Neurophysiology of the Parieto-Frontal System During Target Interception

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ABSTRACT

We studied the functional properties of neurons of two elements of the parieto-frontal system: area 7a of the PPC and the motor cortex (M1), during an interception task of stimuli moving in real (RM) and apparent motion (AM). The stimulus moved along a circular path with one of 5 speeds, and was intercepted at 6 o'clock by exerting a force pulse on a joystick. A smooth stimulus motion was produced in RM, whereas in AM 5 stimuli were flashed successively at the vertices of a pentagon. The results showed, that a group of neurons in both areas of the cortex responded not only during the interception but also during a NOGO task in which the same stimuli were presented in the absence of a motor response. Most of these neurons were tuned to the stimulus angular position. In addition, we found that the time-varying neuronal activity in both areas was related to various aspects of stimulus motion and hand force, with stimulus-related activity prevailing in area 7a and hand-related activity prevailing in M1. Interestingly, the neural activity was selectively associated with the stimulus angle during RM, whereas it was tightly correlated to the time-to-contact during AM. Thus, the results suggest that area 7a was processing high level features of the circularly moving stimuli and was involved in the production of an early command signal for stimulus interception, whereas M1 was still processing some aspect of the visual stimulus that were used to trigger the interception movement using a predictive mechanism.

KEY WORDS

Motor cortex, Posterior parietal cortex, Interception.

INTRODUCTION

The interception of a moving target is a complex process that requires the analysis of visual motion information (target direction, velocity, position and travel time) [Van Donkelaar, 1992] and the use of a predictive strategy in order to determine where and when the target is going to be at the end of the interception movement [Van Donkelaar, 1992] [Lee, 1976] [Port, 1997]. Two main variables can be used in this predictive process to control the initiation of the interception movement: the position of the target [Van Donkelaar, 1992] and the time-to-contact [Port, 1997] [Lee, 1976] which corresponds to the first-order estimate of the time to arrival. Here we studied the neural mechanisms of two areas in the parieto-frontal system underlying the interception behaviour. An important number of studies have demonstrated the tight anatomo-functional link between particular regions of the posterior parietal cortex and the premotor areas of the frontal lobe [Battaglia-Mayer, 2001]. These cortical areas are involved in reaching and grasping mechanisms [Caminiti, 1998] and have the ability to process high order visual motion [Merchant, 2001] [Merchant, 2003] [Merchant, 2004]. Thus, the parieto-frontal system is a strong candidate to be the neural substrate of target interception. Therefore, in the present study we investigated the neural mechanisms of the sensorimotor integration and predictive processes involved in intercepting moving targets in area 7a and M1. An emphasis was made in the study of the neural representation of the

target position and the time-to-contact for controlling the initiation of the interception movement in these areas.

METHODS

Two male rhesus monkeys (*Macaca mulatta,* 4 and 7 kg BW) were used in these experiments. Animal care conformed to the principles outlined in the Guide for Care and Use of Laboratory Animals (National Institutes for Health publication no. 85-23, revised 1985). These monkeys were trained to intercept stimuli moving in real and apparent motion (Fig. 1A). The stimulus moved along a circular path (15.2 degrees outside diameter and 1.7 degrees width) with one of 5 angular speeds (180, 300, 420, 480 and 540 deg/s), and was back-projected on a tangent screen using a LCD projector (NEC Multisync MT 820/1020). In RM the stimulus was displayed every 16.7 ms, resulting in a smooth stimulus motion that was indistinguishable from a continuously moving stimulus. In AM five stimuli were flashed successively for 16.7 ms at the vertices of a regular pentagon. All the stimuli traveled counterclockwise. The monkeys were trained to intercept the targets at 6 o'clock in its circular trajectory, by exerting a force pulse on a semi-isometric joystick (Measurement Systems Inc., Model 467-G824, Norwalk CT, USA), which controlled a cursor on the screen. This experimental configuration was such that in AM the monkeys intercepted a stimulus that crossed the 6 o'clock position in a perceptual rather than in a physical sense. We provided some feedback to the monkeys about their interception performance. Monkeys received a liquid reward if the angle between the cursor and the stimulus was less than 18 degrees.

Impulse activity of single neurons was recorded extracellularly from area 7a and the proximal arm area of M1 (left hemisphere) (see Merchant et al., 2001b for details). All isolated neuronal potentials were recorded regardless of their activity during the task, and the recording sites changed from session to session. The presentation of the visual stimuli, behavioural control and data collection were carried out by a personal computer. Standard statistical techniques were used for the analysis of the behavioural and neural data including analysis of variance, analysis of covariance and multiple linear regressions analysis. The level of statistical significance to reject the null hypothesis was $\alpha = 0.05$.
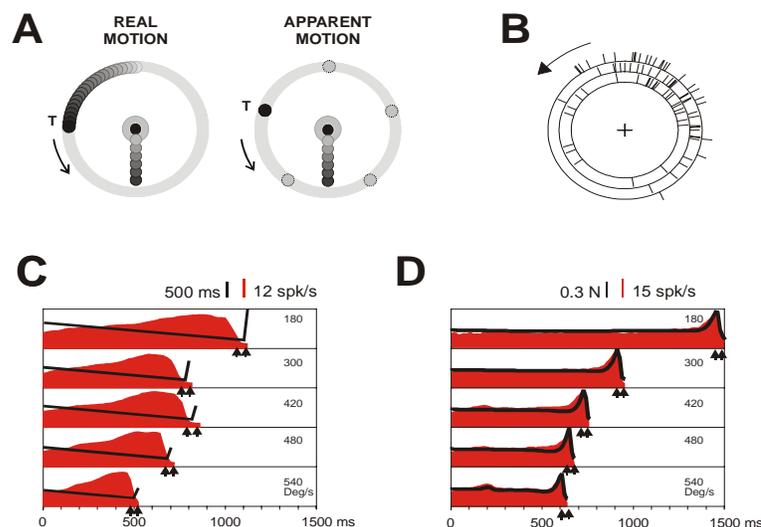
Figure 1. A. Interception task. B. Raster of a neuron tuned to the stimulus angular position. C. Activity profile of a neuron with a response (red) that was inversely proportional to the time-to-contact (black line). D. Neuron with a response (red) with the same profile of the of the hand force (black line).

RESULTS

The analysis of the monkeys' performance in the interception task indicated that the animals could use either the position of the target or the time-to-contact as variables to control the initiation of the interception movement. This is due to the fact that: (1) the location of the target in relation to the interception zone was not constant, and (2) the movement time that defines the time-to-contact, was not constant either. These results were obtained for both real and apparent motion targets. Nevertheless, as we will review, the neurophysiological data indicated that different variables were used to intercept targets moving with real or apparent motion.

The first interesting finding at the neurophysiological level was that neurons in area 7a and M1 responded selectivity to RM or AM in a NOGO task, in which the same stimuli were presented in the absence of a motor response. In area 7a, the neurons with selective responses to RM were tuned to the stimulus angular position (Fig. 1B), whereas the neurons with selective responses during AM showed a periodic entrainment of activation with the period of the inter-stimulus interval of the flashing dots. Hence, these results suggest that during the NOGO task, area 7a could codify the location and the temporality of the stimulus in RM and AM, respectively. In contrast, in the motor cortex the neurons were tuned to the angular position in RM, but did not respond to AM in the NOGO task. This suggests that the motor cortex has access to spatial information of moving stimuli, even in the behavioural context where the stimulus is not used to trigger a motor response. However, the motor cortex did not process the temporal information of the stimuli under these circumstances.

We used a multiple linear regression model in order to determine the explicative power of different sensory and motor parameters on the time-varying activity of the neurons during the interception task. These parameters were the sine and cosine of the target angle, the time-to-contact (τ), the hand force and the hand force velocity. The temporal relation, δ between the neural activity and these sensorimotor parameters was varied systematically. The standardized regression coefficients were used to identify the parameters with the best explanatory power on the neural activation profile. These analyses revealed, first, that the time-varying neuronal activity in area 7a and M1 was related to various aspects of stimulus motion and hand force in both the motion conditions, with stimulus-related activity prevailing in area 7a and hand-related activity prevailing in M1 (Fig. 1D). In addition, a very interesting finding was that the neural activity was selectively associated with the stimulus angle during RM interceptions, whereas it was tightly correlated to the time-to-contact during AM interceptions (Fig. 1C), particularly in M1. The analysis of δ revealed a sensory processing of the angular position and time-to-contact in area 7a, whereas in the motor cortex both variables were processed in a predictive fashion.

Finally, we used a binomial analysis in order to establish whether the processing of sensory variables was associated with the encoding of motor variables during the interception task. The results showed that in M1 during RM the hand force was significantly associated with the hand force velocity and the stimulus angle, whereas during AM the hand force was significantly coupled with τ and the hand force velocity. In addition, in area 7a for RM the stimulus angle was significantly associated with the hand force velocity, and τ was significantly coupled with the hand force velocity. Finally, in AM, area 7a neurons showed significant associations between the stimulus angle and the hand force and force velocity.

DISCUSSION

The results showed that the sensory variables were better represented in the activity of area 7a neurons during interception task, whereas the motor parameters were better accounted for in the activity M1 cells. Nevertheless, the neural activity in area 7a showed a clear modulation by motor variables, and the M1 activity showed also a representation of sensory parameters. These results suggest that area 7a and M1 are

probably part of a parieto-frontal system engaged in the interception of moving targets. Under this framework, neurons in area 7a process the high level features of the circularly moving stimuli and produce an early command signal for stimulus interception. This information can be transmitted through different potential nodes of this distributed system to M1, where some aspects of the visual stimulus are still processed to trigger the interception movement using a predictive mechanism.

On the other hand the results also revealed that during the real motion situation the stimulus angle was the most important stimulus parameter encoded in both areas, whereas during the apparent motion condition the time-to-contact became the parameter with the larger explanatory power in the motor cortex. Based on all this evidence, it is possible that the neural mechanisms that controlled the initiation of the interception movement differed in real and apparent motion. We suggest that the neural representation of stimulus position over time was the signal used to initiate the movement during the interception of real moving stimuli, so that the interception movement could be started when the stimulus position signal reached a specific value, a mechanism that will follow the distance threshold model [van Donkelaar, 1992]. In contrast, the interception movement in the apparent motion situation was possibly triggered when the neural representation of τ reached a particular value. This neural mechanism, then, will follow the threshold τ model [Lee, 1976].

As far as we know, no imaging studies have been performed during interceptive behavior. Thus, based on our present results we predict that fMRI studies will find that the human parieto-frontal system is also engaged during target interception.

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