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RESEARCH ARTICLE

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Motor planning: effect of directional uncertainty with discrete spatial cues

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Abstract We investigated the effect of spatial uncertainty on motor planning by using the cueing method in a reaching task (experiment 1). Discrete spatial cues indicated the different locations in which the target could be presented. The number of cues as well as their direction changed from trial to trial. We tested the adequacy of two models of motor planning to account for the data. The switching model assumes that only one motor response can be planned at a time, whereas the capacity-sharing model assumes that multiple motor responses can be planned in parallel. Both models predict the same relation between average reaction time (RT) and number of cues, but they differ in their prediction of the shape of the distribution of the reaction time. The results showed that RT increased with the number of cues independently from their spatial dispersion. This relation was well described by the function predicted by both models, whereas it was poorly described by the Hick-Hyman law. In addition, the distribution of RT conformed to the prediction of the capacity-sharing model and not to that of the switching model. We investigated the role that the requirement of a spatially directed motor response might have had on this pattern of results by testing subjects in a simple RT task (experiment 2) with the same cueing presentation as in experiment 1. The results contrasted with those in experiment 1 and showed that RT was dependent on the spatial dispersion of the cues and not on their number. The results of the two experiments suggest that the mode of processing of potential targets is dependent on the spatial constraints of the task. The processing resources can be either divided relative to the spatial distribution of possible targets or across multiple independent discrete representations of these targets.

Keywords Motor preparation · Reaching · Choice reaction time · Hick-Hyman law · Cueing · Processing capacity

Introduction

The ability to respond promptly to environmental events is strongly enhanced by the possibility to anticipate the preparation of the appropriate action. The amount of prediction and preparation of a motor response depends on the information available about the required response (Rosenbaum 1980). In particular, motor preparation is dependent on the extent of the set of possible motor responses.

It is known since the early work of Merkel that choice reaction time (RT) increases with the number of possible responses (Luce 1986). Although the respective contribution of the number of stimuli and of the number of responses can be dissociated (Bernstein et al. 1967), we consider here only the case where both coincide. The relation between RT and number of alternative responses is often described using the Hick-Hyman law, which states that average RT is linearly related to uncertainty (Hick 1952; Hyman 1953). When the alternative responses are equiprobable, the response uncertainty is defined as the base 2 logarithm of the number of possible responses N, therefore according to the Hick-Hyman law:

$$\overline{RT} = a + b\mathrm{Log}_2(\mathrm{N}) \tag{1}$$

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where a and b are empirically determined constants. However, the relation between RT and number of alternative responses does not always obey the Hick-Hyman law (Longstreth et al. 1985; Teichner and Krebs 1974). In particular, this relation is sensitive to factors such as the degree of compatibility between stimulus and response (Brainard et al. 1962; Teichner and Krebs 1974). For example, it was found in conditions in which stimuli and motor responses were highly spatially compatible that RT was either not related or only weakly related to the number of possible responses (Bock and Eversheim 2000; Broadbent and Gregory 1965; Dassonville et al. 1999; Leonard 1959; Longstreth et al. 1985).

We tested two models of motor planning (viz., switching model and capacity-sharing model) that relate RT to the number of possible motor responses. These models predict a different relation between RT and number of alternative responses than the Hick-Hyman law. The switching model assumes that only one motor response can be planned at a time, whereas the capacity-sharing model assumes that multiple motor responses can be planned in parallel. These models were tested using a reaching task in which discrete spatial cues indicated the different locations in which the target could be presented. The number of cues as well as their direction changed from trial to trial and the set of possible motor responses varied accordingly.

Switching model

The switching model is based on the assumption that only one motor response can be intended at a time. In the context of a reaching task with spatial cues, as used in the present experiment, this model assumes that subjects get prepared to move toward one of the cues during the cue period of the task. Whether they select only one of the possible responses or whether they consider different responses alternately during the cue period is not critical here, the important point is that a single motor response is planned at any time. Therefore, there are two possibilities when the target appears, either it is in the location corresponding to the planned motor response or it is in a different location. In the first case, subjects execute the response as planned (i.e., no switch) which takes an amount RT_{NS} to initiate. In contrast, in the second case they have to switch the intended movement, which takes an additional amount of time T_S, therefore RT in this case is:

$$RT_S = RT_{NS} + T_S. \tag{2}$$

A sketch of this model for a two-cue condition is illustrated in Fig. 1 (top). The implication of the switching model is that the distribution of RT, $F(RT)$, is a two-component mixture composed of a distribution $F_{NS}(RT)$ of no-switch trials and a distribution $F_S(RT)$ of switch trials. If each cue has an equal probability to be the target, the probability p_{NS} to be prepared to respond toward the target and the probability p_S to need to switch motor plan are:

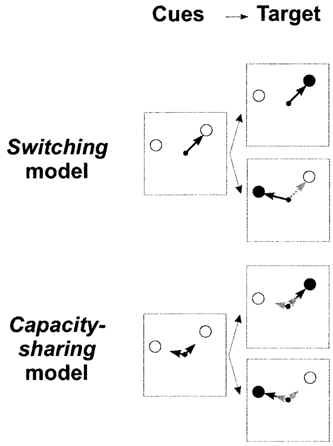

Fig. 1 Schematic illustration of the switching and the capacity-sharing models in a condition with two alternative responses. The two alternative responses are identified by two cues. Subsequently, the target, which appears at one of the cued locations, determines the expected response. The *black arrow* within each inset symbolizes the representation of the direction of response during the preparation and at the onset of the execution of the motor response. *Top*: switching model. One of the alternative responses is prepared before the target is presented. One row illustrates the case where the intended motor response coincides with the direction of the target (i.e., no switch), whereas the other row illustrates the case where the intended motor response has to switch from one direction to the direction of the target. *Bottom*: capacity-sharing model. The processing capacity for motor preparation is shared across the possible responses so that each direction is partially represented. After the target is presented, all the resources are allocated to the representation of the selected motor response

$$p_{NS} = \frac{1}{N} \quad \text{and} \quad p_S = 1 - p_{NS} \tag{3}$$

respectively. The mixture distribution $F(RT)$ is the linear combination of the component distributions weighted by their respective probabilities:

$$F(RT) = p_{NS}F_{NS}(RT) + p_S F_S(RT). \tag{4}$$

The mean RT of the mixture distribution $F(RT)$ is similarly defined (Yantis et al. 1991):

$$\overline{RT} = p_{NS}\overline{RT}_{NS} + p_S\overline{RT}_S. \tag{5}$$

Using the definitions (Eq. 2–4), this relation can be written as:

$$\overline{RT} = a + b\left(1 - \frac{1}{N}\right), \tag{6}$$

where

$$a = \overline{RT}_{NS}$$

and

$$b = \bar{T}_S$$

That is, mean RT corresponds to the average latency of no-switch responses plus the average duration of switching motor plan weighted by the probability that a switch occurs.

Therefore, the switching model predicts a specific relation between mean RT and number of cues that is different from the Hick-Hyman law (Eq. 1). In addition, it predicts that the distribution of RT is a two-component mixture. This switching model has been used to describe the results in perceptual choice reaction time tasks (Longstreth et al. 1985). In addition, a switching mechanism of motor intention was described from the pattern of activity of motor cortical neurons when a monkey had to select a response among several alternatives in a memory-scanning task (Pellizzer et al. 1995).

Capacity-sharing model

In contrast with the serial nature of the switching model in which only one motor response can be intended at a time, the capacity-sharing model includes the possibility that several motor responses be prepared in parallel. The two central assumptions of the capacity-sharing model are that (1) the processing resources available for motor planning can be distributed to prepare multiple responses concurrently and that (2) the strength of the representation of a given motor response is a function of the amount of resources allocated to it. Additional assumptions are necessary in order to infer a functional relation between RT and number of cues. The assumptions made here are that (1) the amount of resources R available for motor planning is constant, (2) if the alternative responses are equiprobable, the amount of resources is divided equally among them, therefore the amount r allocated to a given alternative response is:

$$r = \frac{R}{N}, \tag{7}$$

(3) when the motor response is eventually selected, the total amount of processing resources R is allocated to it, and (4) the time t to change the amount of resources allocated to a given response from the level r to the total amount R is proportional to the difference between the two levels, that is:

$$t = T\frac{(R - r)}{R}, \tag{8}$$

where T is a time constant.

In other words, this means that when there is only one cue, all the resources are allocated to prepare the response associated with it, which means that t=0. Therefore, when the target appears, the response can be executed as planned, which takes an amount say RT_1 to initiate. On the other hand, when there is more than one cue, the resources are divided among the alternative responses. The consequence of sharing resources is that the strength of the representation of each alternative response decreases: the higher the number of alternatives, the weaker their representation (Eq. 7). Therefore, when the target appears, an additional time t is necessary to allocate all the resources to the required response, that is:

$$RT = RT_1 + t. \tag{9}$$

Using the definitions (Eq. 7–8) and assuming that the variables are stochastic, this relation is equivalent to Eq. 6 with

$$a = \overline{RT}_1$$

and

$$b = \overline{T}$$

A sketch of this model for a two-cue case is illustrated in Fig. 1 (bottom). Models similar to the capacity-sharing model have been proposed for visual search (Shaw 1978) and for visual stimuli identification tasks (Eriksen and Yeh 1985).

In summary, each model makes two explicit predictions about the data. One about how the average RT changes as a function of the number of cues and the other about the number of components determining the distribution of RT. Despite the fact that the two models are based on very different assumptions, they predict the same relation between average RT and number of cues. However, they differ in their predictions about the distribution of RT. As shown above, the switching model predicts that the distribution of RT is a two-component mixture, where the relative weight of each component changes with the number of cues. In contrast, the capacity-sharing model is a single-component model, in which it is assumed that its duration varies with the number of cues. Therefore, the capacity-sharing model predicts that the distribution of RT is a single-component distribution regardless of the number of cues. In addition, both models predict that RT depends on the number of cues but not on their spatial distribution. In this study we opted to test primarily these versions of the models as alternatives to the Hick-Hyman law, which relates RT to the number of alternative responses. However, other switching models or capacity-sharing models could be constructed that predict a dependence of RT with the spatial distribution of the cues. Each of these predictions has been explicitly tested in a reaching task using the cueing method (experiment 1). Spatially discrete cues displayed on a screen indicated the locations in which the target could appear. Subjects had to fixate the center of the screen before and during the cue period. When the target was presented, subjects had to move a cursor from the center of the screen to the target using a joystick as quickly and accurately as possible. The path of the motor response had to be within determined spatial limits for the response to be counted as correct.

In addition, we used a simple RT task as control experiment (experiment 2). In the simple RT task, cues were presented as in the reaching task. However, when the target was presented, the response required was always the same (viz., release of a push-button). Therefore, in contrast to the reaching task, the simple RT task did not require the selection of a spatial response in relation to the target.

Methods

Experiment 1: reaching task with discrete spatial cues

Subjects

Fifteen human adult subjects took part in this experiment (11 males and 4 females, age range: 19–37 years). All were naive relative to the purpose of this study. Subjects used their preferred hand to respond (12 subjects used their right hand and 3 their left hand). A signed informed consent was obtained from each subject. The experimental protocol was approved by the Institutional Review Board of the Veterans Affairs Medical Center (Minneapolis, MN).

Apparatus

A personal computer was used to control the display of stimuli on a 14-in. color monitor and to record the position of the joystick and the direction of gaze in real time. The two-dimensional coordinates of the position of the joystick, which were sampled at a 200-Hz frequency, determined the position of a red cursor on the monitor. The direction of gaze was processed at a 60-Hz frequency using a video-based tracking system (Iscan Inc., Burlington, Mass., USA). The digital coordinates of gaze direction were transformed into an analog signal and sampled at 200 Hz in synchrony with the sampling of the joystick position. The monitor was refreshed at 60 Hz.

Procedure

Subjects were seated in front of the monitor with the head against a chin rest. The center of the monitor was at eye level and the distance between the eyes of the subjects and the monitor was 45 cm. The vertically oriented joystick was placed in the midsagittal plane of the subject and at a comfortable location to be grasped. The direction of gaze was calibrated before each task.

Subjects initiated a trial by placing the red cursor within a circular window (radius=0.3° of visual angle) in the center of the display for a 1-s center-hold period. This was followed by a cue period randomly varying between 0.5 and 1 s, after which the target was presented. The target was a white disc of 0.75° radius of visual angle and was presented at 4° of visual angle from the center of the display. During the cue period a number of white circles indicated the locations at which the target could appear. These circles were the size of the target and they were located at 4° of visual angle from the center. The number of cues presented were n=1, 2, 4, 8, or 16. In one-sixth of the trials no cue was presented during the cue period. Trials from the different conditions were randomly mixed. We did not use a small set of fixed directions, neither for the cues nor for the target. In each trial, cues were randomly selected in any of the 360° directions around the center. Since the target was randomly selected from any cue, the target could be also in any direction. When multiple cues were presented, they could be at any angle from each other but they could not overlap. When 16 cues were present, they were contiguous and covered the 360° circular range. The presentation of the target consisted in filling one of the cues. When more than one cue was present on the screen, the cues that were not the target remained on the screen after target onset.

Subjects were instructed to fixate the center of the display during the center-hold and cue periods and they were informed that they could move their eyes after the target presentation. Any gaze displacement outside a center window of 2° radius during the center-hold and cue period aborted the trial. However, gaze direction was not constrained after the presentation of the target. The subjects were instructed to move the cursor as quickly as possible from the center to the location of the target as soon as the target appeared. They were informed that the trajectory of the cursor had to stay within unseen straight boundaries from the center to the target, otherwise it was counted as a movement direction error. The boundaries formed a straight path that matched the width of the target. The cursor had to stop on the target for at least 500 ms. The reaction time was defined as the time elapsed between the onset of the target and the exit of the cursor from the center window. Reaction times shorter than 100 ms or longer than 2000 ms were counted as reaction time errors. When an error occurred, a trial of the same cue condition was presented again at a random position in the sequence of the remaining trials. Subjects received a feedback every 30 trials about the overall average reaction time of the correct trials done up to that point. Twelve correct repetitions per cue condition were obtained for each subject. A schematic example of the task is illustrated in Fig. 2A, and the coordinates of the cursor and gaze direction during one trial of the task are plotted in Fig. 2B. Before the experimental trials, subjects did 30–50 practice trials in order to get familiar with the task and, in particular, with the constraints on gaze direction and on movement trajectory.

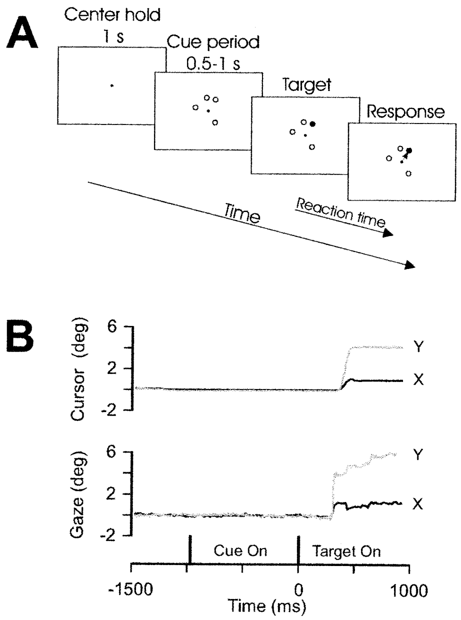

Fig. 2 A Schematic example of the reaching task (experiment 1). The subjects controlled a cursor on a screen using a joystick. They had to place the cursor in the center window during a 1-s period to initiate a trial (center-hold period). This was followed by a randomly variable delay of 0.5–1 s in which the subjects were cued about the possible location of the upcoming target (cue period). The number of cues was either n=0, 1, 2, 4, 8, or 16. Subjects had to fixate the center of the screen during the center-hold and cue periods. When the target was presented at one of the cued locations, the subjects had to respond by moving the cursor from the center to the location of the target. The trajectory of the cursor had to stay within an unseen straight path from the center to the target. **B** Time-varying X and Y coordinates of the cursor and gaze direction in one trial of the task. The *vertical lines* on the abscissa indicate the onset of the cues and the onset of the target. The units of the ordinates are degrees of visual angle with the center of the screen corresponding to 0°

Data analyses

Data were analyzed using standard statistical techniques (Snedecor and Cochran 1989; Sokal and Rohlf 1995). Directional variables were processed using directional statistics (Mardia and Jupp 2000). In all analyses, effects that had a $P<0.05$ were considered significant. ANOVA and ANCOVA analyses of RT data were performed using a within-subject univariate model using all correct repetitions. In contrast, for the functional analysis of the relation between average RT and number of cues as predicted by the models, we performed regression analyses in which we used the average RT across repetitions for each condition and subject. For this purpose we computed the harmonic mean of RT, which is robust to outliers and has been shown to be reliable under various distribution conditions (Ratcliff 1993). To determine the effect of cueing, we compared the data from each condition in which a cue was presented with the data in the no cue condition using Dunnett multiple comparisons test (Dunnett 1955). The ANOVA, ANCOVA, and regression analyses were implemented using the GLM procedure from SPSS (release 10.0, SPSS Inc., Chicago, Ill., USA).

The analysis of the shape of the distribution of RT was performed by pooling the individual distributions using the vincentization method (Ratcliff 1979). This is a pooling method that preserves the shape of the individual distributions provided that they belong to the same family of distributions (Ratcliff 1979; Genest 2000). For this purpose, we ranked the 12 repetitions of RT in ascending order for each subject in each condition. Each rank *i* was given the value of (*i*- 0.5)/12 percentile. The vincentized distribution of RT for each condition was obtained by averaging the RT from each percentile across subjects.

In addition, we have analyzed the frequency of the following three types of errors: (1) anticipated responses, which were defined as responses that were initiated either during the cue period or in the initial 100 ms after target onset, (2) eye fixation errors, which occurred when an eye movement was made during the cue period, and (3) directional errors, which corresponded to trials in which the response trajectory did not stay within the path boundaries between the center and the target. Since these analyses were made on counts of errors, the averages and statistical analyses were computed using square-root transformed values to stabilize their variance (Snedecor and Cochran 1989).

Besides the number of movement direction errors, we have also analyzed the signed error of the initial movement direction. The initial movement direction was defined as the direction of movement between the moment when the acceleration exceeded a threshold of 5% of maximum acceleration and the moment of the first maximum of acceleration. The analyses on the error of the initial movement direction were made using correct trials and directional error trials to prevent introducing a bias in the results.

Experiment 2: simple RT task with discrete spatial cues

This control experiment was the same as experiment 1 except for the mode of response. It was performed several weeks after experiment 1. The following information is specific to experiment 2.

Subjects

Fifteen subjects participated in this experiment (11 males and 4 females, age range: 19–37 years). Eleven subjects were the same as those of experiment 1. A signed informed consent was obtained from each subject. The experimental protocol was approved by the Institutional Review Board of the Veterans Affairs Medical Center of Minneapolis.

Procedure

The experimental conditions were identical to those in experiment 1 except that the joystick was replaced by a press-button. The subjects had to press the button to initiate a trial and keep it pressed during the cue period. They were instructed to release the button as soon as the target was presented.

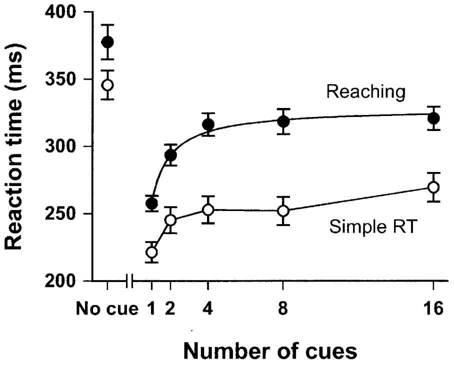

Fig. 3 Mean RT across subjects is plotted against number of cues. The data from the reaching task (experiment 1) are represented by *solid symbols*, whereas the data from the simple RT task (experiment 2) are represented by *open symbols*. The *vertical error bars* indicate the standard error of the mean. The *solid line* passing through the data points of experiment 1 is the least-square fit of Eq. 6 predicted by the switching and the capacity-sharing models

Results

Experiment 1: reaching task with discrete spatial cues

Effect of discrete spatial cues on RT

The average RT is plotted as a function of number of cues in Fig. 3 (filled symbols). First of all, it can be seen that RT in any of the cued conditions was shorter than in the no cue condition (all Dunnett tests with $P<0.05$) and second that RT changed as a function of the number of cues ($F_{(4,881)}=58.531$, $P<0.0005$).

However, the effect of the number of cues on RT could be a side effect of the spatial dispersion of the cues. This is because the spatial arrangement of the cues on a circle is constrained by their number: The greater the number of cues, the greater their spatial dispersion is on average. Therefore, RT could be related to the spatial dispersion of the cues rather than their number. To test for this possibility we performed an ANCOVA with the number of cues as factor and the cues circular variance (Mardia and Jupp 2000) as covariate. In addition, the duration of the cue period was also included as covariate because of its common effect on RT (Luce 1986). The results of this analysis confirmed the effect of the number of cues on RT. We found that the number of cues had a significant effect on RT ($F_{(4,879)}=14.105$, $P<0.0005$) but not the cues circular variance ($F_{(1,879)}=0.031$, $P=0.859$). The duration of the cue period had also a significant effect on RT ($F_{(1,879)}=19.865$, $P<0.0005$): RT decreased by 0.049 ms for every ms of the cue period, which varied randomly between 500 and 1000 ms.

The directional dispersion of the cues can also be evaluated using the circular range (viz., smallest angle that contains all the cues; Mardia and Jupp 2000). The circular variance used in the previous analysis is analogous to the variance in linear statistics and carries more information about the directional distribution than the circular range. Nevertheless, we have also executed an ANCOVA substituting the circular range to the circular variance as covariate. The results obtained were similar to those of the previous analysis (number of cues: $F_{(4,879)}$=11.105, P<0.0005; cues circular range: $F_{(1,879)}$= 0.034, P=0.854; cue period duration: $F_{(1,879)}$=19.857, P<0.0005).

We tested further for a possible effect of the cues spatial dispersion on RT by analyzing the subset of trials in which only two cues were presented. In this specific condition, the angle between the two cues completely defines their directional disparity. Therefore, for this analysis we performed a linear regression analysis between RT and the angle between the two cues. Subjects were considered as a dummy factor in the analysis. We found that the angle between cues had no significant effect on RT ($F_{(1,164)}$=0.004, P=0.951).

Therefore, the various analyses performed on RT point to the same conclusion, which is that the number of cues, but not their spatial dispersion, had a significant effect on the RT of reaching movements. In addition to this effect it was found that RT decreased as the cue duration increased. The effect of number of cues on RT is independent of the effect of cue duration since the latter varied randomly across trials. The functional relation between number of cues and RT is analyzed in more in detail in the following section.

Functional relation between RT and number of cues

The two models described in the "Introduction" predict a specific relation between mean RT and number of cues (Eq. 6). We examined this prediction in the following analyses. The plot of mean RT against number of cues (Fig. 3, filled symbols) shows that RT increased initially sharply with number of cues and then reached a plateau. Evidently a straight line does not fit the data, but neither does a logarithmic function (viz., Hick-Hyman law). We tested the fit of the Hick-Hyman law to these data by calculating for each subject the regression of the harmonic mean of RT against the logarithm of the number of cues (Eq. 1). The examination of the residuals revealed a systematic lack of fit (Fig. 4A). Therefore, this indicates that in this task RT did not obey the Hick-Hyman law. In other words, the results showed that RT was not a linear function of the amount of uncertainty provided by the spatial cues.

In contrast, we found that the relation between RT and number of cues was well described by Eq. 6. In this case the residuals were symmetrically distributed around zero for all conditions (Fig. 4B), which indicates that it was appropriate to describe these data. The correlation coefficient of the regression using Eq. 6 ranged from 0.631 to 0.9998 across subjects. The average correlation coefficient computed using Fisher's z-transformation (Snedecor and Cochran 1989) was 0.967. These results indicate that Eq. 6 provided a good description of the functional relation between RT and number of cues. The average parameters of Eq. 6 across subjects were a=259 ms and b=70 ms (Fig. 3). The standard error of the mean (SEM) of a and b was 6 ms and 8 ms (n=15 subjects), respectively.

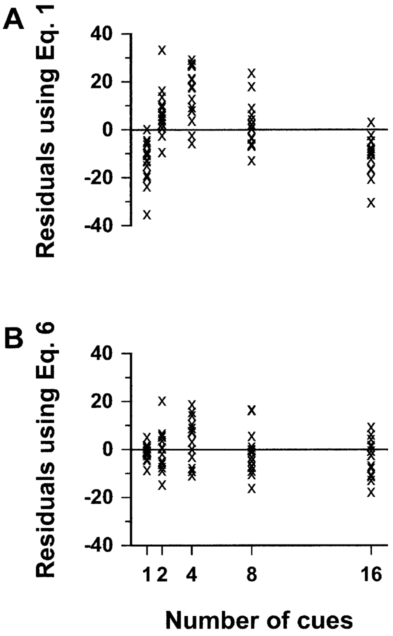

Fig. 4A, B Distribution of residuals across conditions of the reaching task (experiment 1) for (**A**) the least-square fit of Eq. 1 (viz., Hick-Hyman law) and (**B**) the least-square fit of Eq. 6 predicted by the switching and the capacity-sharing models

Analyses of the distribution of RT across conditions

The analysis of the relation between mean RT and number of cues showed that Eq. 6 fitted the data well. However, this equation was predicted by both the switching model and the capacity-sharing model and, therefore, it cannot be used to differentiate the two models. However, the two models can be differentiated on their predictions regarding the shape of the distribution of RT. The prediction of the switching model is that the distribution of RT is a two-component mixture distribution. As seen in the "Introduction," the proportion of each component depends on the number of cues (Eq. 4). Therefore, the switching model implies that not only mean RT changes across conditions, but the shape of the distribution of RT changes as well. In contrast, the capacity-sharing model assumes a change of mean RT across conditions associated with a single-component distribution. In this case, the distribution of RT changes across conditions essentially by shifting along the abscissa, i.e., the distribution of RT should correspond to the same type of one-component distribution across conditions.

On these bases, we have examined the distribution of RT across conditions and compared them to the predictions of these two models. A prominent characteristic of a distribution is its variance. The variance *Var(RT)* of a two-component mixture is predicted by the following equation (Yantis et al. 1991):

$$Var(RT) = p_{NS}Var(RT_{NS}) + p_S Var(RT_S) + p_{NS}p_S\left(\overline{RT}_{NS} - \overline{RT}_S\right)^2, \quad (10)$$

where $Var(RT_{NS})$ is the variance of RT_{NS} and $Var(RT_S)$ is the variance of RT_S. Equation 10 indicates that the variance of the mixture distribution is dependent on the weighted sum of the variance of the components and on the difference between the means of the component distributions. This equation predicts that the variance of RT be typically an inverted u-shaped function. In the case where $\mathrm{Var}(RT_S) \approx \mathrm{Var}(RT_{NS})$ then Var(*RT*) would be the smallest in the n=1 condition (i.e., p_S=0 and p_{NS}=1), the largest in the n=2 cues condition (i.e., p_S=p_{NS}=0.5) and in between for the other conditions.

We tested these predictions by analyzing the standard deviation rather than the variance because the distribution of the latter deviated greatly from a normal distribution (Snedecor and Cochran 1989). The results from the ANOVA indicated that the standard deviation of RT across conditions from n=1 to n=16 cues did not vary significantly ($F_{(4,56)}$=0.906, P=0.467). The average standard deviation of RT was 40 ms (SEM=3 ms, n=75, 15 subjects × 5 conditions). Therefore, the results of this analysis did not support the prediction of the switching model that the dispersion of RT changes across conditions.

A more comprehensive analysis of the distribution F of RT resides in examining its shape. If we can estimate the distribution functions of the components $F^*_{NS}(RT)$ and $F^*_S(RT)$, then we can predict the distribution of the mixture distribution in any number of cues condition using Eq. 4. The distribution of RT in the n=1 cue condition is the best estimate of $F^*_{NS}(RT)$, since in this case subjects know where the target will be and therefore never need to switch motor plan, therefore:

$$F^*_{NS}\left(\overline{RT}\right) = F_{N=1}(RT). \quad (11)$$

In contrast, there is no condition in which a switch of motor plan always occurs. However, the distribution $F^*_S(RT)$ can be estimated from any distribution of RT where the number of cues is greater than one, i.e., in conditions where, according to the switching model, switches of motor plan should occur. The most reliable condition for this estimation is the n=16 cues condition in which the expected proportion of trials where a switch occurs is 94% (i.e., 15/16), and the proportion of trials where there is no switch is 6% (i.e., 1/16):

$$F_{N=16}(RT) = \frac{15}{16}F^*_S(RT) + \frac{1}{16}F^*_{NS}(RT). \quad (12)$$

Therefore using Eqs. 11 and 12, $F^*_S(RT)$ can be estimated as follows:

$$F^*_S(RT) = \frac{16}{15}F_{N=16}(RT) - \frac{1}{15}F_{N=1}(RT). \quad (13)$$

The estimated functions $F^*_{NS}(RT)$ and $F^*_S(RT)$ can be used to predict the distribution of RT in any cue condition. However, of particular interest is the condition with n=2 cues given that in this case the two component distributions have the same weight and therefore their presence in the mixture distribution is expected to be the most evident. The expected distribution $F^*_{N=2}(RT)$ was calculated as follows:

$$F_{N=2}(RT) = \frac{1}{2}F^*_{NS}(RT) + \frac{1}{2}F^*_S(RT). \quad (14)$$

We compared the predicted distribution $F^*_{N=2}(RT)$ with the observed distribution $F_{N=2}(RT)$ using the following procedure. The cumulative distribution function (CDF) of RT in each condition was obtained using the vincentization method (see “Methods”). Each vincentized CDF was fitted with a Weibull function using nonlinear regression (DRNLIN subroutine from the IMSL Fortran libraries version 4, Visual Numerics Inc, Houston, Tex., USA). The Weibull function was selected because it fits the skewed distribution of RT data generally quite well (Luce 1986). The vincentized distributions for the conditions with n=1, n=2, and n=16 cues and their respective fitted functions are plotted in Fig. 5A. Goodness-of-fit tests indicated that the Weibull function provided a good description of the data in all conditions (all δ-corrected Kolmogorov-Smirnov tests with P>0.9, Sokal and Rohlf 1995). In contrast, we found that the expected distribution $F^*_{N=2}(RT)$ differed significantly from the observed distribution $F_{N=2}(RT)$ (δ-corrected Kolmogorov-Smirnov test, P=0.0004). To illustrate this result, we plotted in Fig. 5B the probability distribution functions (PDF) derived from the fitted Weibull functions for the two estimated components $F^*_{NS}(RT)$ and $F^*_S(RT)$, the predicted distribution $F^*_{N=2}(RT)$, and the observed distribution $F_{N=2}(RT)$. It can be seen clearly that the PDF of the observed distribution $F_{N=2}(RT)$ did not match the predicted distribution $F^*_{N=2}(RT)$.

In summary, both the analysis of the standard deviation of RT and the analysis of the shape of the distribution did not support the hypothesis of a mixture distribution of RT. In other words, the analyses of the distribution of RT rejected the switching model. Furthermore, it was found that the same type of function described well the distribution of RT in each condition, which supports the capacity-sharing model.

Analyses of movement time and errors

Movement time (MT) and directional errors were analyzed to investigate the question of whether the change of RT across conditions was associated with a time-accuracy tradeoff. In addition, we analyzed the occurrence of anticipated responses and eye fixation errors as an indication of the level of preparation to initiate a

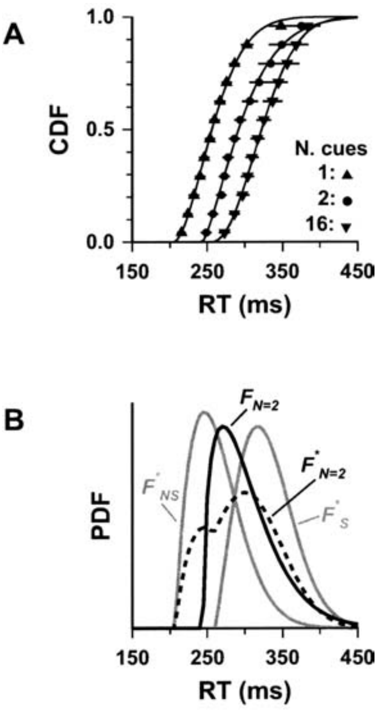

Fig. 5 **A** Cumulative distribution functions of RT in the n=1, 2, and 16 cues conditions of the reaching task (experiment 1). The *horizontal bars* indicate the standard error of the mean. **B** The probability density functions of the two components F^{*}_{NS} and F^{*}_{S} assumed by the switching model (Eqs. 11 and 13) are plotted as *light gray lines*. The *dashed black line* corresponds to the distribution $F^{*}_{N=2}$ predicted by the switching model in the n=2 cues condition (Eq. 14), whereas the *continuous black line* shows the distribution $F_{N=2}$ actually obtained in that condition

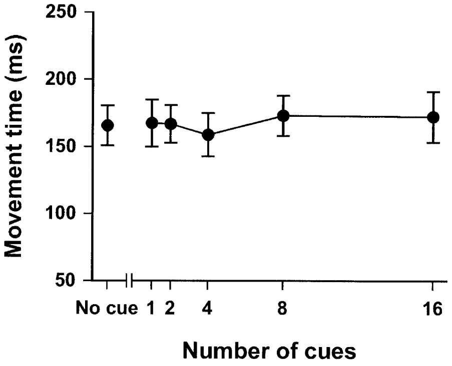

Fig. 6 Mean MT across subjects is plotted against number of cues. The *vertical error bars* indicate the standard error of the mean

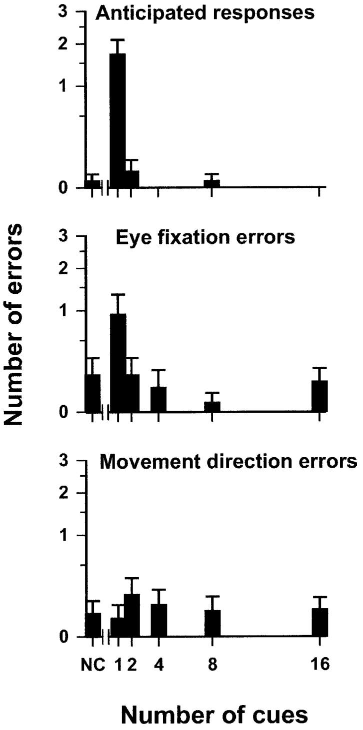

Fig. 7 Mean number of anticipated responses, eye fixation errors, and directional errors across subjects for each condition of the reaching task (experiment 1). The *error bars* represent the standard error of the mean. Note that the ordinates are in a square-root scale

response. The average MT is plotted as a function of condition in Fig. 6, whereas the average number of anticipated responses, eye fixation errors, and movement direction errors are plotted in Fig. 7.

We found no significant effect of the experimental conditions on MT. First, Dunnett tests did not show any significant difference between MT in the no cue condition and MT in any of the cued conditions (all Dunnett tests with P>0.05). In addition, the ANOVA did not reveal any significant effect of the number of cues on MT ($F_{(4,881)}$=0.822, P=0.511). The average MT across all conditions and subjects was 167 ms (SEM=6 ms, n=90, 15 subjects × 6 conditions).

Regarding the spatial accuracy of the response, we found that the number of movement direction errors was small and that it did not vary significantly across conditions ($F_{(4,56)}$=0.537, P=0.709). In addition, none of the condition with cues were significantly different from the no cue condition (all Dunnett tests with P>0.05). We extended the analysis of directional error by examining the initial movement direction (see “Methods”). Consistent with the analysis of the number of errors, we found that the average error of the initial movement direction (i.e., constant error) and its standard deviation (i.e., variable error) were not significantly different between the no cue condition and any of the condition with cues (all Dunnett tests with P>0.05). In addition, the analyses of the average initial direction error and of its standard deviation showed no significant difference across conditions with cues either ($F_{(4,56)}$=1.420, P=0.239 and $F_{(4,56)}$=1.239, P=0.284, respectively). The average error of the initial movement direction across all conditions and subjects was 1.9° (SEM=0.6°, n=90), whereas the standard deviation of the error was on average 13.9° (SEM=0.6°, n=90). Similar results were obtained when the movement direction error was evaluated at a later point during the trajectory, specifically at the moment of maximum speed (data not shown).

It could be argued that, when there are several cues, the effect of interference of the cues on the direction of movement is canceled out. For this reason we analyzed data in the simpler condition with two cues. We arranged the data so that a negative error indicated a movement that deviated away from the cue that was not the target, whereas a positive error was a movement that deviated toward that cue. We performed a regression analysis of the error of the initial movement direction as a function of the angle between the two cues. Subjects were a dummy variable in this analysis. We found that the intercept was not significantly different from zero ($F_{(1,172)}$=0.184, P=0.668), which indicates that there was no overall tendency to deviate toward or away from the cue that was not the target. In addition, there was no significant effect of the angle between cues ($F_{(1,172)}$=0.008, P=0.928), which indicates that the error did not change significantly with the angular separation between the cues. Similar results were obtained when the analysis was performed on the error of movement direction evaluated at the moment of maximum speed (data not shown).

In contrast with the directional errors, we found that the number of anticipated responses was significantly different across cued conditions ($F_{(4,56)}$=50.333, P<0.0005). In addition, Dunnett tests indicated that only the condition with n=1 cue had a significantly higher number of anticipated responses than the no cue condition (P<0.0005).

Similar results were obtained for the number of eye fixation errors during the cue period. The ANOVA indicated that the number of cues had a significant effect on the number of eye fixation errors ($F_{(4,56)}$=6.007, P<0.0005), but only the single cue condition had significantly higher number of eye fixation errors than the no cue condition (Dunnett test, P=0.007).

The analyses of the errors indicate that anticipated responses occurred more often in the n=1 cue condition, either with an eye or with an arm movement, than in any of the other conditions. Regarding the question of a possible speed-accuracy tradeoff, we found that the number of directional errors, the error of the initial movement direction, and MT were not affected by the experimental conditions. Therefore, the change of RT across conditions was not associated with a change of accuracy of the motor response.

Experiment 2: simple reaction time task with discrete spatial cues

Effect of discrete spatial cues on RT

The average RT across subjects is plotted against number of cues in Fig. 3 (open symbols). Similarly to the reaching task, RT was shorter in any condition with cues than in the no cue condition (all Dunnett tests with P<0.05).

In addition, as can be seen in Fig. 3, RT changed with the number of cues ($F_{(4,881)}$=17.332, P<0.0005). So, at first sight the results seem similar to those obtained in the reaching task (experiment 1). However, we analyzed the data using the same model of ANCOVA as in experiment 1 and found that, in contrast to the results obtained in experiment 1, the spatial distribution of the cues rather than their number was a determinant factor of RT in experiment 2. The results were that the number of cues had no significant effect on RT ($F_{(4,879)}$=1.034, P=0.389), whereas the cues circular variance had a significant effect ($F_{(1,879)}$=5.136, P=0.024). In addition, as in experiment 1, the duration of the cue had a significant effect on RT ($F_{(1,879)}$=44.429, P<0.0005). The parameter estimates from the ANCOVA indicate that RT increased by 31 ms for a unit increase of circular variance, whereas it decreased by 0.094 ms for every ms of cue duration, which varied between 500 and 1000 ms.

Since many subjects included in experiment 2 participated in experiment 1 before, it could be that practice had influenced the pattern of results obtained in experiment 2. To test for this possibility, we performed an ANCOVA similar to that described above but with the additional factor of subjects group. Subjects were divided into two groups depending on whether they participated in experiment 1 or not. The analysis did not show any significant effect of group ($F_{(1,12.998)}$=0.423, P=0.527) or of interaction number of cues × group ($F_{(4,876)}$=0.216, P=0.930). On the other hand, the same pattern of results was found regarding the number of cues and the covariates as above (number of cues: $F_{(4,875)}$=1.109, P=0.351; cues circular variance: $F_{(1,875)}$=5.206, P=0.023; cue period duration: $F_{(1,875)}$=44.015, P<0.0005). Therefore, this analysis did not support the hypothesis that the two groups of subjects performed differently in experiment 2

In order to illustrate the differential effect of the cues circular variance on RT in experiments 1 and 2, we partitioned the data as follows. For each subject and cue condition, we ordered the trials according to the cues circular variance and we divided the sequence of trials in four equal partitions. For each partition, we computed the average circular variance of the cues and the harmonic mean of RT. The conditions with n=1 cue and n=16 cue have by definition only one value of cues circular variance and therefore had only one partition of data each. The mean cues circular variance and mean RT for each partition and condition are plotted in Fig. 8. The open symbols correspond to the data from the simple RT task (experiment 2), whereas the solid symbols correspond to the data from the reaching task (experiment 1). The figure shows that RT increased linearly with cues circular variance in experiment 2, whereas it was best described by plateaus at different levels for each number of cues condition in experiment 1. The lines across the data correspond to the predictions from the regression models.

These analyses have shown that RT in experiment 2 was affected by the spatial dispersion of the cues as estimated by their circular variance and not by the number

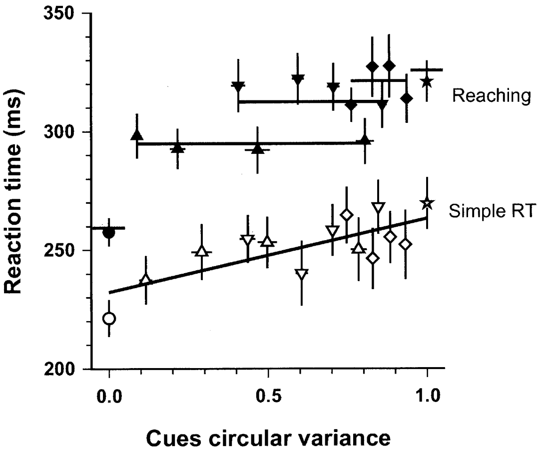

Fig. 8 Mean RT across subjects is plotted against partitions of circular variance of the cues for the different number of cues conditions. The data from the reaching task (experiment 1) are represented by *solid symbols* (n=1: ●; 2: ▲, 4: ▼, 8: ◆, and 16: ★), whereas the data from the simple RT task (experiment 2) are represented by *open symbols* (n=1: ○; 2: △; 4: ▽; 8: ◇, and 16: ☆). The *horizontal error bars* indicate the standard error of mean circular variance, whereas the *vertical error bars* indicate the standard error of mean RT. The *solid lines* across the data indicate the predictions from the regression models

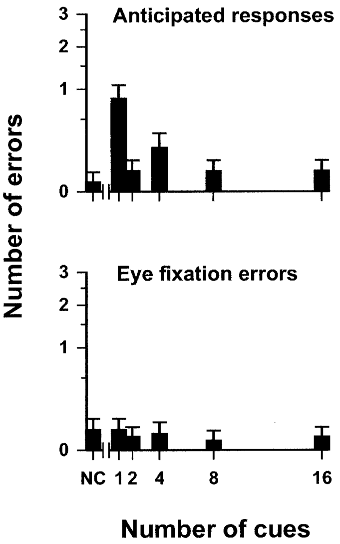

Fig. 9 Mean number of anticipated responses and eye fixation errors across subjects for each condition of the simple RT task (experiment 2). The *error bars* represent the standard error of the mean. Note that the ordinates are in a square-root scale

of cues. This result is in contrast with the result obtained in experiment 1, in which the number of cues and not their dispersion had an effect on RT.

Analyses of errors

Error trials were analyzed as in experiment 1. Evidently, only anticipated responses and eye fixation errors could be analyzed, since there is no directional error possible in the simple RT task. The average number of anticipated responses and of eye fixation errors per condition are plotted in Fig. 9. It can be seen that in all conditions the average number of errors was quite low. Nevertheless, the number of anticipated responses was significantly different across cued conditions ($F_{(4,56)}$=7.269, P<0.0005). In addition, Dunnett tests indicated that only the condition with n=1 cue had a significantly higher number of anticipated responses than in the no cue condition (P<0.0005).

In contrast, the analysis of the number of eye fixation errors indicated that there was no significant difference across cued conditions ($F_{(4,56)}$=0.228, P=0.922), nor were these conditions significantly different from the no cue condition (all Dunnett tests P>0.05).

These analyses have shown that the number of anticipated responses had a pattern similar to that found in experiment 1. The number of anticipated responses was higher when there was only one cue than in any other condition. In contrast, the number of eye fixation errors had a different pattern in the two experiments. The number of eye fixation errors did not differ significantly across condition, whereas in experiment 1 it was significantly higher in the one cue condition.

Discussion

We investigated the effect of spatial uncertainty on motor planning using the cueing method in a reaching task (experiment 1). Discrete spatial cues defined the set of possible motor responses in each trial. After a variable cue period, one of the cues became the target and the subjects had to reach it with a joystick-controlled cursor. The subjects were instructed to fixate the center of the display during the center-hold and cue periods. In addition, the trajectory of the response had to stay within spatial limits to be valid. The RT was used as an indicator of the level of preparation to initiate a response in a given experimental condition. In addition, we investigated the role that the requirement of a spatially directed motor response might have had on the pattern of results obtained in experiment 1 by removing such a requirement in a simple RT task (experiment 2).

Effect of cueing on RT

The average RT in any of the cued conditions was lower than in the no cue condition, both in the reaching task and in the simple RT task. This result indicates that subjects effectively used the information provided during the cue period to prepare the response. Surprisingly, however, the results showed a benefit of cueing relative to the no cue condition even when the cues provided very little information about the direction of the upcoming target (i.e., n=16 cues). In this condition the cues were contiguous, but the center of the cues is more relevant for a successful motor response than the point of contact between two contiguous cues. This creates some nonuniformity in the probability distribution of responses, which provides potentially useful spatial information. It could be that subjects were able to extract this spatial information to prepare for the possible motor responses. In addition, although the distance of the target from the center was constant, the presence of the cues may have helped subjects determine the amplitude of the movement in advance relative to the no cue condition.

An additional factor that could have contributed to this effect is that the presentation of the cues acted as a warning signal regardless of any spatial information. It is known that the presence of a warning signal often shortens RT by presumably arousing the attention of the subjects (Luce 1986). Therefore, even if subjects could not have extracted spatial information from the n=16 cues condition, the presentation of the cues would have given a warning signal that provided an advantage relative to the no cue condition.

Relation between RT and number of cues in the reaching task

We found that RT in the reaching task increased with the number of cues and that this increase was not associated with a change in movement time or in spatial accuracy of the response. Therefore, the change of RT across cue conditions cannot be accounted for by a speed-accuracy tradeoff. In addition, we showed that the change of RT was a function of the number of cues and not of their spatial dispersion. This latter result is in contrast with the result obtained in the simple RT task, which is discussed later.

Furthermore, the functional analysis of the relation between RT and number of cues in the reaching task showed that it was not well described by the Hick-Hyman law. This was not unexpected and is consistent with the results obtained in other spatially compatible motor tasks (Bock and Eversheim 2000; Broadbent and Gregory 1965; Dassonville et al. 1999; Leonard 1959; Longstreth et al. 1985). In contrast, we found that the relation between RT and number of cues was well predicted by the function derived from the switching and the capacity-sharing models (Eq. 6). Both models predicted the same relation and, consequently, were equally supported by this finding. However, the adequacy of the two models could be discriminated on the basis of their prediction about the distribution of RT.

Distribution of RT in the reaching task

The analyses of the distribution of RT in the reaching task did not support the hypothesis that the distribution is a two-component mixture and therefore they rejected the switching model. In contrast, the distribution of RT was well described by a one-component distribution in each cued condition, which supports the capacity-sharing model. The hypothesis of the capacity-sharing model is that the processing resources are shared to prepare alternative motor responses concurrently. The consequence of this sharing of resources is that the strength of the representation of each alternative response decreases as their number increases. When the expected motor response is defined, the processing resources are reallocated in order to initiate the response. The duration of this process is a function of the difference between the neural representation during the cue period and that required for initiating the response. Therefore, the duration of this process increases with the number of cues and can be described by a one-component distribution regardless of the number of cues. The results supported this view. In this context, it should be noticed that the results support a class of models that conform to the assumptions of the capacity-sharing model. Additional predictions about RT, such as an analytic prediction of the distribution function, would require more assumptions than those that were presented here. Other studies, particularly on the dynamics of the transformation of the neural representation between the planning and the execution of the motor response, are needed to specify the capacity-sharing model further.

The cues did not affect the execution of the reaching response

Tipper and colleagues have shown that the presence of a visual distractor influenced the movement trajectory to a target (Tipper et al. 1998). This interference is thought to result from the competition between two neural representations of action, one related to the target and one to the distractor. This view is consistent with the capacity-sharing model in which multiple alternative responses can be prepared in parallel. However, unlike Tipper and colleagues, we did not find any influence of the cues on the trajectory of the response. There are good reasons to think that this difference is determined by the timing between the presentation of the target and the presentation of other visual stimuli. In experiment 1, the target was presented after a cue period of 0.5–1 s, whereas in the Tipper et al. (1998) experiments, target and distractor were presented simultaneously. It is known that attention is captured by the onset of visual stimuli (e.g., Yantis and Jonides 1996); therefore, the simultaneity of the presentation of target and distractor creates an initial competition of orientation of attention and an overlap in time with the selection of the response. Accordingly, it has been shown that a visual distractor influences the movement trajectory when it appears simultaneously with the target but not when it is present before the target appears (Castiello 2001).

Comparison between the reaching task and the simple RT task

We found that the spatial distribution of the cues had no significant effect on the RT of the reaching task (experiment 1), whereas it had a significant effect in the simple RT task (experiment 2). This dissociation can be attributed to the type of response since the presentation of the cues was identical in both tasks. The reaching task required a spatially directed motor response that had to be selected on the basis of the location of the target. In addition, the response trajectory had to be within spatial boundaries from the starting point to the target. In contrast, the response in the simple RT task was the same (i.e., release of a push-button) in every trial regardless of the location of the target. This suggests that the task constraints relative to the motor response determined how the cues were processed and consequently affected the relation between cue factors and RT. This will be discussed further below.

Moreover, the patterns of anticipated responses and eye fixation errors provide an additional indication of the different nature of motor preparation during the cue period in the two tasks. In the reaching task, both the number of anticipated responses and the number of eye fixation errors were higher in the n=1 cue condition than in any other condition. In that condition, subjects had all the information to completely prepare the response during the cue period. The pattern of errors indicates that subjects used that information and that they prepared a directional response both with the arm and the eyes before the onset of the target. The level of preparation of the directional response occasionally led subjects to initiate a response during the cue period. The similarity of the patterns of hand and eye anticipated errors is consistent with the view that the planning of arm and eye directional responses are linked (Carey 2000).

In contrast, the patterns of hand and eye anticipated errors were different in the simple RT task. The number of anticipated responses was higher in the n=1 cue condition than in any other conditions, but not the number of eye fixation errors. That is, subjects were prepared to respond manually but not to make a saccade. This underlines the different nature of response preparation in the two tasks, a directional response in the reaching task, which linked arm and eye motor preparation, and a stereotypical response in the simple RT task, which did not require a directional processing of hand and eye motor responses. Overall, these results suggest that the differential effect of cues factors (i.e., number of cues vs cues spatial dispersion) on RT was determined by the difference in motor preparation associated with each task.

Spatial constraints of the task and relation between RT and cue factors

In the reaching task, i.e., when the target defined the spatial constraints of the motor response, the number of cues had an effect on RT but not their spatial dispersion. In contrast, in the simple RT task, i.e., when the target did not constrain the spatial dimension of the motor response, the number of cues did not affect RT but their spatial dispersion did. This dissociation provides a framework to compare with the results of other experiments related to the planning of reaching movements.

In a number of studies on reaching movements with controlled endpoint accuracy, Fitts and colleagues found that RT increased with response uncertainty (Fitts et al. 1963; Fitts and Peterson 1964). These results are consistent with those found in the reaching experiment (experiment 1) presented here. However, the outcome of other experiments seems at odds with these results. Notably, it was reported that the spatial dispersion of the possible target location, rather than the number of locations, had a significant effect on the preparation of reaching movements (Bock and Arnold 1992; Bock and Eversheim 2000; Favilla 1996, 2002; Ghez et al. 1997). Although this seems to be in conflict with the findings from the present experiment, the examination of the spatial constraints of the tasks used shows that the conflict is only apparent.

Using the timed response paradigm, Ghez and colleagues found that the specification of reaching hand trajectories was dependent on the spatial disparity between the possible targets (Ghez et al. 1997). The specification mode was qualified as continuous for narrow target separations and as discrete for wider target separations (see also Lee 1999). Furthermore, Favilla (2002), using the same paradigm, showed that the spatial configuration of the possible targets within a fixed angular range affected the specification mode of the response, whereas the number of possible target locations did not affect it (Favilla 1996). It is necessary to examine the spatial constraints of the timed response paradigm to determine whether these, as we suggested above, determined the cue factors that affected motor preparation. In these experiments subjects were trained to initiate a motor response in synchrony with the last of a regular series of tones and the target was presented at variable intervals before the last tone. The consequence was that the shorter the interval between the presentation of the target and the last tone, the less the response was related to the location of the target. In other words, subjects had to be prepared to make a default response that was unrelated to the location of the target. This implies also that the trajectory of the response could not be constrained spatially. Therefore, the examination of the spatial constraints of the timed response paradigm suggests that the effect of the spatial dispersion of the cues on response preparation occurs when the spatial constraints on the response trajectory are lax. This is similar to what we found in the simple RT task. Clearly, the levels of spatial constraints associated with the simple RT task and the timed response paradigm are different, but each one is much less constrained than the reaching task used in experiment 1.

Furthermore, Bock and colleagues investigated the effect of number of cues and of their spatial range on motor preparation using the cueing method (Bock and Arnold 1992; Bock and Eversheim 2000). In one series of experiments, two or five cues were presented (Bock and Eversheim 2000). The two cues were either 15° or 60° apart, whereas the five cues covered a single arc size of 60°. It was found that the size of the arc rather than the number of cues affected the RT of reaching responses. The task for the subjects consisted in placing the index finger at a starting position at the bottom of the display and pointing at the target after it had been presented. The response was made without visual control on the position of the hand. In addition, although subjects were instructed to respond quickly and accurately, there was no criterion regarding response accuracy neither for the trajectory of the movement nor for its final position. Therefore, the spatial constraints on the motor response in the task used by Bock and Eversheim (2000) were less stringent than in the reaching task presented here (experiment 1). In addition, Bock and Eversheim (2000) tested subjects in a simple RT task using the same cues described above. They found also an effect of dispersion of the cues, which corresponds to what was found in the simple RT task presented here (experiment 2). Therefore, these results are compatible with the proposal that the effect of the spatial dispersion of the cues occurs when the spatial constraints on the motor response are lax, whereas the effect of number of cues occurs when these constraints are strict.

This analysis indicates that whether the number of cues or their spatial dispersion has an effect on the preparation of the motor response rests on the spatial constraints of the task. This outcome is consistent with several studies that have shown that different task constraints induce different modes of specification of reaching movements (Favilla 2002; Ghez et al. 1997; Lee 1999; Pellizzer and Georgopoulos 1993; Pellizzer et al. 1995).

Processing modes during motor planning

The analyses described above showed that motor preparation can be either independent or dependent on the spatial distribution of discrete alternative motor responses. In both cases, the results support the capacity-sharing model. The first case corresponds to the capacity-sharing model described in the “Introduction” and tested in experiment 1. We found that the results supported the hypothesis that the processing resources were divided across multiple discrete and independent representations of alternative reaching responses. Instead, the second case is compatible with the results of experiment 2 and those of other studies (Bock and Arnold 1992; Bock and Eversheim 2000; Favilla 1996, 2002; Ghez et al. 1997), which suggest that the processing resources are allocated as a function of the spatial distribution of the alternative responses. In this case the representations of the alternative responses are not independent, but rather interact as a function of their spatial disparity. Similar effects have been described in relation to the allocation of attention in visual search tasks (Eriksen and Yeh 1985; Podgorny and Shepard 1983).

Taken together, these results indicate that both modes of capacity-sharing of processing resources are available and that, as discussed above, the spatial constraints of the task determine which mode is going to be preferentially engaged. When the spatial constraints on the response are low, the preferential mode of processing seems to be that of sharing the processing capacities as a function of the spatial distribution of the alternative responses. However, when the spatial constraints become stricter, the system is capable of dividing the resources across each alternative response as discrete and independent processes. Furthermore, it should be noted that in some conditions it is also advantageous for the subject to adopt a switching mode of planning. This has been shown to occur when subjects plan a default response before the information about the expected response is given (Favilla 2002; Ghez et al. 1997; Lee 1999; Pellizzer et al., 1995).

If we assume that the mode of processing selected in a given task is the most economic for the system, the characterization of the conditions that engage one or the other mode of processing provides a guide in determining the neural network architecture that underlies these different processing modes.

Neural representation of motor preparation as a function of target uncertainty

Neurophysiological studies using instructed-delay tasks have shown that neuronal activity associated with motor preparation is present across a wide range of central nervous system structures engaged in the planning and execution of arm movements, including cerebral cortical areas (Battaglia Mayer et al. 1998, for a review), basal ganglia (Alexander 1987; Jaeger et al. 1993), and spinal interneurons (Prut and Fetz 1999).

Basso and Wurtz (1998) tested the effect of uncertainty by manipulating the number of possible targets in a saccade task. They found that the activity of superior colliculus neurons in the monkey decreased as the number of stimuli increased. Therefore, the activity of these neurons reflected the probability of a particular movement to be selected. In addition, the level of neuronal activity predicted the latency of the response. These results are compatible with the hypothesis that processing resources available for motor planning are shared to prepare multiple responses concurrently. They do not indicate, however, whether the processing resources are divided across the spatial range of possible targets or across multiple discrete representations of these targets. Consistent with the latter is the recent suggestion that two potential reach targets can be encoded simultaneously by neurons in the dorsal premotor cortex (Cisek and Kalaska 2002). Instead, Bastian et al. (1998) showed that the activity of a population of motor cortical neurons during an instructed delay reflected the spatial uncertainty about the upcoming target. Therefore, these studies are consistent with the results of the experiments presented here. Both lines of evidence suggest that different modes of processing potential targets are available and that the task constraints determine which one is engaged.

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