent attentional capture by abrupt onsets. Hence, this would result in the absence of increment in reaction time between the neutral and the distractor-onset conditions [29, 23, 5, 10].

2.1 Methods

Stimuli and apparatus: The stimuli were gray squares (37, 37 cd/m²) appearing inside a circle of equal luminance. They were presented in a black background (0.034 cd/m²). At a viewing distance of 30 cm, the angular size of each square was of 0.5 × 0.5° and the circle’s radius of 1°. Each square had a discontinuity and was shown in four possible orientations: 0, 90, 180 or 270° to the vertical. The target was rotated in 90 or 270°, whilst the distractors were rotated in 0 or 180°. The stimuli were displayed centrally on a color screen of a Dell Latitude portable computer with a PentiumII 200 MHz processor and an SVGA graphics card. The experiments took place in a dimly illuminated room.

Procedure: A visual search task was proposed. Subjects had to decide whether a square target had a discontinuity on its right or left side. The target appeared inside an outline circle embedded among other circles containing square distractors. No-onset stimuli where camouflaged by square premasks. Two stimuli conditions were tested: a distractor-onset and a neutral. In the distractor-onset condition, an onset item was presented in a previously blank location. This item was always a distractor. In the neutral condition, no onset occurred. At the beginning of a trial, a central dot appeared. After 1000 ms, the standard premask was presented consisting of circles. Each circle contained a square. The premask consisted of three or six circles, which were equally spaced around the fixation point on an imaginary circle whose radius was 4.8°. The six circles formed a hexagon; the three circles formed either an upward pointing or downward pointing equilateral triangle. An endogenous cue (a central arrow) was then presented for 100 ms and pointed the absolute location of the target. The stimulus field was presented 100 ms later. A discontinuity appeared on one side of each square after extinguishing of a single segment. In only one circle the extinguished segment revealed a discontinuity on the right or the left side. The orientation of the square determined the right response key (the ‘J’ key for right and the ‘F’ key for the left side). The display remained present until the response was given. In the distractor-onset condition, at the end of the 100 ms cue period, a circle containing a distractor appeared at one previously blank location of the 4.8° imaginary circle. In each trial, it occupied a position in the hemifield opposite the one containing the target. Display size and conditions were randomly presented. Each subject performed a single block of 96 trials. Each session was preceded by 40 practice trials. No feedback was given.

2.2 Results and discussion

Fig. 2b shows the results of correct reaction times in Section 2 for the R.J. and the matched healthy control subject. No errors were observed for either subjects. Statistical analyses were carried out with the trials as the random variable. Compared to the healthy control, R.J. presented slower reaction times in all conditions (F(1, 46) = 148.17, P < 0.001). There was no main effect of display size (F(1, 46) = 0.26, P < 0.872). It seems that the top–down control of attention is not disturbed when no object is abruptly presented in the visual space. In anticipation to the target event, attention was already directed to the location of the impend-
ing target, suggesting that visual selection took place before the identity of each stimulus was revealed. Therefore, the number of items presented had no reason to produce an increment in reaction time. The main effect of condition was revealed to be significant \(F(1, 46) = 20.71, P < 0.001\), as well as the condition \(X\) subject interaction \(F(1, 46) = 9.82, P < 0.003\). Compared to the neutral condition, R.J. presented significantly slower reaction times in the distractor-onset condition for both three-object \((t(23) = 2.737, P < 0.012)\) and six-object \((t(23) = 2.192, P < 0.039)\) display sizes. This was not observed in the performance of the healthy control subject \((t(23) = 1.461, P < 0.161\) and \(t(23) = 1.867, P < 0.75\) for the three-object an six-object display sizes, respectively). Such a finding suggests that, whilst the control subject is able to ignore the onset of a distracting item, R.J. is not. Even under absolute cueing conditions, the onset item attracted his attention automatically. Furthermore, since an onset captured R.J’s attention, we suspected that the mechanism underlying attentional priority was still functional. The support to this idea comes from the distractor-onset condition in which no significant difference was found between the three-object and the six-object display size for both R.J. and the control subject \((t(23) = 0.425, P < 0.675\) and \(t(23) = 0.855, P < 0.401\), respectively). R.J’s lesion of the right inferior premotor cortex caused a pattern of interference when a dynamic change occurred in his visual field. This suggests that his attention was involuntarily shifted to the location of the onset item [16,2,6]. Thus, R.J exhibited a deficit in the top-down control of attentional capture.

Nevertheless, some interesting questions arise. Firstly, if we consider that the spatial cue was very shortly presented, thus there was not enough time for attention to get focused at the target location, an alternative explanation to R.J’s performance may be proposed. It is possible that both R.J and the healthy control to have shifted attention to the location of the onset, but that R.J was not able to shift his attention back to the location of the target (because of an insufficient focalization) while the control subject was. Section 3 aimed at examining this matter. Secondly, it is possible that the appearance of a distracting element in the distractor-onset condition may have engendered grouping (see Fig. 2A). Is the performance difference between R.J and his control subject due to the group of closely spaced objects, rather than the onset per se? This question is examined in Section 4.

3. Experiment 2

In Experiment 2, we gave subjects the opportunity to well focus attention on the location of the impeding target by prolonging the duration of the cue.

3.1. Method

Stimuli and apparatus: The stimuli and the apparatus were the same to those used in Section 2.

Procedure: The procedure was the same as in Section 2, except that the premask always consisted of three circles, forming an upward pointing triangle. The endogenous spatial cue (an arrow) was presented either for (a) 100 or (b) 200 ms and was followed, 100 ms later, by the search display. Two stimuli conditions were presented: (a) in the distractor-onset condition, a distracting circle was abruptly added to the search display and occupied a previously blank location; (b) in the neutral condition, no distractor was added in the display. All four conditions were randomly presented. Each subject performed a single block of 96 trials. The experimental session lasted for about 8 min. No feedback was given.

3.2. Results and discussion

Statistical analyses were carried out with the trials as the random variable. As in Section 2, R.J presented slower RTs than the healthy control in all conditions \((F(1, 46) = 79.39, P < 0.001)\). Very interestingly, the cue duration \(X\) subject interaction was not found to be significant \((F(1, 46) = 0.139, P < 0.711)\). This result show that both subjects responded in a similar way when the cue was presented for either 100 or 200 ms. The subject \(X\) stimuli condition interaction was found to be significant \((F(1, 46) = 24.75, P < 0.001)\), as well as the main effect of the stimuli condition \((F(1, 46) = 15.37, P < 0.001)\). Statistical analyses carried out on RTs of each subject individually, showed that the cue duration \(X\) stimuli condition interaction was significant only for R.J \((F(1, 23) = 7.66, P < 0.011)\), with a significant main effect of stimuli condition \((F(1, 23) = 25.08, P < 0.001)\) but not for the cue duration \((F(1, 23) = 2.70, P < 0.114)\). Compared to the neutral, R.J presented slower RTs in the distractor-onset condition for both 100 and 200 ms cue durations \((t(23) = 6.42, P < 0.001\) and \(t(23) = 2.18, P < 0.04,\) respectively).

The results observed in Section 2 gave place to a crucial question: was a shortly presented cue (i.e. 100 ms) long enough to permit a correct focalization of attention at the target’s location? The results of Section 3 may definitely answer this question. They clearly suggest that R.J’s defective performance (in both Sections 2 and 3) in the distractor-onset condition is not due to a shortly presented spatial cue, but rather to an irresistible attentional attraction by the sudden onset of a distracting element in space (see Fig. 3). This is directly suggested by statistical analyses which failed to find a significant difference between a condition where a brief cue was presented (100 ms) and a condition where a longer cue was presented (200 ms). Thus, the
question arisen in Section 2, seems to be already answered.

4. Experiment 3

Experiment 3 aimed at examining the second question arisen by the results obtained in Section 2. Is the onset per se responsible for the performance difference between RJ and the healthy control subject, or is there any grouping effect? We introduced a new control condition in which the number and position of stimuli were the same as in the distractor-onset trials in order to determine whether grouping or onset capture was the source of RJ’s attentional deficit in performance.

4.1. Method

Stimuli and apparatus: The stimuli and the apparatus were the same to those used in Section 2.

Procedure: The procedure was the same as in Section 2, except that the premask always consisted of three circles, forming an upward pointing triangle. The endogenous spatial cue (an arrow) was always presented for 100 ms and was followed, 100 ms later, by the search display. Three stimuli conditions were presented: (a) in the distractor-onset condition, a circle was abruptly added to the search display and occupied a previously blank location, (b) in the neutral condition, no distractor was added in the display and (c) in the grouping condition a distractor was present on the screen since the appearance of the premask (thus, the number and position of items was the same as in the distractor-onset condition but there was no onset). All three conditions were randomly presented. Each subject performed a single block of 98 trials. The experimental session lasted for about 10 min. No feedback was given.

4.2. Results and discussion

Statistical analyses were carried out with the trials as the random variable. The results are depicted in Fig. 4. As in the two previous experiments, RJ exhibited slower RTs than the healthy control \((F(1, 70) = 54.45, P < 0.001)\), and the main effect of condition was found to be significant \((F(2, 140) = 4.54, P < 0.012)\). An Analysis of Variance (ANOVA) carried out for each subject, revealed a significant condition effect only for RJ’s performance \((F(2, 70) = 5.27, P < 0.007)\). Paired comparisons showed that RJ responded slower in the distractor-onset condition than in the neutral one \((t(35) = 2.11, P < 0.042)\), as well as compared to the grouping condition \((t(35) = 5.33, P < 0.001)\). Interestingly, no difference was observed between the neutral and the grouping conditions \((t(35) = 0.36, P < 0.723)\).

Section 2 arose the matter of the factor responsible for RJ’s performance. This question seems to find an answer in the present experiment. The results suggest that the main factor responsible for RJ’s loss of control over attentional capture is the sudden appearance of a distracting element, but not the spatial arrangement of stimuli (i.e. a grouping effect). RJ exhibited slower RTs when a distractor was suddenly added to the display but he did not appeared to be disturbed by the presence in the display of a group of closely spaced items.

Taken together, Sections 2 and 3 and Section 3 provide strong evidence on the nature of RJ’s attentional deficit. First of all, it seems fairly logical to propose that RJ’s ability to control attentional capture is defective. Even though he knows where the target is going to be presented, he is not able to avoid an involuntary orienting towards a certainly distracting item which appears in his visual space (Section 2). We considered the possibility that this defective performance might depend on an insufficient attentional focalization on the target. The data obtained in Section 3 do not support this explanation, since RJ exhibited an equal deficit for 100 and 200 ms cues. We also tested the alternative hypothesis that the distracting element...
for RJ is not the onset per se, but rather a group of closely spaced items. Once more, this alternative explanation may be discarded. Section 4 clearly suggests that the RJ’s attention is captured by the onset item but not by the group of items presented in the display. We may, thus, draw our first conclusions which support the idea that RJ does exhibit a deficit in controlling attentional capture only by an onset element.

The performance pattern in Sections 2 and 3 and Section 4 does not, however, offer a satisfactory clarification of the functional origin of RJ’s deficit. If controlling attentional priority intentionally is specifically linked with the control of oculomotor programs, there is need to look for a behavioral evidence exclusively related to the oculomotor system. The meridian effect has been proposed as one such mark of oculomotor activity [9,10]. According to Rizzolatti and colleagues [16,17], attending is achieved by compiling a saccade program specifying the direction and the amplitude parameters required to move the eyes to the attended location. When an onset occurs elsewhere in the visual space, this saccade program has to be modified in a way that its parameters reflect the locus of change. In cases where attention is covertly shifted, this program is compiled but not executed. In Sections 2 and 3 and Section 4, the onset of the distracting item always occurred in the hemi-field opposite the one containing the target. Thus, the interference was produced when attention had to cross the visual meridians [16]. Would we also observe a similar pattern of interference in case where the onset occurred in the same hemi-field?

5. Experiment 4

Experiment 4 aimed at eliciting this question. If the observed interference has nothing to do with oculomotor programming\(^1\), then no meridian effect should be observed: the degree of interference would be the same whether the distractor is presented in the same or the opposite hemi-field. In contrast, if interference reflects RJ’s difficulty to prevent changes in the parameters of his oculomotor program, then the meridian effect should be expected.

5.1. Method

**Stimuli and apparatus:** The stimuli and the apparatus were the same to those used in Section 2.

**Procedure:** The procedure was the same as in Section 2, except that the premask always consisted of four circles, which were displayed on the angles of an imaginary square for 1000 ms. The laterals of this square were of 8.6° and the fixation point was presented in its center. One of the four circles was the impending target and was pre-cued with a central arrow for 100 ms. The search display was presented 100 ms later. Three stimuli conditions were tested: (a) in the same hemi-field distractor-onset condition, a circle containing a distractor appeared in the hemi-field containing the target; (b) in the opposite hemi-field distractor-onset condition, a circle containing a distractor appeared in the hemi-field containing the target; (c) in the opposite hemi-field distractor-onset condition, a circle containing a distractor appeared in the hemi-field opposite the one containing the target; in both distractor-onset conditions, the onset was located above, beneath, on the right or on the left side of the target. The

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\(^1\) Although no eye movements recording was carried out, we employ here the term of oculomotor programming as introduced by Rizzolatti et al. [16] to define the meridian effect.
distance between the target and the onset item was always of 6.1°, thus the distractor could appear outside of the imaginary square (Fig. 5a); (c) in the neutral condition, no onset was generated. All conditions were randomly presented. Each subject performed a single block of 144 trials.

5.2. Results and discussion

Fig. 5b depicts the results of correct reaction times in Section 5 for RJ and his healthy control. Statistical analyses were carried out with the trials as the random variable. As in the previous experiments, RJ presented slower reaction times in all conditions ($F(1, 94) = 241.06$, $P < 0.001$), compared to the healthy control. The main effect of condition was significant ($F(2, 188) = 5.94$, $P < 0.003$), as well as the condition X subject interaction ($F(2, 188) = 5.74$, $P < 0.004$). The analysis revealed no significant condition effect for the healthy control ($F(2, 46) = 2.41$, $P < 0.101$), suggesting, once again, that the regularly valid cues prevent attentional capture. In contrast, this effect was significant for RJ ($F(2, 46) = 4.92$, $P < 0.012$). Compared to the neutral condition, a significant increment in reaction time was observed in RJ’s performance only when the onset occurred in the hemifield opposite the one containing the target ($t(47) = 1.96$, $P < 0.04$), whilst this was not observed when the onset occurred in the same hemifield ($t(47) = 1.47$, $P < 0.146$). Thus, the appearance of an onset in the opposite hemifield captured RJ’s attention. An additional support to this suggestion came from the same/opposite hemifield comparison of reaction times, which revealed that the two conditions were highly significantly different ($t(47) = 3.54$, $P < 0.001$). Thus, interference occurs only when attention has to cross the visual meridians [16].

What really determines the meridian effect? There is evidence [16] that when attention moves to reach a target, a program specifies first the direction of the attentional shift, followed by the exact distance to be covered. Once programmed, changes in distance imply only a readjustment of the preexisting program, whereas changes in direction require an entirely new program to be constructed [16,17]. In the present study, onsets occurring in the hemifield containing the target involve changes in distance, whereas when they occur in the opposite hemifield, attention has to cross a meridian. RJ’s interference pattern seems to be generated only when an item is abruptly presented in the hemifield opposite the one containing the target. In order to optimize the selection of the target, the attentional system has to exert a top–down inhibitory control on the location of the distracting information, so that this information no longer competes for selection. In terms of the premotor theory of attention [16,17], the decrement of the relevance of the distracting information would be achieved by maintaining unchanged the preexisting (oculomotor?) program. This could be possible via activity of the cortical areas sending the necessary information to the SC [17]. Hence, RJ looses attentional control through the meridians and involuntarily attributes attentional priority to abrupt onsets biasing, therefore, his guided search of the target [26].

6. General discussion

Four experiments were carried out aiming at investigating the contributions of the premotor cortex in the control of attentional capture. In all experiments, a visual search task was proposed with an absolute pre-cueing of the location of an impending target. In a critical condition, so called distractor-onset condition, which was present in all experiments, an onset occurred in the visual space just after the spatial cue. In Section 2, the onset constantly occurred in the hemifield opposite the one containing the target, whilst in Section 5, the onset occurred either in the same or the opposite hemifield. In Section 2, a relatively long lasting interference was observed in RJ’s performance when an onset occurred in his visual field, suggesting that he had difficulties to maintain attention at the appropriate locus. The abrupt onset automatically captured RJ’s attention, and this capture was equal irrespectively to the display size. This finding suggests that the data-driven orienting component of RJ’s attentional system is still intact. In addition, the voluntary orienting component seems also to be intact, since no difference was found as a function of the display size. The possibility to explain RJ’s distraction as the results of a defective attentional focalization or of an attraction exerted by closely spaced objects may be discarded given the results obtained in Section 3 and Section 4, respectively. Section 5 confirmed the findings obtained in Section 2 and offered arguments in favor of an oculomotor component of the attentional control system: the interference pattern was observed only when the onset occurred in the hemifield opposite the one containing the target, thus when involuntary attentional shifts had to cross the visual meridians.

RJ’s performance might be explained if we suppose that he is not able to maintain constant the parameters of the oculomotor program which was compiled just after the presentation of the spatial cue. Let us consider the sequence of events in a single trial. Focusing on the fixation point results in the observer drawing a vertical and a horizontal virtual meridians. As soon as the brief endogenous spatial cue is presented, a program for a saccade towards the expected
location is prepared. If no onset occurs in the visual field (i.e. the neutral condition), the saccade parameters (i.e. amplitude and direction) remain the same, hence, the stimulus appearing in that location is adequately processed. In case where the onset occurs in the hemifield containing the target, a quick readjustment of the amplitude parameter is automatically accomplished. Thus, the program is relatively maintained unmodified and, therefore, the control of attentional priority may be successfully carried out [16]. In contrast, when the onset occurs in the hemifield opposite the one containing the target, the direction parameter has to be modified. This change requires the construction of a completely different program, hence, delaying the manual response. RJ’s inability to maintain the already existing program, results in the automatic construction of a new one by the SC, reflecting the spatial location of the onset item. This radical change in the program would be the origin of the meridian effect observed in RJ’s performance [16,17].

RJ’s deficit inform us on the contribution of the premotor cortex in the top-down control of attentional priority to new objects and, thus (although indirectly) on the way it might control oculomotor programs. Our data suggest that, under normal conditions, voluntary selection of a stimulus via its location requires a cortical control of the program which specifies its spatial coordinates [26]. This would be accomplished by preventing changes in these parameters. As a result, dynamic changes in the visual space do not interfere.

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References


