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RESEARCH NOTE

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Motor planning: effect of directional uncertainty with continuous spatial cues

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Abstract We have investigated the effect of directional uncertainty on the planning of reaching movements. For this purpose, we have used sections of annuli as spatial cues to indicate the directional range within which the target would be presented. The results showed that the reaction time of the reaching response increased with cue range and with the angle between the center of the cue and the target. In addition, the initial direction of movement was biased toward the center of the cue. These results conformed to the predictions of the capacity-sharing model. This model assumes that the processing resources used for motor planning are limited and distributed as a function of the range of directions indicated by the cue, and that when the target appears, these resources are reallocated to represent the response to be executed.

Keywords Motor preparation · Reaching · Reaction time · Processing capacity

Introduction

When information about the action that will need to be performed is available in advance, aspects of the response can be processed beforehand. This motor preparation is revealed, at the behavioral level, by a change in the latency of response (e.g., Rosenbaum 1980) and, at the neurophysiological level, by a pattern of neural activity that reflects the intended response. Neuronal activity associated with motor preparation has been found across the distributed network of the central nervous structures subserving motor behavior (e.g., Riehle and Requin 1995).

Typically, information is presented to subjects in experimental conditions using the precuing method (Rosenbaum 1980). That is, a cue provides information about some aspects of the response before the signal to respond occurs. The effect of the cue on reaction time (RT) is assumed to reflect the amount of processing of the response that had been completed before the response signal. For example, Rosenbaum (1980) found that cueing the direction of a reaching movement produced greater benefits on RT than cueing the amplitude of the movement. This result was interpreted as indicating that the direction of movement needs to be specified before its amplitude. This interpretation was subsequently supported by the analysis of the activity of neurons in the premotor and motor cortex of monkeys performing in reaching tasks (Fu et al. 1993; Riehle and Requin 1989). For example, Fu et al. (1993) found that the activity of motor and premotor neurons reflects initially the direction of the reaching response and then progressively its amplitude. Therefore, the analysis of the pattern of RT as a function of the information provided by the cues offers an important basis of inference of the brain processes associated with the planning of a motor response (Luce 1986).

Recently, we have tested the effect of the degree of uncertainty about the direction of the upcoming target on motor preparation (Pellizzer and Hedges 2003). The possible location of a reaching target was indicated by one or more discrete spatial cues. As the number of cues increased, the degree of uncertainty about the upcoming location of the target increased as well. We tested the predictions of two models of motor planning: a capacity-sharing model, which assumes that multiple motor responses can be planned in parallel (Shaw 1978), and a switching model, which assumes that only one motor response can be planned at a time (Longstreth et al. 1985). The results supported the predictions of the capacity-sharing model.

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The main assumptions of the capacity-sharing model are that the processing resources for motor planning are limited and that they can be divided to prepare alternative motor responses concurrently. The consequence of this division of resources is that the strength of the neural representation of each alternative response decreases as the number of alternative responses processed increases. When the expected motor response is defined, the processing resources are reallocated in order to initiate the response. It is assumed that the duration of this reallocation of resources is a function of the difference between the neural pattern of activity associated with motor preparation and the pattern of activity for initiating the response. In other words, the duration of the reallocation of resources is expected to be a negative inverse function of the number of alternatives (Pellizzer and Hedges 2003).

The analyses of both the relation of RT with the number of discrete cues and of the shape of the distributions of RT supported the predictions of the capacity-sharing model (Pellizzer and Hedges 2003). In addition, we found that the spatial dispersion of the cues did not affect RT or the initial direction of movement. Therefore, these results suggested that the processing resources were divided across multiple discrete and independent representations of alternative reaching responses. However, the capacity-sharing model predicts different results when the target is expected within a continuous range of directions rather than at some discrete locations.

In the present experiment we investigated the effect of directional uncertainty as determined by continuous spatial cues. The cues indicated the directional range in which the upcoming target would appear. In this context, the capacity-sharing model predicts that the processing resources of motor preparation are distributed as a function of the directional range indicated by the cue. In other words, motor preparation reflects the probability distribution of the response (Bock and Arnold 1992; Erlhagen and Schöner 2002; Pellizzer and Hedges 2003; Shaw 1978). As the range increases, the processing resources are spread further, which increases the duration of the reallocation of the processing resources when the response to be executed is determined. Therefore, it is predicted that RT increases as a negative inverse function of the directional range (Pellizzer and Hedges 2003). In addition, the processing resources need to be reallocated as a function of the direction of the target within the cue. Therefore, the representation associated with motor preparation requires a transformation both in range and location (Fig. 1B). In other words, RT should increase both as the spatial range increases and as the angle θ between the direction of the target and the center of the cue increases. The results supported these predictions.

Materials and 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. They had a normal or corrected-to-normal vision and no known neurological or motor impairment. Each subject signed an informed consent before the experiment. The experimental protocol was approved by the Institutional Review Board of the Minneapolis VAMC.

Apparatus

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 that they grasped with their preferred hand (right hand: 12 subjects; left hand: 3 subjects). The direction of gaze was monitored using a video-based eye tracking system (Iscan Inc., Burlington, MA). The position of the joystick and the direction of gaze were recorded at 200 Hz.

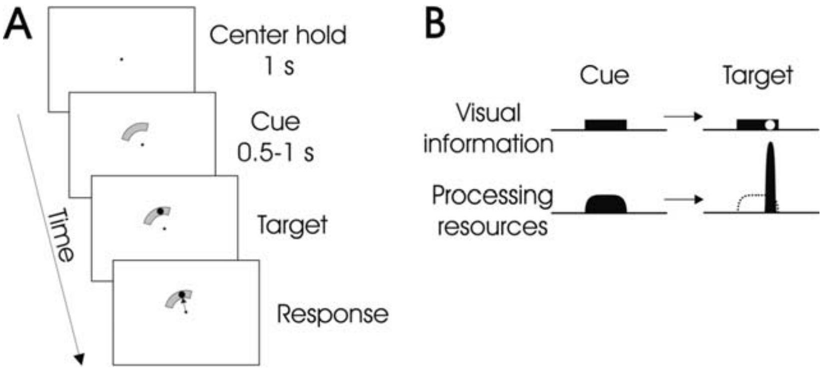

Fig. 1 **A** Schematic example of a trial. The subjects controlled a cursor on a screen using a joystick. After the center-hold period, the cue indicated the range of directions in which the target would appear. Subjects had to fixate the center of the screen during the center-hold and cue periods. When the target was presented, the subjects had to move the cursor from the center onto the target. The trajectory of the cursor had to stay within an unmarked straight path from the center to the target for the response to be counted as correct. The width of the path matched the width of the target. **B** Capacity-sharing model. The processing resources (*bottom left*) are distributed as a function of the directional range indicated by the cue (*top left*). When the target is presented (*top right*) the processing resources are reallocated through a transformation in range and location to define the response (*bottom right*)

Procedure

Subjects were seated and had their head against a chin-rest. They initiated a trial by placing the cursor within a circular window of 0.23 cm radius (i.e., 0.3 deg of visual angle) in the center of the display for a 1-s center-hold period. A cue period of 0.5–1 s followed. The cue was formed by a sector of annulus that had its center coinciding with the center of the screen and a radius of 3.15 cm (i.e., 4 deg of visual angle). The sector covered an angle of 22.5, 45, 90, 180 or 360 deg that indicated the range of directions in which the target would appear. On each trial the direction of the cue relative to the center of the screen was randomly selected in any direction around the circle. In addition to the cued conditions, a no cue condition was also presented in 1/6th of the trials. Trials from different conditions were randomly mixed. Subjects were instructed to fixate the center of the display during the center-hold and cue periods. Any eye movement outside a center window of 2 deg radius during these periods aborted the trial. After the cue period, a target was presented (white disc of 0.53 cm radius, i.e., 0.75 deg of visual angle). The target could be in any direction within the cue as long as the whole disc was within the cue. The 22.5 deg cue could contain the target only in its center and therefore provided complete information about its location. In contrast, the 360 deg cue provided no information about the direction of the target. After the target appeared, the subjects had to move the cursor as quickly as possible from the center to the location of the target and leave the cursor on the target for at least 0.5 s. The trajectory of the cursor had to stay within unmarked straight boundaries from the center to the target. The boundaries formed a straight path that matched the width of the target. Trials in which the trajectory went out of these boundaries were counted as directional errors. The reaction time was defined as the latency between the onset of the target and the exit of the cursor from the center window. To eliminate responses that were indicative of anticipation or distraction, we considered RTs shorter than 100 ms or longer than 2 s, respectively, as errors. The movement time (MT) was defined as the duration between the moment the cursor exited the center window and the moment it reached the target. When an error occurred, a trial with the same cue range was presented again at a random position in the sequence of the remaining trials. Twelve correct repetitions per cue range were obtained for each subject. A schematic example of the task is illustrated in Fig. 1A with an instance of the 90 deg cue range condition.

Data analyses

The data were analyzed using standard statistical techniques (Snedecor and Cochran 1989) including within-subject univariate GLM models (Rutherford 2001). Analyses of RT and MT data were performed using all correct repetitions, whereas the functional analyses of RT were done using the harmonic mean (Ratcliff 1993). The accuracy of the response was assessed by counting the number of directional errors (see “Procedure”) and by measuring the error of the initial direction of movement. The initial direction of movement was defined as the movement direction from the moment when the acceleration exceeded a threshold equal to 5% of the maximum of acceleration and the moment of the first maximum of acceleration. The analyses of the counts of directional errors were performed on the square-root transformed data (Snedecor and Cochran 1989).

Results and discussion

First of all, we tested the effect of the presence of the cue on RT. For this purpose, we compared RT in the no cue condition with every cued condition using the Dunnett test (Dunnett 1955). The results showed that RT in the no cue condition was significantly greater than RT in all of the cued conditions (all Dunnett tests with $P<0.0005$). These results indicate that the cue had the effect of decreasing RT even when it did not provide any directional information (i.e., cue range=360 deg). This effect can be seen in Fig. 2A where mean RT is plotted for the no cue condition and for each cued condition. Similar results were found also with discrete cues (Pellizzer and Hedges 2003). There are two explanations that are not mutually exclusive for this effect. First, even though the amplitude of the movement was the same in all conditions, it is possible that the presence of the cue helped the subjects to determine in advance the amplitude of the movement more precisely than in no cue condition, thereby shortening the duration of movement specification after the presentation of the target (Rosenbaum 1980). Second, the cue may have acted as warning signal regardless of any spatial information and helped in that way subjects to respond more promptly (Luce 1986).

A more central question for this experiment is whether RT changed significantly with the cue presented. The analysis showed that cue range had a significant effect on RT ($F_{(4,881)}=36.932$, $P<0.0005$). It can be seen in Fig. 2A that mean RT increased with cue range. The orthogonal polynomial contrasts showed a significant linear ($P<0.0005$), quadratic ($P<0.023$) and cubic effect ($P<0.012$). In other words, the increase of RT with cue range is more complex than a straight line. It can be seen in Fig. 2A that RT is a monotonically increasing quasi-concave function of cue range (Borowski and Borwein 1991). A qualitatively similar result was found by Bock and Arnold (1992) in a comparable task. However, Bock and Arnold (1992) chose to analyze only the linear trend of the data because there was no hypothesis on how to account for the curvilinear function. In contrast, the capacity-sharing model provides a possible explanation for the curved functional relation between RT and cue range. Indeed, it is assumed that the duration of the specification of the response is a negative inverse function of the dispersion of resources (Pellizzer and Hedges 2003). However, before testing this hypothesis we need to analyze the effect of the angle θ between the direction of the target and the center of the cue on RT. We excluded from this analysis the data in which this angle cannot be calculated unequivocally (i.e., 360 deg cue range). The analysis showed that RT increased both with the angle θ ($F_{(1,701)}=4.673$, $P=0.031$) and with cue range ($F_{(3,701)}=6.046$, $P<0.0005$). To illustrate these effects, we divided the trials in each cue range condition into two groups. One group was formed by the trials in which the target was at or near the center of the cue, whereas the other group was formed by the trials in which the target was toward the periphery of the cue. For this purpose, the trials of each subject in each condition from 45 deg to 180 deg cue range were ranked according to the distance of the target from the center of the cue. The lowest half of the ranked trials was assigned to the center group whereas the other half was assigned to the periphery group. The trials from the 22.5 deg cue condition were inevitably all in the center of the cue and none in the periphery. Using this procedure, each group had an equal number of

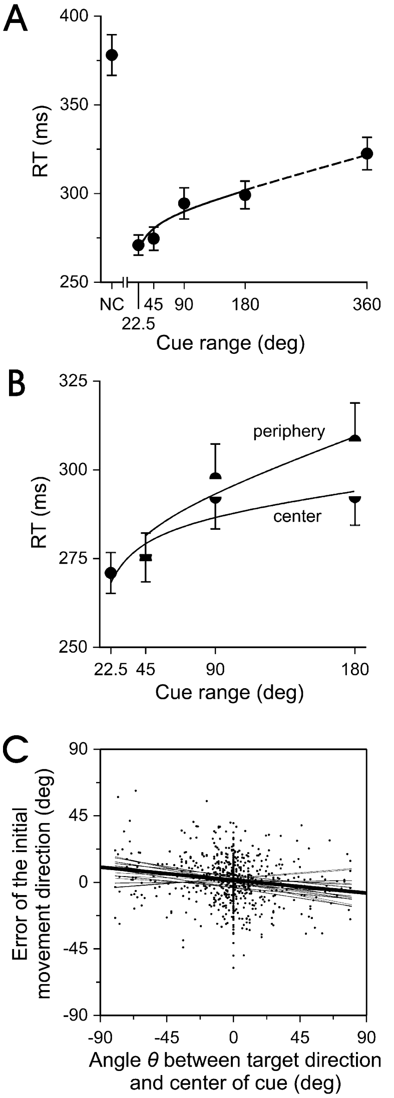

Fig. 2 **A** Mean RT (± SEM) across subjects in the no cue condition (*NC*) and as a function of cue range. The *continuous line* through the data corresponds to the fit of Eq. 1 (see "Results and discussion"). The *dashed line* is the extrapolated portion of the same function. **B** Mean RT (± SEM) across subjects as a function of cue range for the trials in which the target was near the center of the cue and for the trials in which the target was near the periphery of the cue. The *lines passing through the data* correspond to the least-square fit of Eq. 1. **C** Scatter plot of the error of the initial direction of movement against the angle θ between the direction of the target and the center of the cue for all trials of all subjects in the conditions with cues of 22.5, 45, 90 and 180 deg. Negative values correspond to clockwise directions, whereas positive values correspond to counterclockwise directions. Each *thin line* represents the linear regression of the data for each subject separately, whereas the *thick line* is the average linear regression across subjects

observations per subject in order to avoid biases in the subsequent analyses. Therefore, the boundary between center trials and periphery trials could be different from subject to subject although it was on average at mid-distance between the center and the periphery of the cue. Average RT for each group of data (i.e., center and periphery) is plotted against cue range in Fig. 2B. This figure shows that RT increased with cue range and that this increase was greater when the target was presented in the periphery of the cue than when it was presented in the center of the cue. The functional relation between mean RT and the variables cue range and angle θ was described using:

$$\overline{RT_i} = a + b\frac{360}{\text{Cue range}} + c\overline{\theta_i}, \qquad (1)$$

where $\overline{RT_i}$ is the average RT for the group of data i, $\overline{\theta_i}$ is the average angle between target and cue center for the same data and a, b and c are constants determined empirically. Equation 1 is composed of a component that reflects the distribution of the processing capacities as a function of cue range (i.e., inverse of the proportion of the range of directions cued) and a component that reflects the relocation of the processing resources centered on the cue toward the direction of the target (i.e., θ). Subjects were entered as a dummy variable in the analysis (Rutherford 2001). The least-square fit of Eq. 1 described the data well (R^2=0.730, $F_{(16,88)}$=14.839, P<0.0005) with parameters a=287.6 ms (SEM=5.6 ms), b=−1.23 ms (SEM=0.54 ms) and c=0.41 ms/deg (SEM=0.13 ms/deg). The function is plotted for the center and periphery groups of data in Fig. 2B. The same function is plotted for mean RT against cue range in Fig. 2A. In the latter figure, it can be seen that the extrapolated function beyond 180 deg predicted well the mean RT for the 360 deg cue condition.

These results provide support for the capacity-sharing model, which assumes that the processing resources during motor preparation are distributed as a function of the spatial distribution of the possible location of the target. The hypothesis of distribution of processing resources has found support also in other experiments, including reaching (Bock and Arnold 1992; Erlhagen and Schöner 2002; Pellizzer and Hedges 2003), detection (Castiello and Umiltà 1990; Pellizzer and Hedges 2003), discrimination (Podgorny and Shepard 1983) and visual search experiments (Eriksen and Yeh 1985; Shaw 1978). In the context of the present task, it is assumed that, when the target is presented, the processing resources are reallocated to define the reaching response. This reallocation is performed through an adjustment of the dispersion and location of the processing resources, thereby affecting RT.

The next question is whether the execution of the response was affected by the experimental conditions. For this purpose we analyzed MT, the count of directional errors and the error of the initial movement direction. In contrast with RT, we found that MT was not significantly affected by the cues. First, MT was not significantly different in the no cue condition compared to the cued conditions (all Dunnett tests with at least P>0.2). Second, MT was not significantly affected by cue range ($F_{(4,881)}$=0.089, P=0.986). Mean MT across all conditions and subjects was 163 ms (SEM=6 ms, N=90=15 subjects × 6 conditions). Concerning the directional errors, we found that their number was very small in all conditions. The overall mean (computed using the square-root transformed counts and then squaring the mean) was 0.040 directional errors across subjects and conditions (95% confidence interval=0.011−0.088, N=90). So, on average there was far less than one directional error per subject and condition. The analyses showed no significant difference of number of directional errors between the no cue condition and the cued conditions (all Dunnett tests with P>0.9) and no significant effect of cue range ($F_{(4,56)}$=0.178, P=0.949). In contrast with the previous analysis, we found that the error of the initial movement direction was affected by the experimental conditions. All trials in the 22.5–180 deg cue range conditions were used in this analysis whether the direction of response was counted as correct or not. We found that the error of the initial direction of movement was not affected significantly by cue range ($F_{(3,717)}$=1.976, P=0.116), whereas it varied significantly with the angle θ between the target and the center of the cue ($F_{(1,717)}$=19.255, P<0.0005). The effect of θ on the error of the initial direction of movement can be appreciated in Fig. 2C. The figure shows that the error of the initial direction of movement was biased toward the center of the cue. The parameter estimates indicate that this bias amounted on average to 10% (SEM=2%) of the angle θ. This result contrasts with the absence of effect on movement trajectory when discrete cues were presented (Pellizzer and Hedges 2003), but is similar to results obtained in some reaching tasks with distractors (Lee 1999; Tipper et al. 1998). This result is also consistent with the hypothesis of continuous specification of the parameters of a motor response (Bock and Arnold 1992; Erlhagen and Schöner 2002; Ghez et al. 1997; Lee 1999) and suggests that the intended direction of response was centered on the cue during the cue period and that it was transformed toward the direction of the target during RT (Fig. 1B). The bias in the initial direction of movement reveals the tail of the transformation, which was then completed during the execution of the movement. Indeed, we found that the error in movement direction decreased during its execution. The bias toward the center of the cue was still significant at the moment of maximum velocity ($F_{(1,717)}$=5.208, P=0.023) but was reduced at 3% (SEM=2%), whereas it was not significant at the end of the movement ($F_{(1,717)}$=0.924, P=0.337). Both the analyses of RT and of the initial movement direction indicate that the intended direction of movement during the cue period was directed toward the center of the cue and then transformed progressively to be directed toward the target. This transformation is similar to that revealed by visuomotor mental rotation tasks (Georgopoulos and Pellizzer 1995) and was also suggested as occurring during drawing and writing movements (Pellizzer 1997).

Conclusions

The results supported the qualitative and quantitative predictions of the capacity-sharing model regarding the relation of RT with cue range and with the angle θ between the target and the center of the cue. Therefore, the results were consistent with the hypothesis that the processing resources engaged during motor planning are limited and distributed as a function of the probability distribution of the target and that these resources are reallocated when the response is defined. The reallocation of resources was assumed to require a transformation in range and location of the representation of the response. The effects predicted when the resources are spread across a continuous spatial range, which was induced in this experiment by the continuous cues, are different than those predicted when the resources are divided in independent representations, which was induced by discrete spatial cues in a previous experiment (Pellizzer and Hedges 2003). The results have supported the predictions. In conclusion, these results suggest that the neural patterns associated with the representation of the intended direction of movement are modulated by the probability distribution of the target. This is consistent with neurophysiological experiments that have shown neural activity varying as a function of the uncertainty of the motor response (Basso and Wurtz 1998; Bastian et al. 1998; Riehle and Requin 1989).

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