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Time-dependent effects of discrete spatial cues on the planning of directed movements

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Abstract The degree of preparation of a motor response varies with the information available regarding the response that will need to be executed and with the time provided to process that information. In experiment 1 we investigated the time-course of processing the information specified by discrete spatial cues regarding the upcoming target of directed movements. For this purpose we varied the number of cues that indicated the possible locations of the target and the duration of the cue period preceding the target. The results showed that the effects of processing the information provided by the cues developed progressively and stabilized after 0.2 s. In addition, the level of motor preparation reached was a function of number of cues. However, the effect of number of cues occurred even in the no cue period condition, i.e. when subjects could not have benefited from the information provided by the cues to prepare the response. Further analyses suggested the hypothesis that, in the no cue period condition, the effect of number of cues resulted from the cues acting as distractors (i.e., interference) whereas, with longer cue periods, the effect resulted from the motor preparatory process (i.e., facilitation). This hypothesis was tested in experiment 2 where the number of cues and the number of distractors were varied inversely. Cues and distractors were the same type of stimuli and differed only in their relation to the time of presentation of the target. Subjects performed in a directed response task and in a

control detection task. It was predicted that the facilitatory effect of the cues and the interference effect of the distractors on the planning of the directed response would oppose each other and produce a non-monotonic change of RT across conditions. The results conformed to the prediction and, therefore, supported the hypothesis of independent effects of facilitation and interference. In addition, we found that the pattern of RT across conditions in the detection task differed radically with that in the directed response task. This result indicates that the time-dependent effects of cues and distractors are contingent on the type of motor response required in the task, and, in particular on the spatial requirement on the motor response.

Keywords Pointing · Reaching · Detection · Motor preparation · Distractors · Spatial attention

Introduction

The level of preparation of a directed movement depends on the amount of information available in advance regarding the motor response that will need to be executed (Basso and Wurtz 1997; Bock and Arnold 1992; Bock and Eversheim 2000; Dassonville et al. 1999; Favilla 2002; Ghez et al. 1997; Pellizzer and Hedges 2003, 2004; Rosenbaum 1980) and on the time provided to process that information (Favilla 2002; Ghez et al. 1997). In experimental conditions, the amount of information given to a subject before the presentation of the target to reach can be manipulated using the cueing method (Rosenbaum 1980).

In a previous experiment, we found that the reaction time (RT) of directed movements changed with the number of discrete spatial cues but not with their spatial dispersion (Pellizzer and Hedges 2003). In addition, we found that the results supported a capacity-sharing model which assumes that the processing resources for motor planning are limited and that they can be distributed to prepare multiple responses in parallel (Pellizzer and Hedges 2003, 2004; Shaw 1978).

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Here, we sought to characterize the time-course of processing the information provided by discrete spatial cues regarding the target of directed movements. In experiment 1, we tested the effect of the duration of the cue period when 1, 4 or 16 spatial cues were presented. We selected six cue periods ranging from 0 to 1.6 s, which provided different amount of time for processing the information provided by the cues. These cue periods vary between two extremes: the cue period of 0 s which does not provide any information before the target and, therefore, cannot facilitate motor preparation, and the period of 1.6 s which gives ample time to process the information provided by the cues and to use that information to prepare for the upcoming response.

Experiment 1: effects of cue period and number of cues

Methods

Subjects

Fifteen human subjects participated in this experiment (11 males and 4 females; age range 19–37 years). All subjects were naive relative to the purpose of this study and signed an informed consent before their participation. The experimental protocol was approved by the Institutional Review Board of the Minneapolis VAMC.

Apparatus

The experimental setup was the same as described before (Pellizzer and Hedges 2003). The visual stimuli were presented on a 14 in. color monitor placed 45 cm in front of the subjects. They controlled the position of a red cursor using a joystick (Model H0000-N0/N04, CTI electronics corp., Stratford CT) that they grasped with their preferred hand (right hand: 12 subjects; left hand: 3 subjects). The position of the joystick was recorded at 200 Hz. The direction of gaze was monitored using a video-based eye tracking system (Iscan Inc.).

Procedure

Subjects were seated with the head against a chin-rest. They initiated a trial by placing the red cursor within a circular window in the center of the display for a 1 s center-hold period. This was followed by a cue period of 0, 0.1, 0.2, 0.4, 0.8 or 1.6 s after which the target was presented. During the cue period a number of white circles (0.75° radius) located at 4° of visual angle from the center of the display indicated the locations where the target could appear. The number of cues presented were $N_{\text{CUES}} = 1, 4$ or 16 . Trials of different cue periods and number of cues conditions were randomly mixed. The direction of each cue was selected randomly with the constraint that cues did not overlap. Since the retinal eccentricity of visual stimuli could affect RT, it was

important to constrain the direction of gaze during the presentation of the visual stimuli. Therefore, subjects were instructed to fixate the center of the display during the center-hold and cue periods. Any eye movement outside of a center window of 2° radius during the center-hold and cue period aborted the trial. When the target appeared (white disc of 0.75° radius), the subjects had to move the cursor as quickly as possible from the center to the location of the target. The change of position of the cursor from the center of the screen to the target corresponded to a change of position of the tip of the joystick of 2 cm. The trajectory of the cursor had to stay within a straight path from the center to the target (Fig. 1b). The path had the same width as the target. Although the path was not visible to the subjects, they were instructed about the spatial constraint on the trajectory of their response and were familiarized with it during practice trials. A directional error was counted when the trajectory of the cursor exited from this path. The cursor had to stay on the target for at least 0.5 s. The reaction time was defined as the latency between the onset of the target and the exit of the cursor from the center window. Trials with reaction times shorter than 100 ms or longer than 2 s were considered as reaction time errors. Responses that were initiated during the cue period or in less than 100 ms after the target presentation were counted as anticipated responses. Movement time (MT) was defined as the time between the exit of the cursor from the center window to the reach of the target. Correct trials were signaled by a computer-generated high-pitch tone, whereas error trials were signaled by a low-pitch tone. The detection of any type of error aborted the trial and a trial with the same cue duration and the same number of cues was presented again at a random position in the sequence of the remaining trials. Twelve correct repetitions per condition were obtained for each subject. A schematic example of the task is illustrated in Fig. 1a (top).

Data analyses

Data were analyzed using standard statistical methods (Snedecor and Cochran 1989). In particular, the effects of the factors number of cues and cue period were determined using a within-subject ANOVA (Rutherford 2001). In some cases orthogonal polynomial contrasts were used to estimate the degree of the model that best relate RT with the independent variable. In those cases, the polynomials appropriate to the unequal spacing between levels of the independent variable were used.

For each subject, we computed the average RT in each condition using the harmonic mean which is robust to outliers (Ratcliff 1993). The analyses of the number of anticipated responses (see above) and of the number of directional errors were performed on the square-root transformed counts to stabilize their variance (Snedecor and Cochran 1989). In addition, we evaluated the straightness of the response trajectory using the path

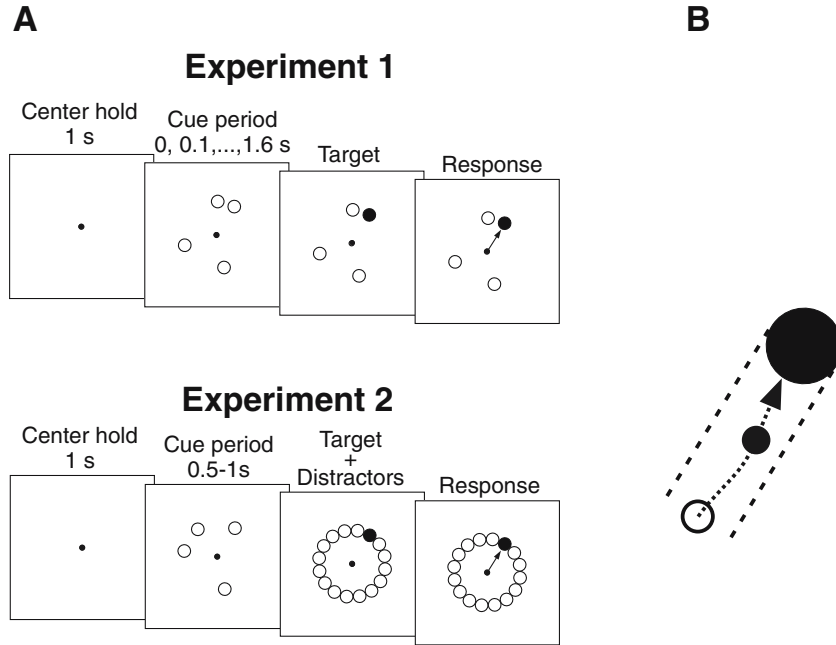


Fig. 1 a Top Schematic example of a trial in experiment 1. The subjects controlled the position of a cursor on a screen using a joystick. After the center-hold period, 1, 4, or 16 cues were presented during a cue period of 0, 0.1, 0.2, 0.4, 0.8 or 1.6 s. The cues indicated the possible locations of the upcoming target. Subjects were instructed to fixate the center of the screen during the center-hold and cue periods. When the target was presented, the subjects had to respond by moving quickly the cursor from the center onto the target. The reaction time was measured from the onset of the target to the time when the cursor exited the center window. **a** Bottom Schematic example of a trial in experiment 2. After the center-hold period, 0, 1, 2, 4, 8 or 16 cues were presented

during a cue period that varied randomly between 0.5 and 1 s. The target was presented simultaneously with distractors. The distractors were identical in shape to the cues and appeared in the interstices between cues which resulted in a ring of 16 contiguous stimuli. In the directed response task, subjects had to move the cursor from the center to the target (like in experiment 1), whereas in a control detection task subjects had to release a push-button after the presentation of the target. **b** In both experiments, the trajectory of the cursor from the center to the target had to stay within parallel boundaries that matched the width of the target. Subjects did not see the boundaries but were instructed about the spatial requirement on their response

linearity index defined by Atkeson and Hollerbach (1985). This index was computed first by measuring in each trial the largest deviation of the trajectory normal to the line joining the initial position and the final position of the movement. Then, we computed the path linearity index as the ratio between this deviation and the length of the line between the initial position and the final position. Finally, we evaluated the average error and dispersion of the initial direction of movement in the different conditions. The initial direction of movement was defined as the direction traveled by the cursor from the time point in which the acceleration exceeded 5% of its maximum and the time of the first maximum of acceleration (Pellizzer and Hedges 2003, 2004). All statistical analyses were performed using SPSS 13.0 (SPSS Inc., Chicago, IL, USA).

Results

Reaction time

Average RT is plotted against cue period for each number of cues condition separately in Fig. 2. It can be seen that RT changed in an orderly fashion both with

cue period and number of cues. The analysis of variance indicated that RT was significantly affected by cue period ($F_{(5,70)} = 43.21$, $P < 0.0005$), number of cues ($F_{(2,28)} = 84.30$, $P < 0.0005$) and by their interaction ($F_{(10,140)} = 2.69$, $P = 0.005$). The functional relation between average RT and cue period T was well described in each number of cues condition i by the following exponential decay function:

$$\overline{RT}_i(T) = a_i + b_i e^{-k_i T}, \quad (1)$$

where a_i , b_i and k_i are empirically determined constants. The parameters of the functions were obtained using a nonlinear regression procedure (Levenberg–Marquardt method) and are indicated in Table 1. The fitted functions are plotted in Fig. 2 as continuous lines passing through the data points. The results of these analyses showed that, for each number of cues condition, RT decreased markedly for cue periods going from 0 to 0.2 s and then leveled off for longer cue periods. In addition, the level at which RT stabilized (i.e., parameter a_i in Eq. 1) was determined by the number of cues: the higher the number of cues, the higher the level of RT. In addition, the step increase of RT with number of cues is larger between the 1 and 4 cues conditions than between

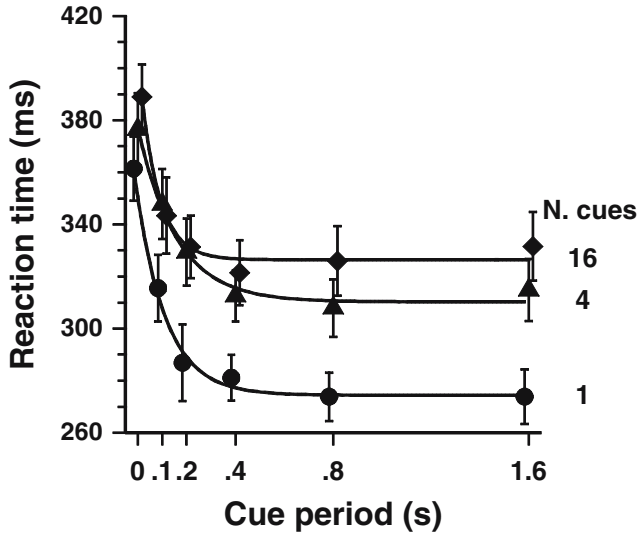


Fig. 2 Experiment 1: average RT across subjects as a function of cue period for each number of cues condition. The data for each number of cues conditions were slightly shifted from each other along the abscissa to reduce the overlap of symbols. The vertical error bars indicate the standard error of the mean ($N=15$ subjects). An exponential decay function (Eq. 1) was used to describe average RT as a function of cue period in each number of cues condition. The parameters of the functions are indicated in Table 1

Table 1 Parameters (and their standard error of the mean in parenthesis) of the exponential decay function (Eq. 1) that relates average RT (in ms) with cue period (in ms) for each number of cues condition

Number of cues	a	b	k	R^2
1	274.4 (2.3)	87.5 (4.1)	8.2E-3 (0.9E-3)	0.993
4	310.2 (2.6)	67.1 (4.3)	6.3E-3 (0.9E-3)	0.988
16	326.4 (2.4)	62.7 (4.9)	13.2E-3 (2.7E-3)	0.982

4 and 16 cues conditions. These effects of number of cues on RT are similar to those found in a previous experiment (Pellizzer and Hedges 2003).

However, the data plotted in Fig. 2 show also that there was an effect of number of cues in every cue period conditions and not only for the longest cue periods. We examined this aspect of the data further by analyzing the effect of number of cues for each cue period separately. The results confirmed that number of cues affected RT significantly in every cue period conditions (all $F_{(2,28)} \geq 9.50$, $P \leq 0.001$ for each cue period). This means that the effect of number of cues on RT occurred whether or not there was time for a preparatory process to take place. Therefore, these results lead to the question of whether a single process can be invoked to explain the effect of number of cues occurring in all cue period conditions or whether there is evidence for two independent processes which would be engaged at different times after the presentation of the visual stimuli.

Experiment 1 was not designed to answer this question, which will be addressed with experiment 2. In

particular, the factor number of cues had only three levels which prevented any detailed functional analysis of the relation between RT and number of cues across different cue periods. Nevertheless, we examined the effect of number of cues on RT further by analyzing the orthogonal polynomial contrasts in each cue period condition. This analysis indicates whether the relation between RT and number of cues is better described by a straight line (i.e., linear component) or a curved one (i.e., quadratic component). The results showed that the linear component was significant in all cue period conditions (all $F_{(1,14)} \geq 8.02$, $P \leq 0.013$ for each cue period), whereas the quadratic component was significant in all conditions except the 0 s cue period condition (all $F_{(1,14)} \geq 17.42$, $P \leq 0.001$ for cue periods between 0.1 and 1.6 s; $F_{(1,14)} = 2.31$, $P = 0.151$ for the 0 s cue period). These results indicate that the relation between RT and number of cues is better described by a straight line in the 0 s cue period condition and by curved lines in all the other cue period conditions. Furthermore, we examined the proportion of variance accounted for by the quadratic polynomial component in each cue period condition. The proportion of variance explained is given by the eta-squared which is plotted for each cue period condition in Fig. 3. The results show that the variance accounted for by the quadratic component was small for the 0 s cue period condition and that it increased abruptly from the 0 s to the 0.1 s cue period conditions and stayed consistently high for longer cue period conditions. Therefore, these analyses indicate that the relation between RT and number of cues is better described

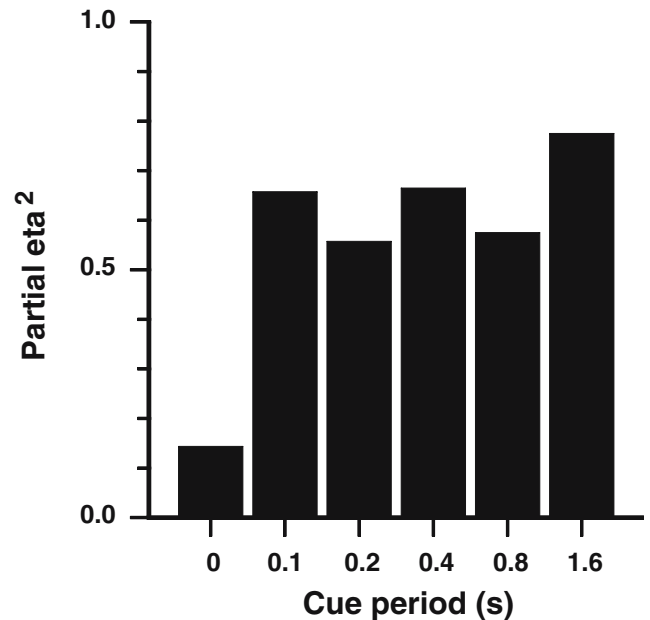


Fig. 3 Experiment 1: Partial eta-squared of the quadratic component of the polynomial contrasts between RT and number of cues for each cue period condition. It corresponds to the proportion of variance of RT accounted for by the quadratic polynomial component in each cue period conditions

by a straight line in the 0 s cue period condition and by a curved one in all the other cue period conditions.

In summary, the results from these analyses indicate that there was a qualitative change in the relation between RT and number of cues between the 0 s cue period condition and the other cue period conditions. Therefore, these results suggest that two different processes were responsible for the effect of number of cues on RT, one in the 0 s cue period condition and the second one in all the other cue period conditions. It can be suggested that, when the cues and the target appear simultaneously, the effect of number of cues on RT would reflect some interference effect of the stimuli that are not the target, whereas when the cue period is long enough for processing the information provided by the cues, the effect of number of cues on RT would reflect the preparatory process. This suggestion will be addressed further in experiment 2.

Anticipated responses

An additional indication of a preparatory process taking place during the cue period is the tendency to produce anticipated responses. When subjects are prepared to move toward a location in space and are waiting for the signal to respond, they initiate the prepared response occasionally before the signal. Therefore, the occurrence of anticipated responses is an indication of the readiness to respond. The analysis of the number of anticipated responses was performed on the square-root transformed counts (Snedecor and Cochran 1989). The analysis showed significant effects of cue period ($F_{(5,70)}=24.28$, $P<0.0005$), number of cues ($F_{(2,28)}=143.29$, $P<0.0005$) and of their interaction ($F_{(10,140)}=26.75$, $P<0.0005$). The average number of anticipated responses across subjects is plotted against cue period for each number of cues condition in Fig. 4 (top). It is clear from the figure that the number of anticipated responses increased with cue period in the 1 cue condition only. In addition, the number of anticipated responses increased essentially between the cue periods of 0.1 and 0.4 s. These results indicate that subjects were prepared to respond in the 1 cue condition after about 0.2 s. Therefore, these results are consistent with the proposal that the preparatory process is time-consuming and that its effect can be detected only after enough time has passed for the process to take place. In contrast, the effect of number of cues when there is no cue period would not be related to the preparatory process but to an effect of interference.

Movement time

The analysis of MT indicated that it was affected by cue period ($F_{(5,70)}=4.69$, $P=0.001$) but not by number of cues ($F_{(2,28)}=0.05$, $P=0.950$) nor by the interaction cue

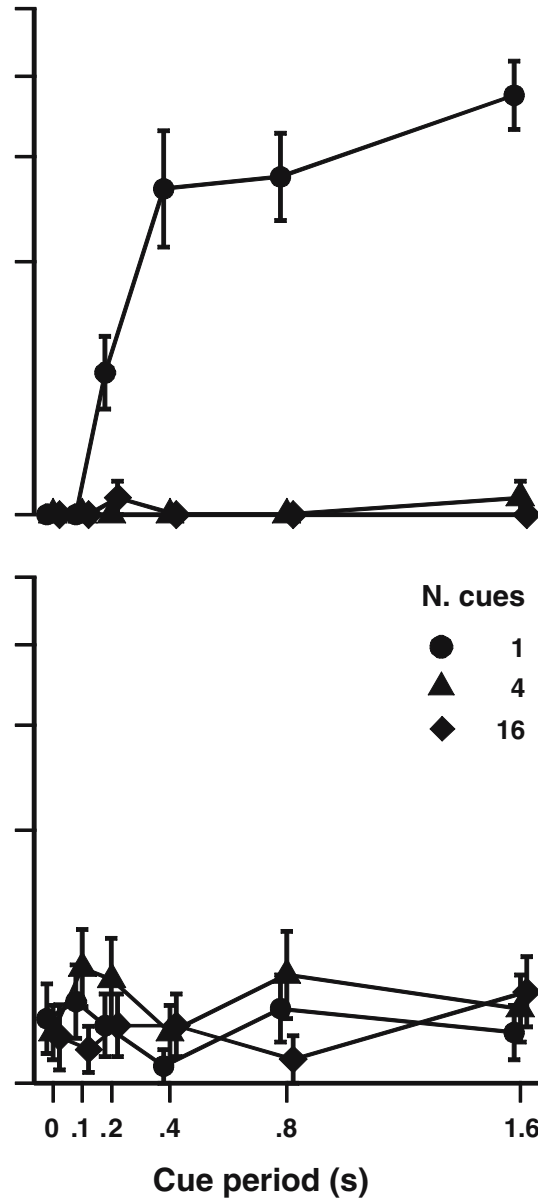


Fig. 4 Experiment 1: *top* average number of anticipated responses across subjects as a function of cue period for each number of cues condition. *Bottom* average number of directional errors across subjects as a function of cue period for each number of cues condition. In each plot the data for the different number of cues conditions were slightly shifted from each other along the abscissa to reduce the overlap of symbols. The vertical error bars indicate the standard error of the mean ($N=15$ subjects). Notice that the ordinate is a square-root scale

period $\times$ number of cues ($F_{(10,140)}=0.80$, $P=0.633$). Average MT across subjects is plotted against cue time in Fig. 5. It can be noticed in the figure that MT decreased abruptly between the 0 s cue period condition and the 0.1 s cue period condition, whereas for cue periods between 0.1 and 0.4 s, MT did not change noticeably. Finally, MT increased progressively between the 0.4 and 1.6 s cue period conditions.

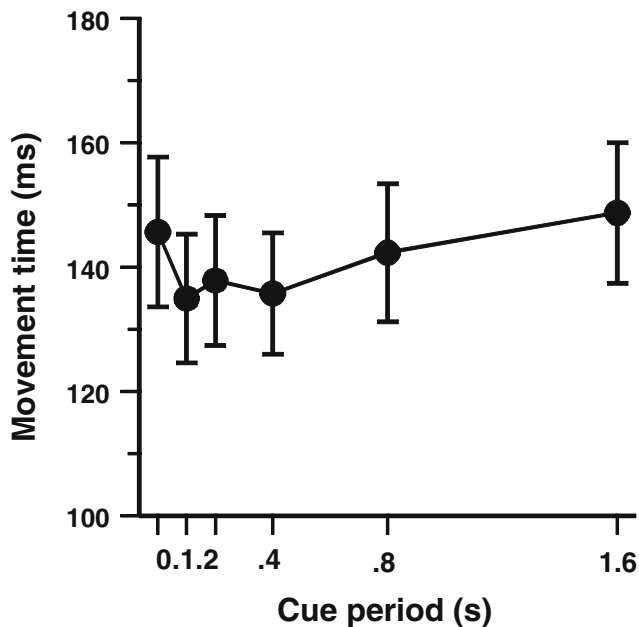


Fig. 5 Experiment 1: Average MT across subjects as a function of cue period. The vertical error bars indicate the standard error of the mean ($N=15$ subjects)

Initial direction of movement

The analysis of the average error of the initial direction of movement indicated that it was not significantly affected by the factors cue period ($F_{(5,70)}=0.82$, $P=0.543$), number of cues ($F_{(2,28)}=2.25$, $P=0.124$) or by their interaction ($F_{(10,140)}=1.38$, $P=0.196$). The average error of the initial direction of movement was 13.1° ($SE=0.4^\circ$, $N=15$ subjects). Similarly, the analysis of the standard deviation of the initial direction of movement did not reveal any significant effect of cue period ($F_{(5,70)}=0.85$, $P=0.517$), number of cues ($F_{(2,28)}=0.91$, $P=0.416$) or of their interaction ($F_{(10,140)}=1.61$, $P=0.111$). The average standard deviation of the initial direction of movement was 15.8° ($SE=0.6^\circ$, $N=15$ subjects). In addition, we investigated whether the initial direction of movement was biased by the average direction of the cues or by the direction of the cue closest to the target. This analysis was limited to trials from the condition with 4 cues in which the average direction of the cues and the closest cue to the target are unambiguously defined. For this purpose, we performed an analysis of covariance using the single trials with cue period and subject as factors and the angle between the direction of the target and the direction of the cues mean resultant as well as the angle between the target and the closest cue to the target as covariates. The results of the analysis did not reveal any significant effect of cue period ($F_{(5,1088)}=0.94$, $P=0.456$) and more importantly did not show any significant effect of the angle between target and cues mean resultant ($F_{(1,1088)}=1.81$, $P=0.179$) nor of the angle between the target and its closest cue ($F_{(1,1088)}=0.077$, $P=0.781$).

Path linearity

The analysis of the path linearity index indicated that the straightness of the response trajectory was not significantly affected by cue period ($F_{(5,70)}=0.83$, $P=0.532$), number of cues ($F_{(2,28)}=0.43$, $P=0.658$) or by the interaction cue period $\times$ number of cues ($F_{(10,140)}=0.91$, $P=0.525$). The average path linearity index across subjects was 0.12 ($SE=0.004$, $N=15$ subjects).

Number of directional errors

The number of directional errors was small in all conditions and for all subjects (see Fig. 4, bottom). The average number of directional errors per condition across subjects was 0.30 (standard error, $SE=0.09$, $N=15$ subjects). The analysis of the number of directional errors was performed on the square-root transformed counts (Snedecor and Cochran 1989) and it showed that there was no significant effect of cue period ($F_{(5,70)}=0.72$, $P=0.611$), number of cues ($F_{(2,28)}=1.22$, $P=0.312$) or of their interaction ($F_{(10,140)}=0.97$, $P=0.470$).

Discussion

We investigated the time-course of processing spatial information provided by discrete spatial cues regarding the direction of the upcoming directed response. The results showed that, in each number of cues condition, RT decreased sharply between the 0 s and the 0.2 s cue period conditions and that it leveled off with longer cue periods. The relation between RT and cue period was well described by an exponential decay function (Eq. 1). These results indicate that the motor preparatory process developed progressively and that it required over 0.2 s to stabilize.

In addition, the results showed that the level at which RT stabilized was a function of the number of cues: the larger the number of cues, the longer RT. These results indicate that a different level of motor preparation was achieved depending on the number of cues: it was the highest in the 1 cue condition and it decreased as the number of cues increased. This relation between RT and number of cues is consistent with the one found in a previous experiment (Pellizzer and Hedges 2003) and is well predicted by the capacity-sharing model mentioned in the Introduction. Moreover, the conclusions based on the analyses of RT are consistent with those reached with the analyses of the number of anticipated responses, which showed that subjects were more susceptible to initiate an anticipated response in the 1 cue condition and after a cue period of 0.2 s. In the 1 cue condition subjects could specify fully the response during the cue period thereby being ready to execute the response more promptly and occasionally in advance

from the target. In contrast, in the 4 and 16 cues conditions, the response could not be fully specify which explain that it was unlikely to be anticipated. However, after 0.2 s of cue period, the level of RT between the 4 and 6 cues conditions were different indicating that a different level of motor preparation was achieved in these two conditions.

The analyses of path linearity and the different analyses of directional error (i.e., number of errors and initial direction of movement) did not show any significant effect of conditions. In particular, it should be noticed that there was no statistical difference in response accuracy between the 1 cue condition and the other cue conditions, which indicates that the cues that were not the target did not influence significantly the direction of the response. This conclusion is consistent with the one reached in a previous experiment with similar cueing and response conditions (Pellizzer and Hedges 2003). These results suggest that subjects initiated their response only after it was sufficiently specified to reach the target within the spatial constraints defined in the task. Since responses were accepted only when they were in the direction of the target, there was no incentive to initiate the response before it was specified enough to meet the accuracy requirements. Therefore, RT was a reliable estimate of the time necessary for planning responses of similar accuracy across conditions.

In contrast, the analysis of MT indicated that it varied with cue period but not with number of cues. It could be that in some conditions, the response was partially specified during its execution thereby lengthening MT. However, the level of preparation of the response as indicated by RT changed both with cue period and number of cues, whereas MT changed only with cue period. This dissociation is not consistent with the hypothesis that the specification of the response was completed during its execution. Instead, the effect of cue period on MT could be an effect of the dynamic properties of the neuronal activity of the populations of neurons engaged during the preparation and the execution of a motor response.

Another result of the analyses on RT was that an effect of number of cues occurred also when there was no cue period. In other words, the effect of number of cues occurred even when subjects did not have time to process the information provided by the cues to prepare the response. These results force the question of whether a single factor can explain the effect of number of cues in all cue period conditions, which would rule out motor preparation as an explanatory cause, or whether different factors were at the origin of the effect of number of cues depending on cue period. The functional analysis of the relation between RT and number of cues suggested that the effect of number of cues on RT changed depending on the cue period condition. One type of effect on RT occurred when there was no cue period and was better described by a straight line function (i.e., linear) of number of cues. This effect can be interpreted as an

interference effect of the visual stimuli that are presented simultaneously with the target. This means that all the visual stimuli that are presented with the target are processed and the greater their number the greater their effect. The second type of effect on RT occurred in all the other cue period conditions and was better described by a curvilinear function (i.e., quadratic) of number of cues. This second type of relation is consistent with the relation predicted by the capacity-sharing model (Pellizzer and Hedges 2003).

The capacity-sharing capacity-sharing model assumes that the processing resources for motor planning are limited and that they can be distributed to prepare multiple responses in parallel (Pellizzer and Hedges 2003, 2004; Shaw 1978). These assumptions led to the prediction that average RT, $\overline{RT}$, is related to the number of cues, N_{CUES} , as follows:

$$\overline{RT} = a + b \left(1 - \frac{1}{N_{CUES}} \right), \quad (2)$$

where a and b are empirically determined constants. Eq. 2 is a negatively accelerated function, i.e., RT increases with N_{CUES} but with smaller steps as N_{CUES} increases. This prediction was tested in a previous experiment in which the factor number of cues was varied more systematically than in the current experiment and the results supported well the predictions (Pellizzer and Hedges 2003).

Since processing information is time-consuming, it was expected that the effect of motor preparation would become observable after some time following the presentation of the cues. The results show that the effect of motor preparation was observable after as little as 0.1 s and evolved over 0.2–0.4 s before stabilizing. On the other hand, the interference effect has different dynamic characteristics than the effect of the preparatory process. The results suggest that its effect is transient and occurs when visual stimuli are presented simultaneously with the target. In this perspective, it is suggested that the effect of number of cues originated from an interference effect in the no cue period condition, whereas it originated from the motor preparatory process when a cue period was present. The hypothetical effects of interference and of facilitation of the cues are confounded to some extent in experiment 1 since both effects predict an increase of RT with an increase of number of cues. Consequently, we sought to test more specifically the presence of facilitation and interference effects in a second experiment.

Experiment 2: effects of number of cues and number of distractors

In this experiment, we varied inversely the number of cues and the number of distractors with the purpose of putting their respective hypothetical effects into opposition. Spatial cues were presented for a duration long

enough for the subjects to process the information, whereas distractors were presented simultaneously with the target to maximize their effect of interference. These distractors were formed of stimuli identical to the cues and they were presented in the interstices between the cues, which resulted in an ensemble of contiguous visual stimuli of which one was the target (Fig. 1a, bottom). As a consequence, the resulting visual display when the target appeared was the same across conditions regardless of the numbers of cues and distractors. Therefore, any effect on RT in experiment 2 can be attributed only to the number of cues and/or to the number of distractors but not to the total number of stimuli present on the screen when the response was made.

Furthermore, the effect of number of cues and distractors on RT can be predicted quantitatively. Considering that the effect of cues on the planning of directed movements was well described by Eq. 2 (Pellizzer and Hedges 2003) and that the hypothetical effect of interference in experiment 1 was better described by a first-degree polynomial with respect to the number of stimuli, it is possible to predict how RT should vary across conditions in experiment 2. Indeed, if the effect of facilitation of the cues and the effect of interference of the distractors are independent, then average RT is the linear combination of the two effects, that is:

$$\overline{RT} = a + b \left(1 - \frac{1}{N_{\text{CUES}}} \right) + c N_{\text{DISTRATORS}} \quad (3)$$

where a , b and c are empirically determined parameters. Therefore, in experiment 2 we tested the respective contribution of number of cues and of number of distractors by testing how the data were fitted by Eq. 3. Since the number of cues and the number of distractors were made to vary in opposite directions, their effects were expected to counter each other, which, according to Eq. 3, should produce a non-monotonic change of RT across conditions.

In addition, we included a detection task as a control in which the same stimuli presentation was used but subjects had to release a push-button when the target appeared. The detection task will indicate whether the effects obtained in the directed response task are dependent on the subjects planning a directed movement or whether these effects are related to a general spatial attention process engaged similarly by directed and non-directed motor responses.

Methods

Subjects

Fifteen subjects participated in this experiment (11 males and 4 females; age range: 19–37 years). Eleven subjects had participated previously in experiment 1. All subjects signed an informed consent. The experimental protocol was approved by the Institutional Review Board of the

Minneapolis VAMC. Subjects participated in both the directed response task and the detection task. The order of the tasks was assigned randomly.

Apparatus

For the directed response task, the experimental setup was identical to the one described for experiment 1. For the detection task, the joystick was replaced by a push-button.

Procedure

The procedure was similar to that described for experiment 1, therefore only the specific aspects of experiment 2 are described here. After a 1 s center-hold period, $N = 1, 2, 4, 8$ or 16 cues were presented. The direction of each cue was randomly selected around the center with the constraint that multiple cues were at an integer multiple of 22.5° of interval from each other. The duration of the cue period varied randomly between 0.5 and 1 s. The target was presented simultaneously with visual distractors. The visual stimuli used as distractors were circles identical to the spatial cues and were positioned on the circle in the interstices between cues; therefore the cues plus the distractors formed a ring of 16 contiguous stimuli around the center of the screen. Consequently, the number of distractors changed inversely with the number of cues (i.e., $N_{\text{DISTRATORS}} = 16 - N_{\text{CUES}}$). The example of a trial is sketched in Fig. 1a (bottom). The constraints on gaze fixation were identical to those described for experiment 1. The required motor response in the directed response task was as described for experiment 1, whereas in the detection task subjects had to push on the push-button to start the trial and then had to release the button as soon as they detected the target. Twelve correct repetitions per cue condition were obtained for each subject in each task.

Results

Reaction time

Directed response task: Average RT across subjects is plotted against condition in Fig. 6. The analysis of variance indicated that RT was significantly affected by condition ($F_{(4,56)} = 13.78$, $P < 0.0005$). As can be seen in Fig. 6 (top), RT changed in a non-monotonic way across conditions. We evaluated the least-squares fit of Eq. 3 to the data using a model with $1 - 1/N_{\text{CUES}}$ and $N_{\text{DISTRATORS}}$ as covariates and Subject as ‘dummy’ variable (Rutherford 2001). The results show that the model fitted the data well ($R^2 = 0.801$, $F_{(16,58)} = 14.56$, $P < 0.0005$). That is, Eq. 3 provided a good description of the non-monotonic change of RT across conditions. The fitted line is plotted across the data points at the top

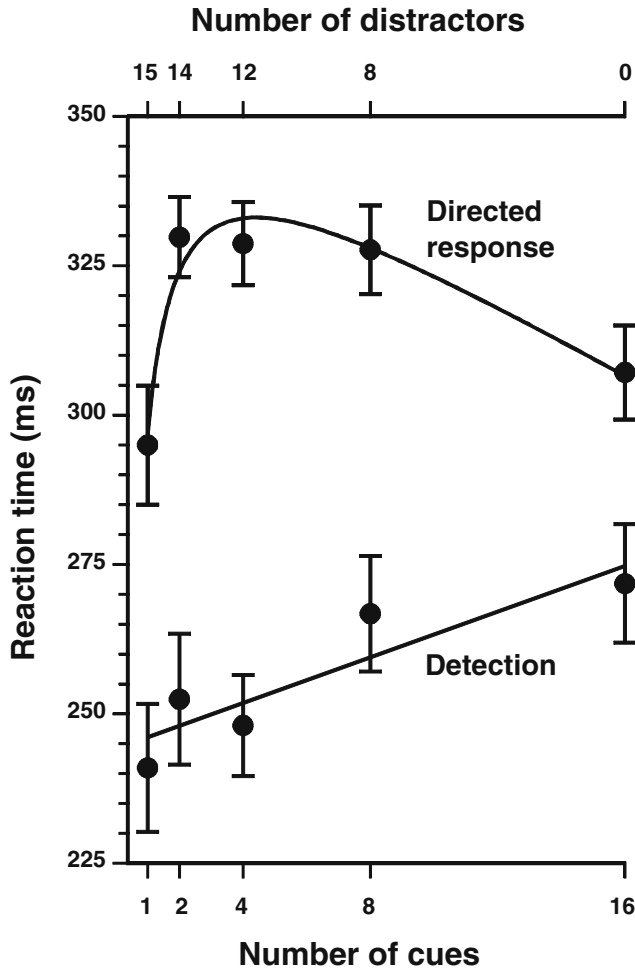


Fig. 6 Experiment 2: average RT across subjects for each condition and task. The vertical error bars indicate the standard error of the mean. The solid line passing through the data points of the directed response task is the least-squares fit of Eq. 3

of Fig. 6. In addition, the analysis of covariance showed that the parameter of Eq. 3 associated with the facilitation effect of the cues (parameter b in Eq. 3) and the parameter associated with the interference effect of the distractors (parameter c in Eq. 3) were both significant ($F_{(1,58)} = 50.55$, $P < 0.0005$ and $F_{(1,58)} = 34.73$, $P < 0.0005$, respectively). The estimated parameters of Eq. 3 were $a = 249.6$ ms (SE = 10.0 ms), $b = 60.8$ ms (SE = 8.5 ms) and $c = 3.1$ ms (SE = 0.5 ms). The least-squares fitted model is plotted in Fig. 6 as a line passing through the data of the directed response task. In addition, the fitted model is plotted in Fig. 7 with the components related to the effect of the cues and to the effect of the distractors.

We tested whether the group of subjects that participated in experiment 1 had significantly different results than the group of subjects who did not participate in that experiment, which could indicate a carry-over effect or a practice effect. The ANOVA showed that there was no significant effect of group ($F_{(1,12)} = 0.30$, $P = 0.865$) and no significant effect of the interaction group $\times$ condition ($F_{(4,48)} = 0.332$, $P = 0.855$).

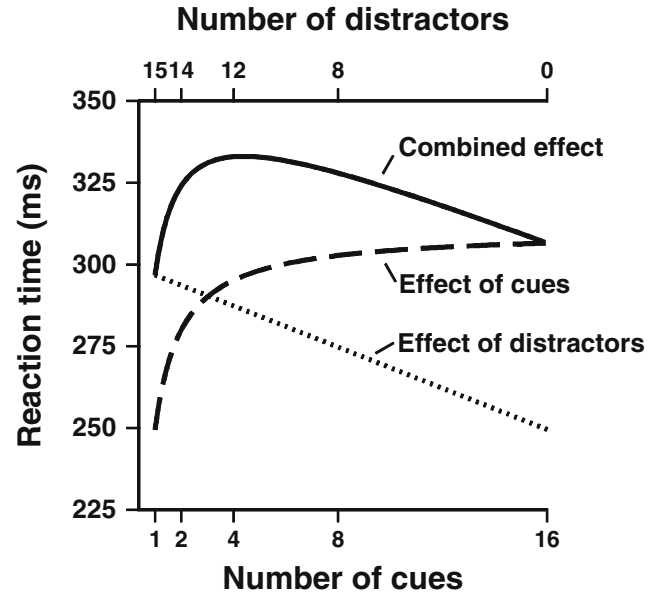


Fig. 7 Experiment 2: components of Eq. 3 related to the effects of the cues and of the distractors on RT of the directed response task. The combined effect is the same function that is plotted in Fig. 6 for the directed response task

Detection task: Average RT across subjects is plotted against condition also in Fig. 6. The analysis of variance indicated that RT was significantly affected by condition ($F_{(4,56)} = 5.40$, $P = 0.001$). However, in contrast to the results found in the directed response task, detection RT changed monotonically across conditions. Orthogonal polynomial contrasts indicated that the linear trend was significant ($F_{(1,14)} = 10.38$, $P = 0.006$) and that no deviation from linearity was significant (quadratic: $F_{(1,14)} = 1.62$, $P = 0.224$; cubic: $F_{(1,14)} = 0.487$, $P = 0.497$; order 4: $F_{(1,14)} = 2.92$, $P = 0.109$). We computed the least-squares fit of a straight line through the data points using a model with N_{CUES} as covariate and Subject as ‘dummy’ variable (Rutherford 2001). The results indicate a good fit of the line to the data ($R^2 = 0.758$, $F_{(15,59)} = 12.31$, $P < 0.0005$). The fitted line is plotted across the data points at the bottom of Fig. 6 (Intercept: 244.1 ms, SE = 3.8 ms; Slope: 1.914 ms, SE = 0.459 ms).

Anticipated responses

Directed response task: The average number of anticipated responses is plotted against condition in Fig. 8 (top). The analysis of variance of the number of anticipated responses was performed on the square-root transformed counts (Snedecor and Cochran 1989). The results indicated that there was a significant effect of condition ($F_{(4,56)} = 21.12$, $P < 0.0005$). Similarly to the results found in experiment 1, subjects produced more anticipated responses when there was 1 cue than in any other condition (all Dunnett tests with $P < 0.0005$).

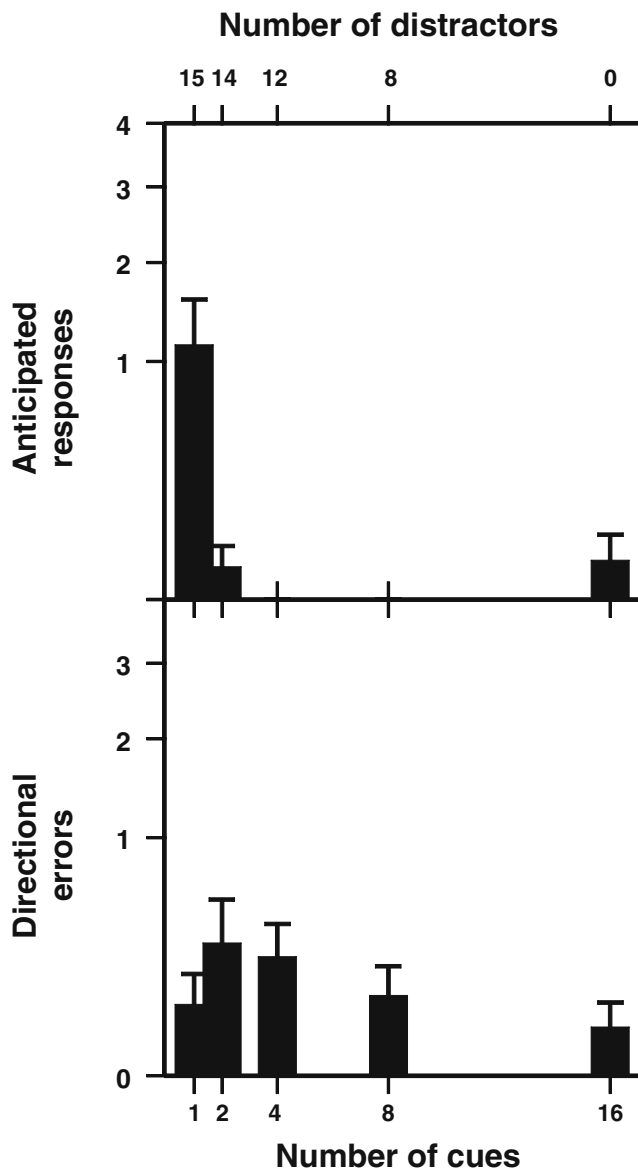


Fig. 8 Experiment 2: *Top* average number of anticipated responses across subjects for each condition. *Bottom* average number of directional errors across subjects for each condition. In each plot the data for the different number of cues conditions were slightly shifted from each other along the abscissa to reduce the overlap of symbols. The vertical error bars indicate the standard error of the mean ($N=15$ subjects). Notice that the ordinate is a square-root scale

Detection task: The number of anticipated responses did not change significantly across conditions ($F_{(4,56)} = 1.01$, $P = 0.408$). The average number of anticipated responses across subject was 0.36 ($SE = 0.10$, $N = 15$) per condition.

Movement time

Directed response task: The analysis of variance showed that there was no significant effect of condition on MT

($F_{(4,56)} = 0.96$, $P = 0.435$). Average MT across subjects was 168.2 ms ($SE = 15.6$, $N = 15$ subjects).

Initial direction of movement

Directed response task: The analysis of the average error of the initial direction of movement showed that it was not significantly affected by condition ($F_{(4,56)} = 1.28$, $P = 0.290$). The average error of the initial direction of movement was 13.7° ($SE = 0.8^\circ$, $N = 15$ subjects). The standard deviation of the initial direction of movement was not significantly affected by condition either ($F_{(4,56)} = 1.52$, $P = 0.209$). The average standard deviation of the initial direction of movement was 16.1° ($SE = 0.8^\circ$, $N = 15$ subjects).

Path linearity

Directed response task: The analysis of the path linearity index indicated that the straightness of the response trajectory was not significantly affected by condition ($F_{(4,56)} = 1.23$, $P = 0.310$). The average path linearity index across subjects was 0.15 (standard error, $SE = 0.006$, $N = 15$ subjects).

Number of directional errors

Directed response task: The average number of directional errors is plotted against condition in Fig. 8 (bottom). The analysis of variance of the number of directional errors was performed on the square-root transformed counts (Snedecor and Cochran 1989). The results indicated that there was no significant effect of condition on the number of directional errors ($F_{(4,56)} = 1.19$, $P = 0.324$). The average number of directional errors across subjects was 0.43 ($SE = 0.10$, $N = 15$ subjects) per condition.

Discussion

We tested the hypothesis that two factors affect independently the time-course of planning directed movements after the presentation of discrete visual stimuli. More specifically, we assumed that discrete spatial cues presented long enough before the target can be used to prepare, at least partly, the upcoming directed response and therefore facilitate motor planning, whereas cues presented simultaneously with the target act as distractors and therefore interfere with the planning of the movement. However, in both of these cases an increase of the number of stimuli is associated with an increase of RT (see experiment 1). Therefore, in experiment 2 we dissociated these effects. By varying inversely the number of cues presented before the target and those presented simultaneously with the target, we expected their respective effects to oppose each other. In

addition, the two factors were assumed to be independent which, by using the results obtained in experiment 1 as well as in previous work (Pellizzer and Hedges 2003), led to Eq. 3. The results from experiment 2 showed that the profile of RT in the directed response task was well described by Eq. 3, which, therefore, supports the hypothesis that two time-dependent factors associated with the number of visual stimuli affected independently the planning of directed movements (see Fig. 7). In addition, the analyses of path linearity, directional error and MT did not show any significant effect of condition. Therefore, the results did not indicate any speed-accuracy tradeoff effect that could explain changes of RT across conditions.

The effect of condition in the detection task contrasted with the effect in the directed response task. In the detection task, RT changed monotonically across condition, whereas in the directed response task RT changed non-monotonically across conditions. The detection task was used as a control to test whether the effects of cues and distractors were dependent on the type of motor response planned or whether they could be related to a general spatial attention process. Since in the detection task and in the directed response task the visual stimuli were the same but the responses were different, the differential effects of the tasks on RT must be related to the different responses. In the detection task, the response was always the same and could be planned in advance, whereas in the directed response task, the response was conditioned by the target. In other words, the results indicated that the effects obtained in the directed response task are dependent on the subjects planning a directed movement and, therefore, reject the hypothesis that these effects could result from a general process of spatial attention.

General discussion

As the number of spatial cues increases, the information about the location of the upcoming target decreases. If subjects use this information to prepare the motor response, then the amount of information available should affect motor preparation. Accordingly, in experiment 1 the reaction time of directed movements increased with number of cues. This indicates that the level of motor preparation was dependent on the number of alternative responses indicated by the cues. In a previous work, we found that a capacity-sharing model of motor planning predicted well the quantitative effects of number of cues on RT (Pellizzer and Hedges 2003). This model assumes that processing resources are limited and that they can be shared to represent multiple responses in parallel. Therefore, as the number of alternative responses increases, the amount of preparation for each alternative response decreases which has the consequence to lengthen the latency of response once the movement goal is selected.

Neural activity in multiple motor-related structures of the monkey central nervous system represents aspects of the upcoming directed response during instructed-delay tasks, including multiple cortical areas (see Battaglia-Mayer et al. 1998 for a review), basal ganglia (Alexander 1987; Jaeger et al. 1993) and spinal interneurons (Prut and Fetz 1999). It was shown that the patterns of neural activity in several motor-related cortical areas during a movement preparatory period change depending on the type of information provided (Miller et al. 1992; Riehle and Requin 1995). In addition, it has been found using a saccade task in the monkey that the level of activity of neurons of the superior colliculus decreased as the number of cues presented increased (Basso and Wurtz 1998). Furthermore, Cisek and Kalaska (2005) have shown, using a two cues instructed-delay task, that the activity of neurons in the most rostral part of the dorsal premotor cortex represented the two potential targets before the target was specified. These studies are consistent with the idea that the level of motor preparation varies with the number of alternative motor responses and that multiple responses can be represented in parallel before one is selected.

In addition, we found that motor preparation evolved gradually and took over 0.2 s to stabilize at a level determined by the number of cues. Similar conclusions were reached by Ghez and colleagues using the timed response paradigm (Favilla 1997; Ghez et al. 1997). In this paradigm subjects were instructed to make a targeted response in synchrony with a timed signal at various delays after the presentation of the target, thereby forcing subjects to respond with various amount of processing of the information provided by the target. It was found that the specification of the response evolved progressively for a period of 0.2 s or more after target presentation. In these experiments, subjects were instructed to respond even if the response was not accurate. In contrast, in the experiments presented here subjects had to respond accurately toward the target for the response to be valid. This constraint forced subjects to initiate their response only after it was sufficiently specified and the results on movement trajectory and directional errors indicate that it was the case. Despite the methodological differences both types of experiment suggest that the neural network engaged during the planning of directed movements take over 0.2 s to engage and reach a stable pattern of activity. The results of experiment 1 showed that the time to reach a stable level of motor preparation is very similar for different levels of information provided by the cues.

In addition, the results from experiment 1 showed that the effect of number of cues occurred even when there could not have been any preliminary processing of information about the location of the target. Therefore, we hypothesized that there are two effects of number of cues on RT that have different dynamic characteristics: a transient effect of interference produced when visual

stimuli are presented and a slower evolving and sustained effect of facilitation resulting from processing the information provided by the cues. The effect of facilitation results from processing the information provided by the cues as discussed above, whereas, the interference effect might be produced by the brief capture of attention triggered by abrupt stimuli onsets (Castiello 2001; Corneil and Munoz 1996; Remington et al. 1992; Riggio et al. 1998).

Experiment 2 was designed to dissociate the effects of facilitation and interference of the visual stimuli. Cues were presented 0.5–1 s before the target, whereas distractors were presented simultaneously with the target. In addition, the number of distractors varied inversely with the number of cues with the purpose of opposing their respective hypothetical effect. We predicted that RT of directed movements would follow a non-trivial profile across condition described by Eq. 3. We found that the results supported the predictions. Therefore, the delay between the presentation of visual cues and the onset of the target determines whether these stimuli facilitate or interfere with the initiation of the directed response. The results suggest also that these two effects acted independently on the onset of directed movements. The neural substrate of the facilitatory effect has been investigated and has been documented across several motor-related areas, as mentioned above. In contrast, the neural substrate of the effect of interference described here is much less well understood. These two effects could be mediated by separate motor-related brain areas projecting on the spinal cord. For example, corticospinal axons originate, not only from the primary motor cortex, but also from dorsal and ventral premotor cortex, the supplementary motor area and several cingulate areas (Dum and Strick 2002).

Finally, the results of experiment 2 clearly showed different effects between the directed response task and the detection task. A similar dissociation was also found in other experiments (Adam and Pratt 2004; Crawford and Muller 1992; Hodgson et al. 1999; Pellizzer and Hedges 2003). Since the visual stimuli were the same in the two tasks, the differentiation must be related to the type of motor response required. In the detection task the motor response does not vary with the target and therefore, it can be prepared in advance and released as soon as the target is detected. In contrast, in the directed response task, the motor response is determined by the target and therefore it needs to be specified before the response is executed. Therefore, the effects observed are not the result of a general process of allocation of attention in space. Instead, these effects are dependent on the type of motor response required in the task, and, in particular on the spatial requirement on the motor response.

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