Neurophysiology of Perceptual and Motor Aspects of Interception

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Merchant, Hugo and Apostolos P. Georgopoulos. Neurophysiology of perceptual and motor aspects of interception. *J Neurophysiol* 95: 1–13, 2006; doi:10.1152/jn.00422.2005. The interception of moving targets is a complex activity that involves a dynamic interplay of several perceptual and motor processes and therefore involves a rich interaction among several brain areas. Although the behavioral aspects of interception have been studied for the past three decades, it is only during the past decade that neural studies have been focused on this problem. In addition to the interception itself, several neural studies have explored, within that context, the underlying mechanisms concerning perceptual aspects of moving stimuli, such as optic flow and apparent motion. In this review, we discuss the wealth of knowledge that has accumulated on this topic with an emphasis on the results of neural studies in behaving monkeys.

INTRODUCTION

The proper control of behavior is essential for animal survival. This control is highly dependent on prediction. In fact, the guidance of effector movements (hands, feet, jaws) to their destination (a ball, a surface, a prey) requires some extrapolation of the sensory signals so that proper adjustments of the movements can be done to cope with task demands. Needless to say, predictive behavior can be based on spatial and/or temporal cues, depending on the current contingencies. On the spatial side, different behaviors such as reaching and grasping use different spatial aspects of the static target to guide the movement (Georgopoulos 2002; Sakata 2003). In addition, interception of moving targets can also use spatial cues to control the initiation and trajectory of the effector movement (Van Donkelaar et al. 1992). On the temporal side, a simple predictive mechanism for movement guidance is to use first-order time-to-contact (tau, τ) information. The tau hypothesis was formulated by Lee (1976) and originally suggested that movement initiation and deceleration to a destination could be controlled using the first-order estimate of the time to arrival to the proper destination. The idea was that in several behavioral contexts, such as target interception and collision avoidance, the movement is triggered when tau attains a particular threshold. A recent reformulation of the tau theory generalizes for movement guidance in practically any circumstance (Lee 1998). The main theory now states that movement guidance can be regarded as the closure of gaps, which, in turn, comprises tau-couplings, i.e., keeping two or more changing taus in constant ratio. Thus tau-coupling could be used to synchronize movements and regulate their kinematics. Tau theory is about the control of behavior using perceptual information from the

environment. This ecological approach to movement control implies that a simple variable such as tau is an affordance that the environment is providing and which animals use to guide their behavior (Gibson 1979).

This review focuses primarily on the neural mechanisms underlying behavioral guidance on the basis of visual-motion signals resulting from any combination of object motion and self-motion of the organism in the environment. Specifically, we review the psychophysical evidence for the use of tau and/or spatial parameters to control interception movements and the results of neurophysiological studies that investigated the interface between spatiotemporal processing of visual information and the motor apparatus engaged in the control of interceptive motor responses.

COLLISION AVOIDANCE AND TAU

To plan a proper reaction, a subject needs to estimate the time remaining before the collision with an approaching object. An estimate of this time is provided by tau, which in this situation, equals the ratio of the size of the retinal image at a given time over the rate of expansion of the image (Fig. 1; Lee 1976; Lee and Reddish 1981). Indeed, this was the original definition of tau (Lee 1976). The time to collision is given exactly by tau when the velocity of the object is constant (Fig. 1). In real life, however, closing velocity is rarely constant. Nevertheless, there is a good number of studies indicating that animals and human subjects trigger specific reactions when tau reaches a particular value (threshold-tau model). For example, it has been observed that gannets close their wings just before entering the water during plunge dive, at a time that correlates with a particular threshold-value of tau, and not with other variables (Lee and Reddish 1981). In addition, a large amount of information indicates that human subjects use tau to estimate time to contact when playing ball games, driving a car, or landing a plane (Regan and Gray 2000; Tresillian 1999; Craig et al. 2000). Finally, it has been shown that, when an object is on a direct collision course, the human visual system uses separate channels for tracking the rate of expansion, the time-to-contact, and the absolute change in size (Regan and Hamstra 1993).

When an object is approaching a subject, its retinal image changes in size. In fact, neurophysiological studies performed in the pigeon and the locust have used looming stimuli to simulate an approaching object (Hatsopoulos et al. 1995; Rind and Simmons 1999). Three types of looming-sensitive neurons
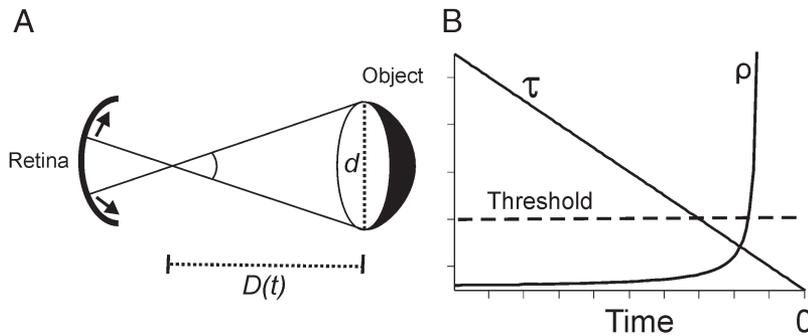

FIG. 1. *A*: spherical object approaching the eye. With an constant approaching velocity, *V*, at time *t* and distance $D(t)$ away from the subject, it subtends a visual angle $\theta(t)$. *B*: time-course of 2 optical variables tau (τ) and absolute rate of expansion (ρ) derived from a spherical object moving at a constant speed directly toward the eye. Horizontal line represents the hypothetical value of the threshold value for onset of neural activity. Modified from Sun and Frost 1998.

have been found in the nucleus rotundus of pigeons, each computing a different optical variable related to image expansion of objects approaching on a direct collision course (Rind and Simmons 1999; Sun and Frost 1998). One group of neurons signals the time-to-contact using tau, a second group signals the absolute rate of expansion (ρ), and a third group signals a complex optical variable that has a distinct peak and a shallower ascending slope for larger objects, which is the opposite of the ρ function (Fig. 1). The absolute rate of expansion is required to compute the two other parameters, whose respective functions probably are to provide precise time-to-collision information and an early warning detection for approaching objects. In the locust there is a pair of synaptically linked neurons that respond to looming stimuli. These neurons are the lobula giant-movement detector (LGMD) and the descending contralateral movement detector (DCMD). The DCMDs are tuned to detect direct collision course (Judge and Rind 1997), whereas the LGMDs are looming-sensitive neurons the response of which depends on the size and the speed of the approaching object (Hatsopoulos et al. 1995). In fact, this last type of response is very similar to the third group of looming-sensitive neurons in the pigeon. Hence, there is direct evidence that an affordance like tau is represented in the nervous system and can be used to drive the response of the subject.

An appealing but unanswered question is whether neurons in the parieto-frontal system of primates use the same type of collision signaling mechanisms observed in pigeons and locusts. There is strong evidence in human subjects and monkeys that the middle superior temporal area (MST) and the posterior parietal cortex (PPC) are involved in optic flow processing (Duffy and Wurtz 1991; Merchant et al. 2001; Orban et al. 1992; Siegel and Read 1997). Neurons in MST are tuned to the

focus of expansion and can code for the direction of heading (Bradley et al. 1996; Duffy and Wurtz 1995). However, the responses of area 7a neurons to optic flow stimuli appear to be more complex than those in MST. Whereas most MST neurons respond selectively to elementary optic flow components [e.g., expansion, contraction, clockwise (CW) or counterclockwise (CCW) rotation], some area 7a neurons respond similarly to CW and CCW rotations (Siegel and Read 1997). Recently, we analyzed the neuronal responses in area 7a to eight different kinds of motion (right-, left-, up-, downward, CW, CCW, expansion, contraction) using hierarchical tree clustering and multidimensional scaling (MDS; Fig. 2). These analytical techniques were used to reveal associations in the activity of neuronal populations driven by elementary optic flow components. Hierarchical tree clustering analyses showed that pairs of opposite stimulus motions (left/right, upward/downward, CW/CCW) were clustered in three separate branches (Fig. 2). The interpretation of these superordinate units is obvious, because they signify horizontal, vertical, and rotatory motions, respectively. In contrast, expansion was in a lone branch, whereas contraction was also separate but within a larger cluster (Merchant et al. 2003a). This finding suggests that radial motion, and, within it, expansion and contraction are represented quite differently in the ensemble. Specifically, the fact that expansion was in a branch stemming directly off the root of the tree indicates a fundamental difference between expansion and all other stimulus motions, which may be related to the prominence of expansion in daily life because of locomotion. The distances among these clusters were subjected to an MDS analysis to identify the dimensions underlying the tree clustering observed. This analysis revealed two major factors (dimensions) in operation. The first dimension separated expansion from all other stimulus motions, which seems
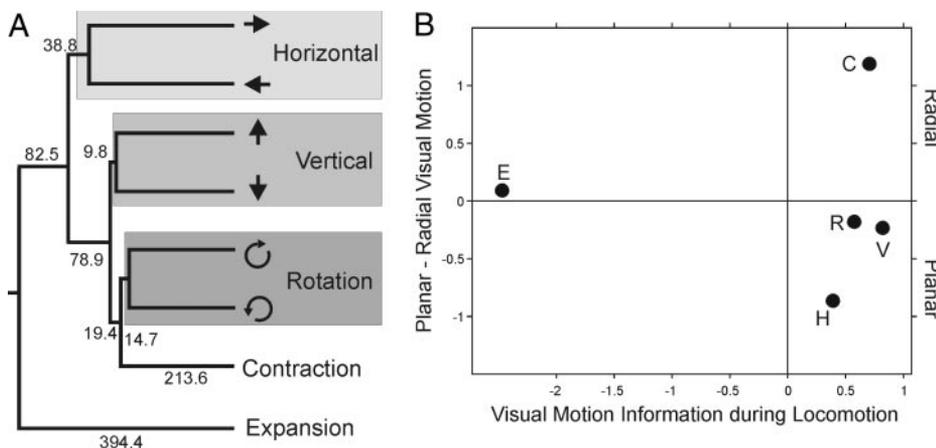

FIG. 2. *A*: dendrogram of the motion condition clustering derived from the normalized (z-score) activity of 150 neurons using the hierarchical tree analysis method. Numbers within the dendrogram correspond to the distance of each cluster in arbitrary units. *B*: results of multidimensional scaling (MDS) analysis. Two-dimensional representation of the 5 superordinate clusters in the tree clustering analysis. The 1st (*x-*) axis represents distinction between expansion and other motion conditions, whereas the 2nd (*y-*) axis dissociates planar from radial motion. H, horizontal; V, vertical; R, rotation; E, expansion; C, contraction. Modified from Merchant et al. 2003a.

to reflect again the prominence of expansion during the common activity of locomotion. Now, the second dimension obviously separated planar from radial motions, a finding not apparent in the tree clustering analysis (Fig. 2; Merchant et al. 2003a). A possible interpretation of the grouping of up/down, left/right, and CW/CCW motions is that all of them correspond to rotations with respect to the three cardinal axes of rotation. For example, to a good approximation, the up/down motions could come from rotation of the eyes or head-plus-eyes about a pitch axis through the head, the left-right motion could come from rotation of the eyes or head-plus-eyes about a yaw axis through the head, and the CW/CCW rotation could come from rotation of the eyes or head-plus-eyes about a roll axis through the head. In addition, the up-down and left-right motions could also come from up/down and left/right translatory movement of the head, respectively. In contrast to these considerations, radial motions can only come from translation in depth, which, in turn, typically comes about from moving in space, a very common activity. We believe that it is this last feature that is captured by the second (*y*-axis) dimension in the MDS plot (Fig. 2). Thus radial motion in general, and expansion in particular, seem to hold a special place in the ensemble processing of visual motion in area 7a, reflecting, most probably, behavioral considerations.

The findings above do not necessarily follow from the existence of a selectivity of single cell discharge to optic flow (Fig. 3). This is evidenced by the fact that such selectivity was also observed in the motor cortex (Merchant et al. 2001), but no clustering was found in that area. Therefore the clustering observed in area 7a seems to rely on specific constraints among cell responses to the different kinds of optic flow stimuli. Finally, although the horizontal, vertical, and rotatory motions were represented individually at the single cell level (Fig. 3), as it was the high preference for the expansion (Fig. 3), the simultaneous grouping of these three motion classes and the segregation of expansion in a unique cluster apparently is an emergent property of the neuronal ensemble.

Thus the posterior parietal cortex can process optic flow information in a very complex, but behaviorally meaningful fashion. It is reasonable to expect that MST and PPC are good candidates for the neural representation of tau in primates. In fact, a recent functional MRI (fMRI) study showed that the parieto-frontal system in humans is specifically activated during perception of time-to-contact judgments (Field and Wann 2005). Interestingly, our group was the first to characterize the neural correlates of tau in area 7a and motor cortex in the monkey.

INTERCEPTION OF TARGETS MOVING WITH RECTILINEAR TRAJECTORIES: PSYCHOPHYSICS AND NEUROPHYSIOLOGICAL EXPERIMENTS

The interception of moving targets is another behavior where prediction is key for success and where tau can play a fundamental role. In this case, however, tau cannot be directly specified as the ratio of the size of the retinal image at a given time over the rate of expansion of the image. Instead, tau should be regarded as the time-to-closure of the gap between the effector and the target-to-be-intercepted, at the current gap closure rate (Lee 1998). During the past 15 yr, we have studied the psychometric performance of human subjects and monkeys

during target interception, as well as the neural mechanisms of target interception in the parieto-frontal system of the monkey. In an initial set of experiments, we trained human subjects to intercept moving targets on a computer screen using a cursor controlled by a two-dimensional (2D) manipulandum (Figs. 4 and 5). The targets could move with 1 of 18 combinations of three acceleration types (constant acceleration, constant deceleration, and constant velocity) and six target motion times, from 0.5 to 2.0 s. In addition, the targets could move from the lower right or left of the monitor with an angle of 45° toward an interception zone located on the vertical meridian 12.5 cm above a starting zone, located on the bottom of the monitor. Thus subjects intercepted the target by moving the cursor upward from the starting point to the interception zone (Figs. 4 and 5). This experimental paradigm was well suited to study the predictive strategy used to control the initiation of the interception movement and the neural underpinnings of that control. Initially we examine whether the interceptive behavior followed one of two strategies, namely a reactive or a predictive strategy. The reactive strategy is based on a threshold-distance model and assumes that the interception movement starts when the target has traveled a constant distance and is further modulated in an ongoing fashion (Van Donkelaar et al. 1992). On the other hand, the predictive strategy is based on a threshold-tau model and assumes that the main element of control is when to start the movement, because the interception movement is ballistic (Port et al. 1997). The psychophysical data indicated that the control of movement initiation was quite complex. In general, for long target motion times, the subjects could use either strategy. In contrast, for short target motion times, the subjects used exclusively the predictive, tau-based strategy (Port et al. 1997). These results underscore the fact that context, accuracy requirements, target kinematics, and subjective preferences are all important in determining the specific strategy adopted in initiating and controlling the interception movement.

Regarding the movement kinematics during the same interception task, we found that, for fast moving targets, human subjects produced a single movement with symmetrical, bell-shaped velocity profiles. In contrast, for slowly moving targets, subjects produced a series of submovements, whose amplitude was controlled to keep the displacement of the hand proportional to first-order estimate of target position (Lee et al. 1997). These data were analyzed further to test the tau-coupling hypothesis, namely that movement guidance can be regarded as the closure of gaps and that the gap closure depends on the principle of tau-coupling: keeping two or more values of tau in a constant ratio (Fig. 4). Surprisingly, we found that subjects achieved the interception by keeping the tau of the gap between the hand and the target coupled with the tau of the gap between the hand and the interception zone (Fig. 4; Lee et al. 2001a). Therefore it appears that, during interception movements, the closure of two or more gaps between effectors and destinations is regulated by constantly sensing the taus of gaps and moving with a kinematics that would keep the critical taus coupled with a constant ratio.

In neurophysiological studies, we recorded cell activity in the primary motor cortex (M1) of rhesus monkeys during the same interception task tested in human subjects, as well as during a NOGO task, in which the same stimuli were presented, but the animals did not produce an interceptive re-
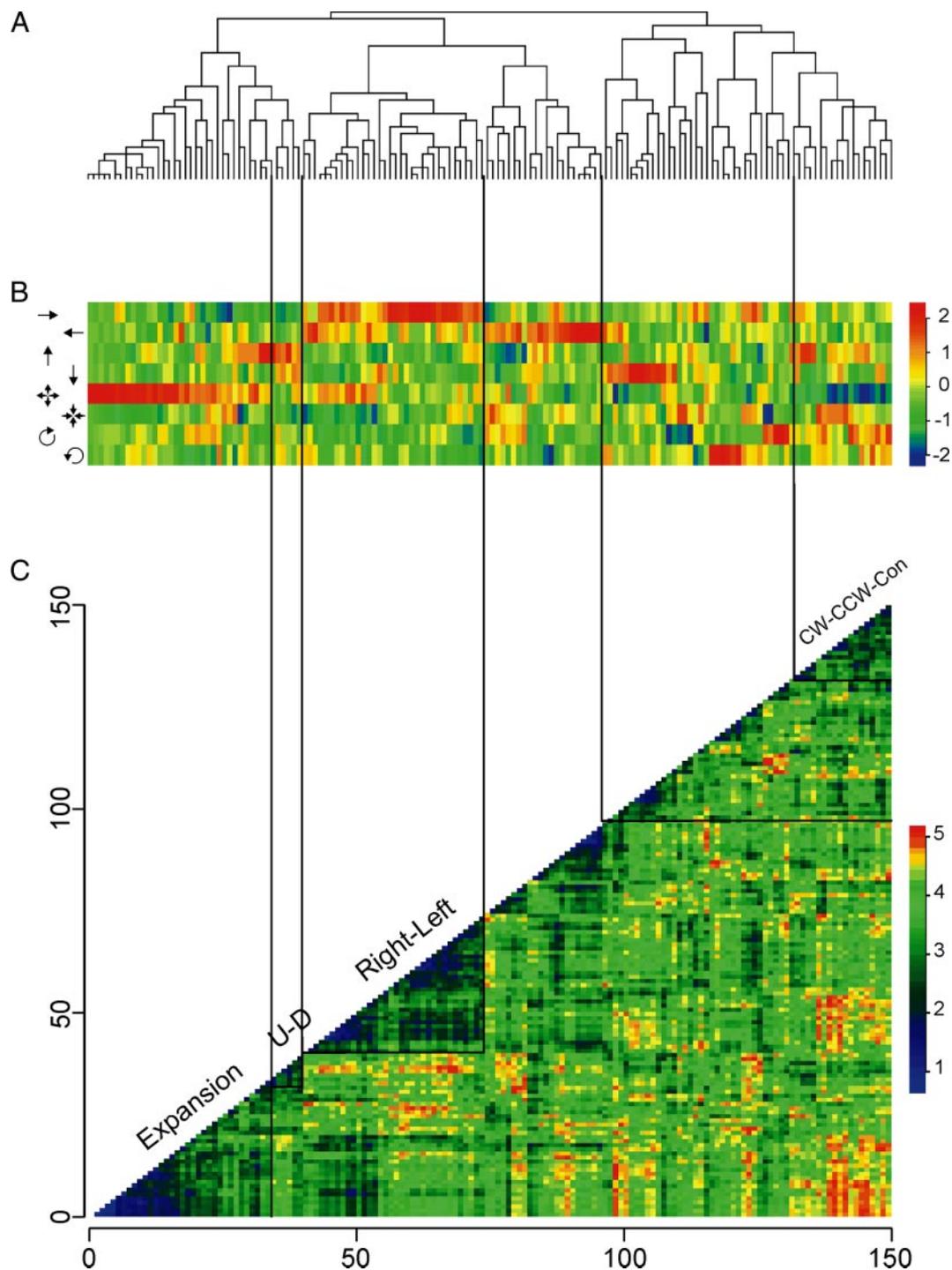
FIG. 3. Hierarchical clustering of 150 neurons in area 7a that showed significant modulation of their activity for motion condition. *A*: dendrogram showing clustering procedure. Each vertical line rising from abscissa corresponds to 1 neuron. Horizontal lines that join the vertical lines represent newly formed clusters and specify distance between the 2 clusters in the ordinate. *B*: z-scored discharge rate for the same neurons ordered according to clustering process. Color scale used ranges from –2 to 2 SD, where 0 is the mean for all motion conditions. *C*: dissimilarity matrix of the Euclidean distance between each possible pair of recordings is displayed in the appropriate cell using a color scale, different from the color scale used in *B*. Cells were also ordered following clustering process. Vertical lines that start at the base of the dendrogram (*A*) and finish in the dissimilarity matrix (*C*) indicate the 5 clusters of cells response patterns: expansion, up-down, right-left, contraction-clockwise (CW)-counterclockwise (CCW) rotation. In the dissimilarity matrix (*C*), groups of neurons with similar response patterns of the optic flow stimuli appear as triangles of dark color (short distance).

sponse (Port et al. 2001). There were three major findings, as follows. First, M1 cell activity was modulated during both tasks by time-varying aspects of target motion, including acceleration profile, direction of target motion, and total travel time (Port et al. 2001). This finding suggests that M1 has access to visual motion information that is relevant for guiding the interception movement. Second, a nonhierarchical cluster analysis on the spike density functions during the interception task classified the temporal pattern of activity in two main groups: *1*) neurons with a temporal profile that followed the
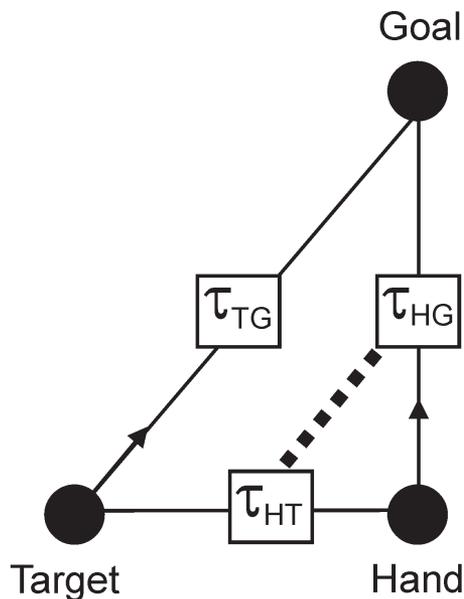
FIG. 4. Tau coupling in an interception task. Target T moved at various constant velocities, accelerations, or decelerations toward the goal G, and the subject had to move the hand cursor H so that it stopped at the goal as the target arrived there. Participants solved the task by tau-coupling τ_{HT} and τ_{HG}. The τs are the time-to-closure at the current closure rate of the gaps HT and HG. Modified from Lee 1998.

kinematics of the interception movement, and, more interestingly, *2*) neurons whose activation patterns conveyed information regarding the initial target velocity and the interval between successive submovements (Lee et al. 2001b). These results underlie the dynamic nature of sensorimotor transformations during interceptive behavior, where different neural subpopulations in M1 representing target and movement parameters are probably in close interaction. Finally, the time-varying activity of neurons in M1 was modulated according to the first-order estimate of the time-to-interception, as revealed using a multiple regression model (Port et al. 2001). These results suggest that M1 could process the tau of the gap between the hand and the interception zone in a dynamic way and that this neural representation could be used to control the interception movement according to the changes in this variable.

INTERCEPTION OF CIRCULARLY MOVING TARGETS: PSYCHOMETRIC MEASUREMENTS

In a more recent set of experiments, we characterized the interceptive behavior of human subjects and monkeys during the interception of circularly moving targets with real or apparent motion. The task required the interception of a moving target at 6 o'clock in its circular trajectory by applying a downward force pulse on a pseudoisometric joystick that controlled a cursor on the computer monitor (Fig. 5; Merchant et al. 2003b; Port et al. 1996). The target could move with one of five speeds, ranging from 180 to 540°/s, in the CCW direction. In the real motion condition, the targets moved smoothly along a low contrast circular path, whereas in the apparent motion situation, the target was flashed successively at the vertices of a regular pentagon, also placed over the circular low contrast path. This last condition was chosen following the work of Shepard and Zare (1983), which showed that the classical rectilinear apparent motion illusion could be extended to curvilinear path-guided apparent motion if a low contrast path was presented between pairs of flashing dots. In this condition, the subjects perceived the dot moving back and forth along that path, and the interstimulus interval (ISI) necessary to produce the apparent motion illusion increased linearly with the length of the path (Shepard and Zare 1983). Accordingly, we determined the detection threshold for our circular path-guided apparent motion in human subjects. To this end, we instructed the subjects to indicate with a key press whether or not they perceived a circularly moving object when the stimuli were flashed successively at the vertices of the pentagon. The stimuli were presented with 1 of 33 speeds (150–600°/s). The average psychometric curve revealed that the threshold for path-guided apparent motion detection was 314°/s, which corresponds to an ISI detection threshold of 229 ms (Merchant et al. 2005).

We used path-guided apparent motion in our interception task for two main reasons. First, we were interested in the study of the psychometric abilities of human subjects and monkeys to intercept an illusory target. The main question here was to understand whether the interceptive strategy and performance were similar during the interception of real and apparent moving stimuli. The second reason was to study the neural bases of target interception under a spatially defined condition, such as real motion, and during apparent motion where the temporal succession of stimuli defines the perception of an illusory motion.

Regarding the interceptive behavior, we found that the interception error, measured as the signed angular difference between the target and the cursor at the interception, increased linearly with target speed and was larger in the apparent than in the real motion condition (Fig. 6*A*; Merchant et al. 2003b; Port et al. 1996). In fact, both human subjects and monkeys showed early interceptions for slowly moving targets and late
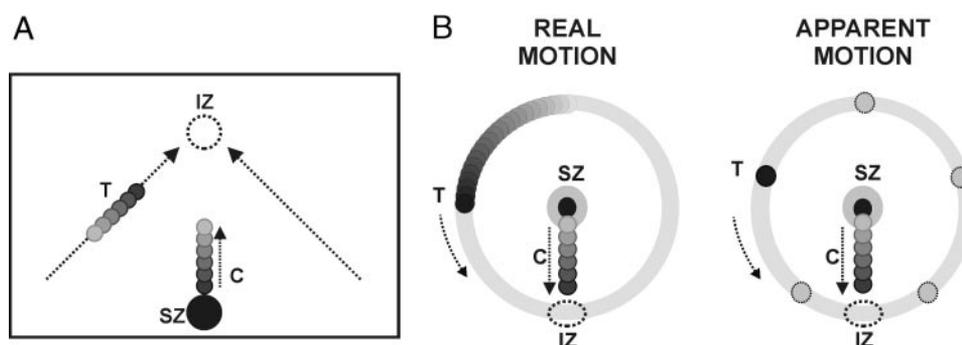

FIG. 5. Interception tasks. *A*: interception of rectilinear moving targets (as in Fig. 3). *B*: interception of circularly moving targets. T represents the smoothly moving target in the real motion condition and the flashing stimulus at the vertices of a regular pentagon in the apparent motion condition. C, cursor; SZ, starting zone; IZ, interception zone.
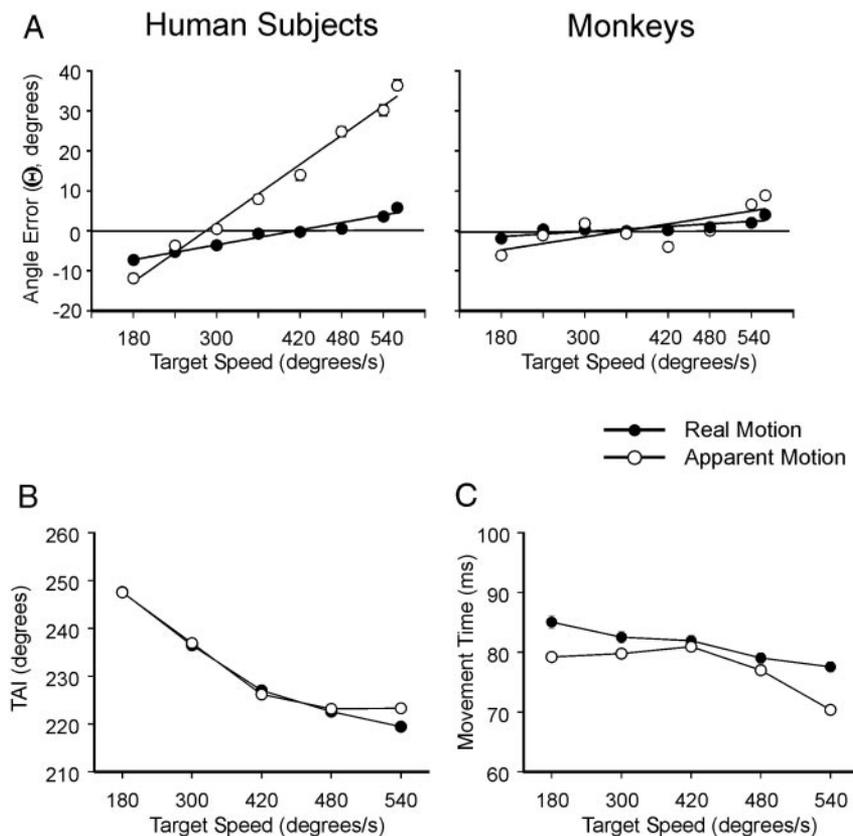
FIG. 6. Behavioral performance during the interception task. *A*: angle error (Θ) of 10 human subjects and 2 monkeys. *B*: position of stimulus at the beginning of the interception movement (TAI), monkey data. *C*: movement time is plotted as a function of the stimulus speed, monkey data. ●, real motion; ○, apparent motion condition. Modified from Merchant et al. 2003b.

interceptions for fast moving ones (Fig. 6*A*). This showed that *1*) subjects can intercept an apparent motion target but, compared with real motion, the performance is somewhat degraded overall; and *2*) there are similarities in performance between the two target motion conditions. More specifically, the fact that target velocity influenced performance in a similar fashion in the two conditions suggests that the motor system can access, and use, the visual information provided by the moving target.

We then studied the possible strategy adopted to control the initiation of the interception movement. For that purpose, we calculated a measure of target distance and a measure of target time-to-contact at the beginning of the interception movement. The former corresponded to the angle (Fig. 6*B*, TAI) and the latter to the movement time. According to a threshold-distance (from interception) model, the interception movement should start at a constant distance from the interception zone, in this case at a constant TAI. In contrast, the threshold time-to-contact model states that the interception movement should start at a constant tau, which implies a constant movement time. However, it was difficult to assign a particular model to the real and apparent motion data. For example, we found that TAI decreased asymptotically as a function of the stimulus speed in both motion conditions and that the movement time decreased slightly as a function of the stimulus speed and was larger in the real than in the apparent motion condition (Fig. 6, *B* and *C*). Nevertheless, as we discuss below, the neurophysiological data collected in the parieto-frontal system suggest the use of spatial cues during real motion and the use of tau to control of movement in the apparent motion condition.

At this point it is important to mention that these behavioral data were not analyzed further in the context of tau-coupling

and closing gaps, because they were for the first interception task. It would be interesting to test whether there is again a tau-coupling involving the tau of the gap between the hand and the real and apparent moving target, and the tau of the gap between the hand and the interception zone (Lee et al. 2001a).

NEURAL REPRESENTATION OF SPACE AND TIME IN THE PARIETO-FRONTAL SYSTEM DURING VISUAL MOTION

After we assessed the psychometric abilities of human subjects and monkeys to intercept real and apparent motion targets, we proceeded to study the visual motion processing in area 7a and the motor cortex during real and apparent motion in a NOGO task. The results revealed two populations of neurons in area 7a (Merchant et al. 2004b). The first comprised cells whose activity was tuned to the angular location of the circularly moving stimulus. These neurons responded in a particular part of the circular trajectory of the stimulus (Fig. 7). Interestingly, most of these responses were selective for real motion, and the preferred angular positions were evenly distributed (Fig. 7). However, there was a subpopulation of neurons that also responded to apparent motion at high stimulus speeds. A detailed visual receptive field analysis was also performed, in which moving visual stimuli were presented to the monkeys, while they fixated their eyes and did not move their arm. The stimuli consisted of random dots moving coherently in eight different kinds of motion (see the optic flow stimuli above) and were presented in 25 square patches on a LCD projection screen. This analysis showed that the relation between angular tuning and the receptive field position varied across the population of neurons, ranging from neurons with
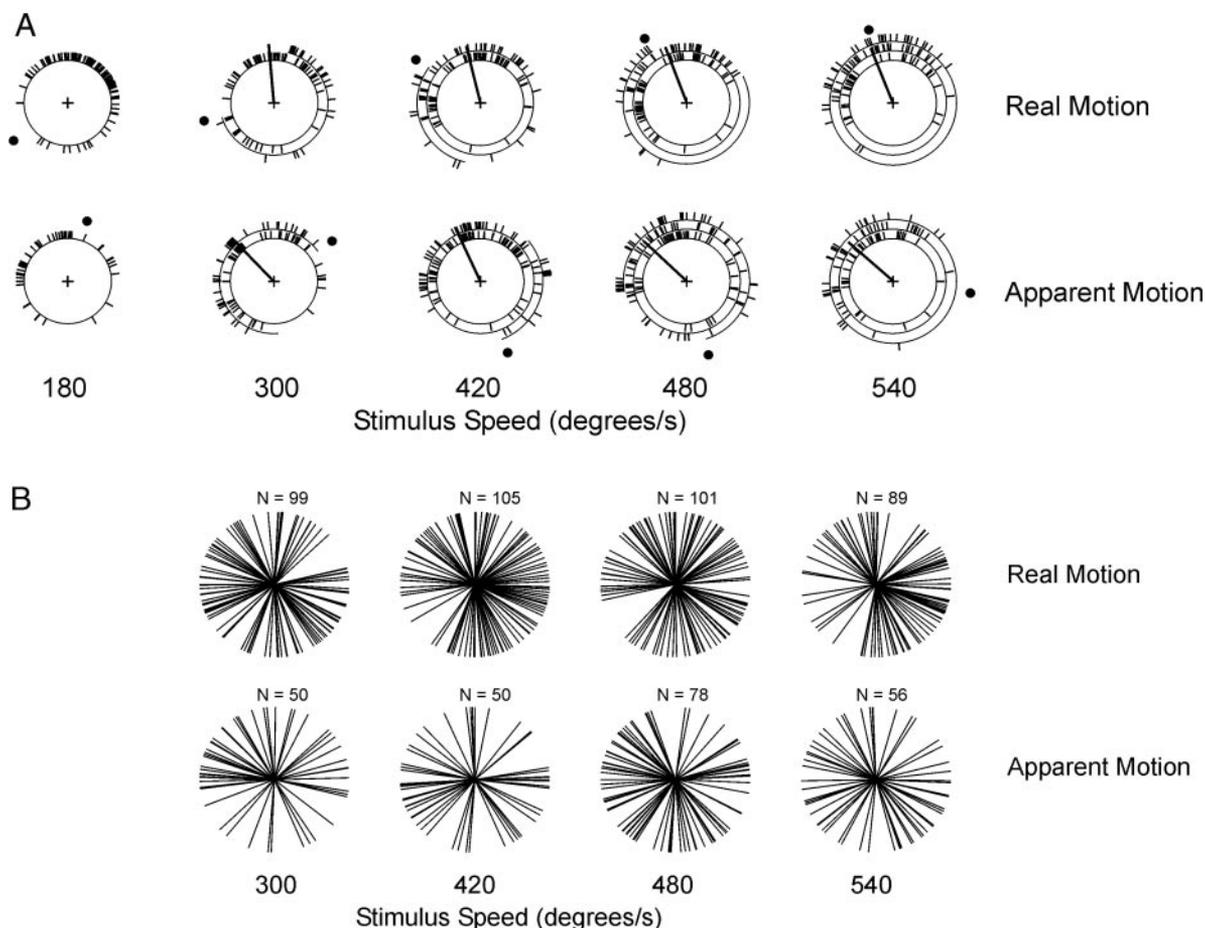
FIG. 7. *A*: circular raster of a neuron in area 7a with a significant preferred stimulus angular location (PSAL) for all stimulus speeds in the real and apparent motion conditions. Vector from the center cross to the circular raster represents significant PSAL. *B*: distribution of neurons in area 7a with PSAL. Modified from Merchant et al. 2004a.

close alignment between the two measures to a large group of cells that showed poor or no overlap between the preferred angular position and the receptive field. We found also a large number of neurons whose receptive field included all the circular trajectory of the visual stimulus (Merchant et al. 2004b). Therefore the observed angular tuning did not depend on the spatial collation of the circularly moving stimulus with respect to the receptive field. Instead, the tuning is probably the result of the dynamic shaping of neural responses in area 7a with respect to the spatial characteristics of the stimulus. The mechanism underlying this new type of cell tuning may depend on feed-forward inhibition generated locally within the parietal cortex, as described in other complex visual responses in area 7a, such as the opponent vector organization (Motter et al. 1987).

The second population of area 7a cells was selective for apparent moving stimuli and showed a periodic entrainment of activation with the period of the ISI of the flashing dots (Fig. 8). These neurons showed significant harmonics at the stimulus ISI frequencies in the spectral analysis (Merchant et al. 2004b). This may reflect a simple passive visual property of neurons in this area, namely that every time that a stimulus is flashed there is a neural response. Alternatively, it is possible that these "periodic" neurons may be involved in time perception and behavioral operations that are time-dependent. Indeed, the successive onset and offset of nearby flashes not only induce

the illusion of apparent motion, but also create a temporal framework where time intervals can be perceived and used to drive the subject's behavior (Merchant et al. 2004a). This was particularly true in this experiment for the following reasons: *1*) the ISIs used were in the range of intervals that can be resolved in time by human subjects (100–1,000 ms; Getty 1975; Ivry and Hazeltine 1995; Wing and Kristofferson 1973), and probably also by monkeys; *2*) the ISI varied across speeds, but the space between the flashing dots and the length of the low contrast path were constant; *3*) it has been shown that PPC neurons are involved in time interval perception (Leon and Shadlen 2003; Rao et al. 2001); and finally, *4*) we have observed that during interception of path-guided apparent motion stimuli, the variable that was better represented in the activation profile of area 7a neurons was the time-to-contact not the target position (Merchant et al. 2004a).

Because we found a group of neurons that were tuned to the angular location in the apparent motion condition, we also studied the capabilities of ensembles of neurons in area 7a to decode continuous circularly moving stimuli (real motion) as well as the perceptual reconstruction of path-guided apparent motion stimuli in the NOGO task (Merchant et al. 2005). To this end, the activity of cells that were tuned to the stimulus angular position in real or apparent motion was used in a multivariate linear regression analysis to recover the stimulus position over time. The hypothesis here was that the fidelity of
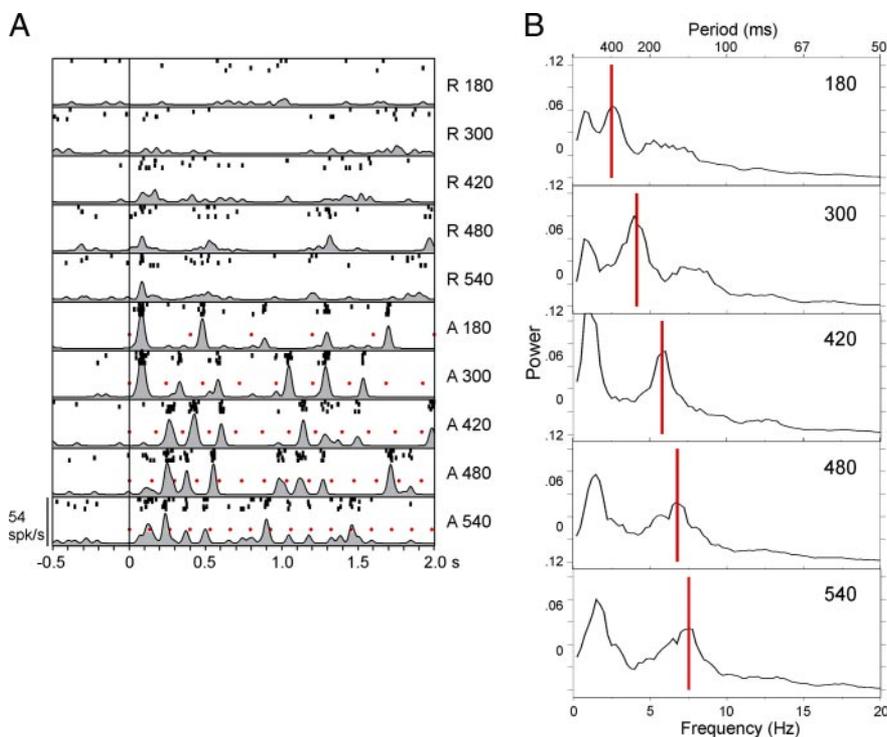
A

B

FIG. 8. Periodic neural activation in area 7a. *A*: neuron in area 7a that showed a clear periodic response to the flashed stimuli (represented as red dots) in the apparent motion condition. *B*: mean spectral densities of 66 neurons for each stimulus speed in the apparent motion condition. Red vertical line represents the interstimulus interval (ISI) of the apparent moving stimuli. Modified from Merchant et al. 2004a.

population representation of circular motion in area 7a would be strictly linked to the perception of real and path-guided apparent circular motion. The results showed that populations of area 7a cells could accurately reconstruct the circular trajectory of real moving stimuli for the range of speeds tested (180–540°/s; Fig. 9). In addition, we found a tight correlation between the neurophysiological and psychophysical responses to path-guided apparent motion, in that the ISI for detection of path-guided apparent motion in human subjects was similar to the ISI at which neural ensembles decoded properly the perceptual reconstruction of the stimulus (Fig. 9). This study assumed, then, that the monkeys perceived apparent motion above a threshold that was similar to the one observed in human subjects. Hence, these results suggest that the posterior parietal cortex is part of a high-level system that is directly involved in the dynamic representation of complex motion.

In summary, the neurophysiological results indicate that in area 7a during the NOGO task there were at least three different levels of neural representation of the circularly moving stimuli: *1*) the angular position of the stimuli in the real motion condition; *2*) the spatial position of the perceptual illusion of apparent motion, i.e., a dynamic representation of the path-guided apparent motion at stimulus speeds that produced the perception of motion in human subjects; and *3*) the temporal sequence of flashed stimuli in the apparent motion condition for all the stimulus speeds tested.

In the motor cortex, a substantial population of neurons showed a selective response to real moving stimuli in the NOGO task (i.e., in the absence of a motor response). This activity was modulated in some cases by the stimulus speed, and some of the neurons were tuned to the angular position of the stimulus (Merchant et al. 2004b). Again, the preferred angular stimulus locations were evenly distributed across this motor cortical neuronal ensemble (Fig. 10). Thus it seems that the motor cortex has continuous access to spatial

information of visual motion, probably because this information has a critical ecological value (Gibson 1979). Moving objects with respect to the subject can potentially demand an immediate action toward them in circumstances such as collision avoidance or interception (Lee 1976), Therefore it is crucial that the motor system has access to the motion parameters of the objects to be able to react toward them in a timely fashion.

An intriguing observation was that relatively few neurons responded to apparent moving stimuli in the motor cortex (Merchant et al. 2004b). Because the neurons in M1 responded to real motion, the question is why they did not respond in the apparent motion condition in our NOGO task. We suggest two hypotheses to account for these observations. The first hypothesis is that the monkeys were able to perceive apparent motion, but the motor cortical neurons did not respond to the perceptual reconstruction of motion in the absence of behavioral response. In this case, we assume that since the visual processing between human subjects and monkeys is very similar, the monkeys perceived apparent motion at stimulus speeds above 314°/s, as did human subjects (Merchant et al. 2005). Hence, even if the monkeys were capable of apparent motion perception, this information was not processed in the motor cortex during the NOGO task. In contrast, we show in the next section that cells in M1 responded during the interception of apparent motion stimuli and that the activity of motor cortical cells was closely related to the target time-to-contact. Therefore the second hypothesis postulates that it is the temporal and not the spatial representation of the stimulus that is the behaviorally relevant variable during apparent motion condition. Then, we suggest that since the time-to-contact is not a meaningful variable in the NOGO task where the stimulus was presented constantly for 2 s, the neurons in M1 did not respond during this motion condition. Of course, these two hypotheses are not mutually exclusive.
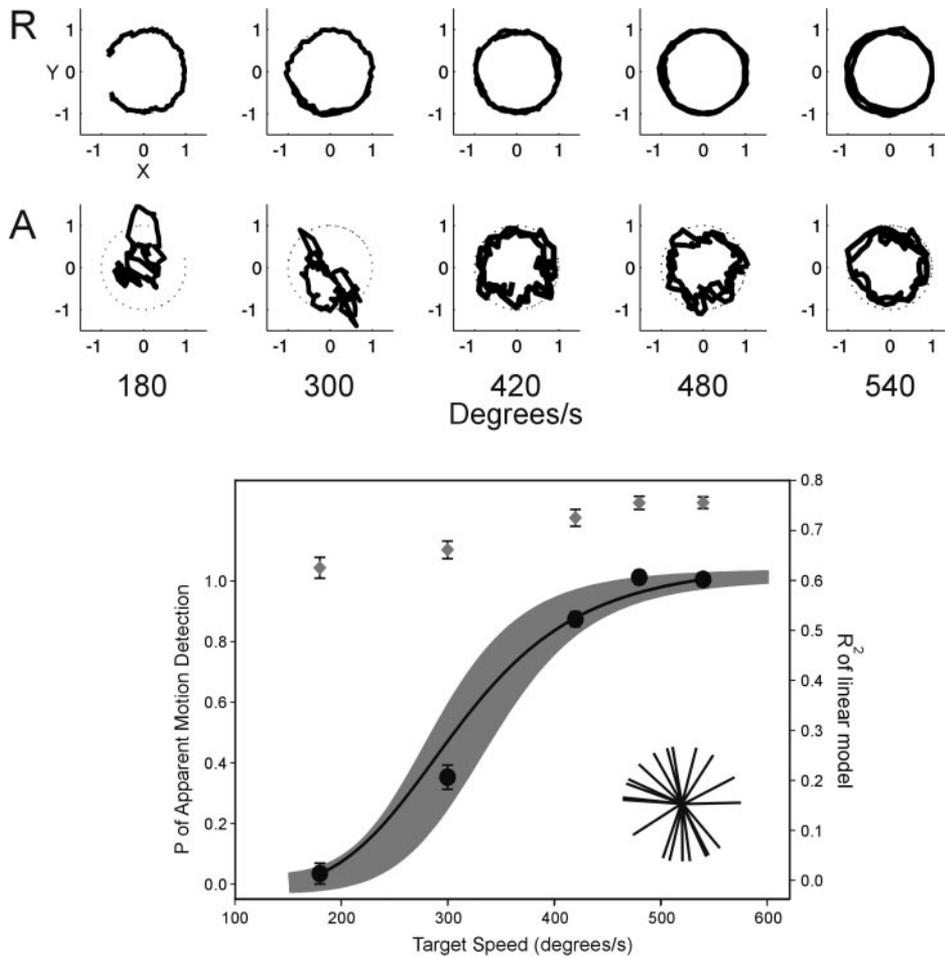
FIG. 9. *Top*: predicted stimulus position using an ensemble of 10 neurons during the real (R) and apparent (A) motion conditions and for the 5 different stimulus speeds. *Bottom*: comparison between the psychometric curve of apparent motion detection as a function of the stimulus speed (mean ± SD, blue lines) with the sigmoidal function obtained from the R^2 (mean ± SD) from the 20 neurons during the apparent motion condition for the different stimulus speeds (black circles and continuous line). The best R^2 (mean ± SD) values of the lineal model during the real motion condition are depicted as solid red diamonds. The preferred angular position for these 20 neurons is shown in the *inset*. Modified from Merchant et al. 2005.

In conclusion, the neural responses in the posterior parietal cortex during the NOGO task were related to spatial aspects of the real motion and to temporal properties of the apparent motion stimuli. In addition, ensembles of cells in this area showed a dynamic coding of path-guided apparent motion at stimulus speeds that produced the illusion of circular motion in human subjects. On the other hand, the motor cortex only responded to spatial properties of the real motion condition during the NOGO task. M1 did not process spatial or temporal information during the apparent motion condition when the stimuli were not used to drive the behavior.
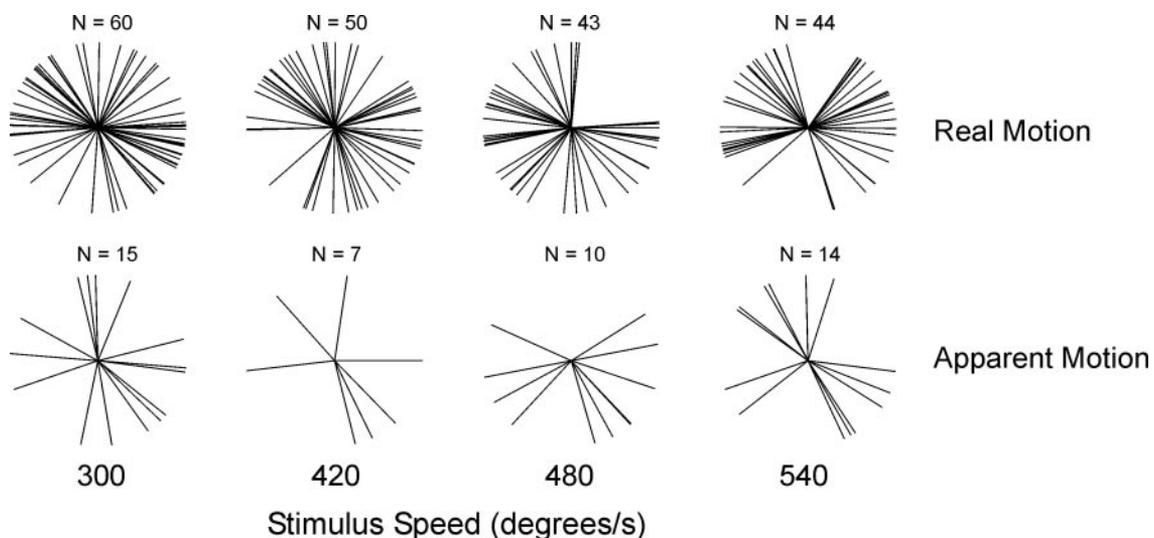

FIG. 10. Distribution of the significant preferred stimulus angular locations of motor cortical neurons. Number of significant cases was larger in the real than in the apparent motion conditions. Modified from Merchant et al. 2004a.

PARIETO-FRONTAL ACTIVITY DURING
INTERCEPTION OF REAL AND APPARENT
MOTION: STIMULUS-DEPENDENT ENCODING
FOR ANGULAR POSITION AND TAU

We used complementary analytical tools to understand the neural mechanisms underlying the interception of real and apparent motion targets. We first followed a descriptive strategy, comparing the functional properties of neurons during three different tasks: the interception, the NOGO, and the center out tasks (in which the monkeys produced similar force pulses toward 8 stationary targets). The objective was to identify the neural ensembles that were associated with the visual motion processing, the implementation of the interceptive response, and the visuomotor transformations inherent to the target interception. We used a quantitative approach in which we measured the explanatory power of different parameters of the target and the motor execution on the time-varying neural activity during the interception (Merchant et al. 2004a).

The results showed, first, that a group of neurons in both M1 and area 7a responded not only during the interception but also during the NOGO task. Most of these neurons were tuned to the angular position of the stimuli (Fig. 11). However, this type of neurons was more common in area 7a than in M1. These findings suggest that M1 and area 7a are differentially involved in the processing of the real and apparent motion stimuli. In addition, a group of motor cortical cells responded during the interception task but not during a center → out task. This group of cells may be engaged in sensorimotor transformations more specific to the interception of real and apparent moving stimuli, including the link of the visual motion signal to the predictive mechanism that controls the initiation of the interception

movement. Nevertheless, the majority of cells responded during both tasks or just during the center → out tasks, emphasizing the well known role of M1 in the preparation and execution of voluntary movements (Georgopoulos 2000). Thus the phenomenological comparison between tasks revealed that despite the fact that the neurons in the motor cortex responded to visual motion stimulation, most of the motor cortical cell activity was driven by the interception movement. In contrast, the neural activity in area 7a was mostly engaged by the sensory aspects of the interception task, and the neural responses in this area were tightly associated with the onset of the stimulus movement. This suggests that the sensory-motor transformations involved in the interception task include a parieto-frontal distributed system that shows functional gradients. These functional gradients may be defined in large part by the connectivity of its elements (Battaglia-Mayer et al. 2001; Johnson et al. 1996; Mountcastle 1978).

Next we determined quantitatively the relation between the temporal pattern of neural activation with different aspects of the target and the motor execution during the interception task. We designed a multiple linear regression model to test the effects of different parameters on the time-varying neural activity. These parameters were the direction cosines of the stimulus angle, the target time-to-contact, the vertical hand force and the vertical hand force velocity. This analysis revealed that the time-varying neuronal activity in area 7a and the motor cortex was related to various aspects of stimulus motion and hand force in both the real and apparent motion conditions, again with stimulus-related activity prevailing in area 7a and hand-related activity prevailing in the motor cortex (Fig. 12). The most important finding was that the neural
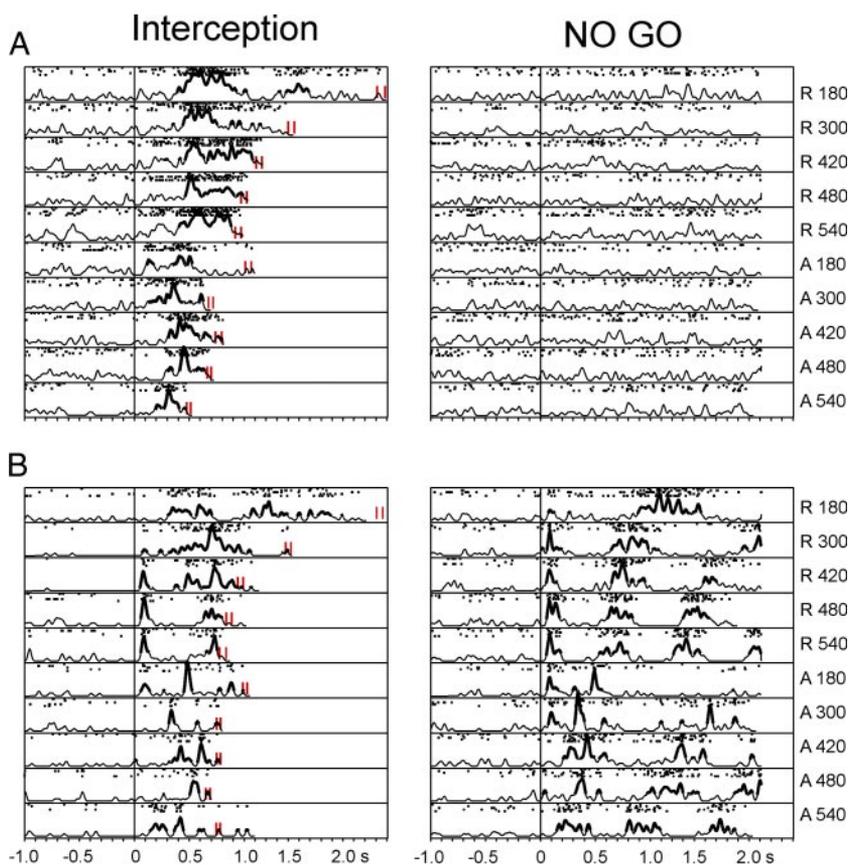

FIG. 11. Rasters of spike trains (*top*) and mean spike density functions (SDFs, *bottom*) for each motion condition and stimulus speed of 2 cells of area 7a during the interception and NOGO tasks. *A*: neuron that responded during the interception but not in the NOGO task. *B*: neuron that was activated during the interception task in both motion conditions that also responded in the real motion condition during the NOGO task. Neural activity of 5 trials was aligned with the onset of the stimulus movement (0 s). Black bold portions indicate that the SDF was greater than the mean ± 3 SD of the control period. Large red vertical lines at the bottom of each raster represent the beginning and end of the interception movement. R, real motion; A, apparent motion. Stimulus speed is in °/s. Modified from Merchant et al. 2004b.
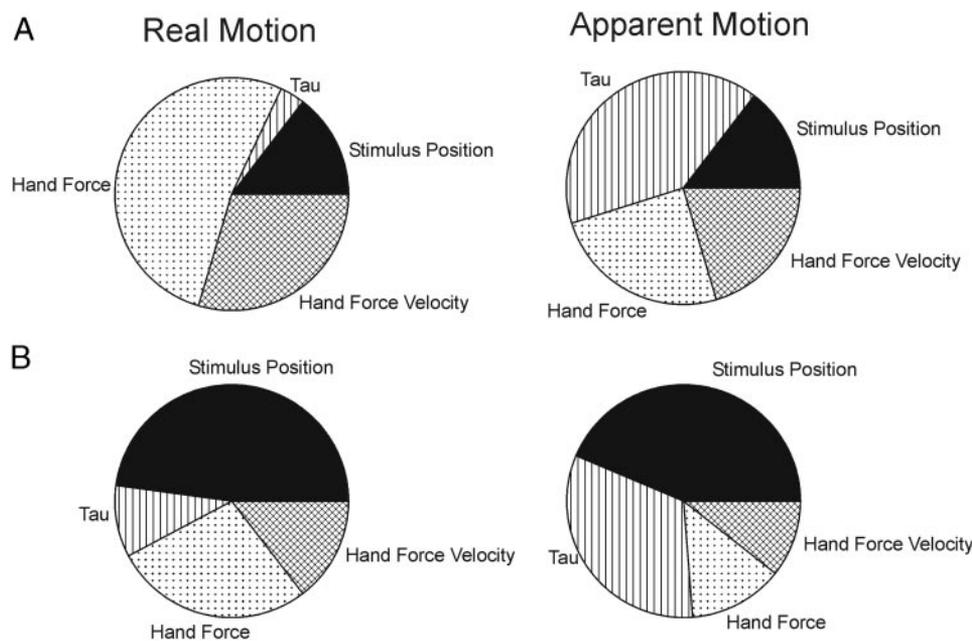
FIG. 12. Percentages of neurons in the real and apparent motion conditions, during the interception for which the noted parameter was ranked 1st using the standardized coefficients obtained from the multiple regression analysis. *A*: motor cortex. *B*: area 7a. Modified from Merchant et al. 2004b.

activity was selectively associated with the stimulus angle during real motion, whereas it was tightly correlated to the time-to-contact in the apparent motion condition, particularly in the motor cortex (Fig. 12).

The prevalence of stimulus position signals during the real motion situation in the multiple regression analysis suggests that neural populations in the motor cortex and area 7a were engaged in processing the stimulus position over time, and that this information was probably used to trigger the interception movement in the real motion condition. This hypothesis is supported by the finding that motor cortical neurons are modulated by the stimulus position during the real but not during the apparent motion conditions in the NOGO task (Merchant et al. 2004b).

The tau was the most important explanatory parameter in apparent motion interceptions in the motor cortex, and it was the second most important in area 7a, preceded by the stimulus angle. This is the first time that a neural correlate of the first-order estimate of the time-to-arrival has been reported in primates. We assumed that in the apparent motion condition the animals intercepted a stimulus that was the perceptual "reconstruction" of motion based on a sequence of stationary stimuli (Port et al. 1996). In fact, the detection threshold for apparent motion in human subjects was 314°/s. However, we cannot rule out the possibility that in this condition the monkeys used the timing between dots to solve the interception task. Indeed, we found a population of neurons in area 7a that signaled the onset of the flashing dots during the NOGO task (Merchant et al. 2004b). Consequently, a suitable hypothesis is that during the interception of apparent moving stimuli the critical variable was time rather than the stimulus location information. Figure 13 shows an example of a neuron where tau was the most important parameter to explain the temporal variation in the neural responses. This neuron shows a linear increase in activity that is inversely proportional to the decrease in the target time-to-contact to the interception zone, and that reaches the activity peak at a similar value of tau for different target speeds. This type of activity "ramp" is the

representation of an elapsed-time accumulator, and in fact, it has been reported in PPC during a time interval discrimination task (Leon and Shadlen 2003). Therefore the tau-ramp recorded in area 7a and particularly in the motor cortex is a neural representation of time-to-contact that, once it reaches a specific magnitude, can be used as the signal to trigger the interception movement.

We observed that most of the neurons in both areas were significantly related to more than one parameter. Therefore we were interested to determine whether particular combinations of variables were associated in the same cell with a frequency that was above chance. Specifically, we sought to establish whether the processing of sensory variables was associated with the encoding of motor variables, and whether there were differences in these relations between the real and apparent motion conditions in both areas. For that purpose, we performed a log-linear modeling analysis to find out which pa-
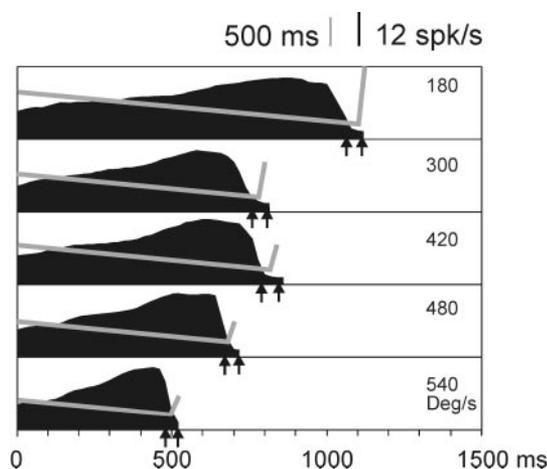

FIG. 13. Motor cortical neuron with a response (SDF, in black) that was inversely proportional to the target time-to-contact (gray line) during the interception of apparent motion targets moving at 5 different speeds. The 1st and 2nd arrows correspond to the beginning and end of the movement time. Activity was aligned to the beginning of the target presentation.
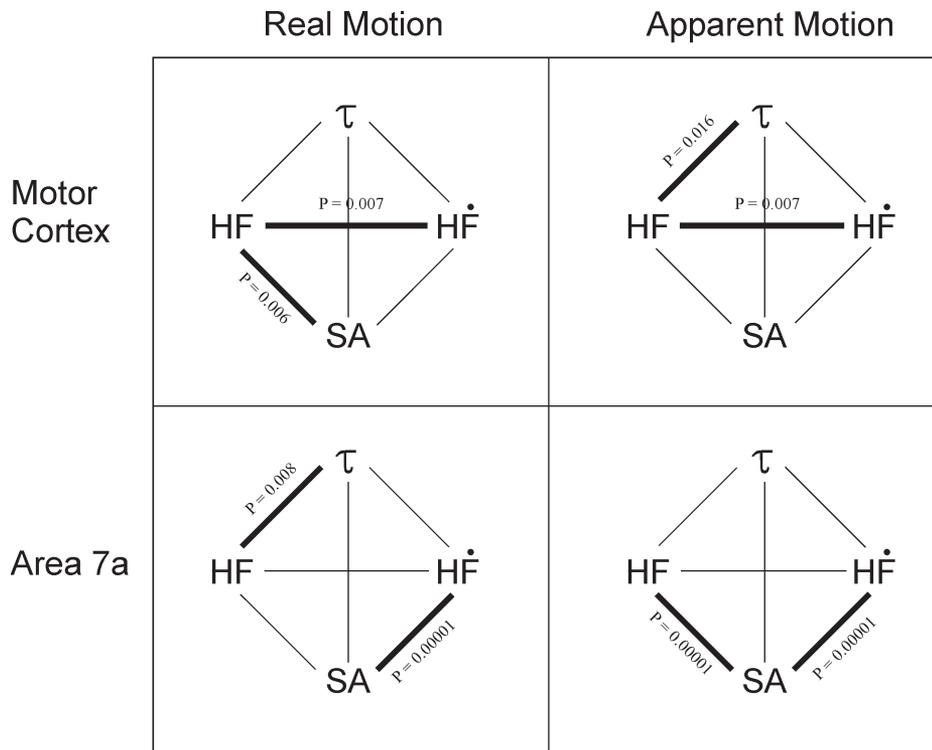
Real Motion   Apparent Motion

FIG. 14. Association of sensory and motor parameters by cells in the motor cortex and area 7a during the real and apparent motion conditions in the interception task. Thick lines connecting pairs of variables indicate significant associations in the 2×2 tables using a χ^2 test. Numbers adjacent to the lines represent the P value of the χ^2 test. SA, stimulus angle; τ, time-to-contact; HF, vertical hand force; HḞ, vertical hand force velocity. Modified from Merchant et al. 2004b.

rameters showed concurrent effects (Fig. 14). The results showed that the association between the sensory and motor parameters was very different in the two areas under both motion conditions. In the motor cortex, during the real motion condition, the hand force was significantly coprocessed with the hand force velocity and the stimulus angle, whereas during apparent motion, the hand force was significantly coupled with tau and the hand force velocity (Fig. 14). In addition, in area 7a for the real motion condition the stimulus angle was significantly coprocessed with the hand force velocity, and tau was significantly coupled with the hand force velocity. Finally, in the apparent motion condition area 7a neurons showed significant coprocessing of the stimulus angle and the hand force and force velocity (Fig. 14). These results confirm the existence of different mechanisms for interception of real and apparent motion targets. In the real motion condition, the stimulus angle was the most important target variable and was coprocessed with the hand force, whereas during the apparent motion the most important target parameter was tau, and it was coprocessed with the hand force.

Taken as a whole, these results indicate that neurons in the motor cortex and area 7a are processing different parameters of the stimulus depending on the kind of stimulus motion and that this information is used in a predictive fashion in the motor cortex to trigger the interception movement.

CONCLUDING REMARKS

The tau theory has its roots in the influential work of Gibson (1958) on visual control of locomotion, in which the basic optical information available to solve this problem was described. Following the Gibsonian ecological approach to perception and motor control, Lee suggested that movement guidance is directly associated to the perception of affordances. The subject is using the information that the environment is

providing to move and respond to stimuli according to ecological demands. In this case, the information is the time-to-contact or tau that is an affordance that can be simply computed by the subjects to guide the movement in practically any circumstance.

The concept of affordances is closely linked with the notion of the development of neural circuits that have been shaped by evolution to process efficiently these affordances. Needless to say, for quite some time, it was necessary to study the neural underpinnings of time-to-contact. The first steps were done in the locust (Hatsopoulos et al. 1995; Judge and Rind 1997) followed by studies of rate of expansion and time-to-contact in the pigeon (Sun and Frost 1998). These papers dealt with the classical definition of tau, an affordance defined as the ratio of the size of the retinal image at a given time over the rate of expansion of the image (Lee 1976). Using looming stimuli it was found that neurons in the nucleus rotundus of pigeons could represent different optical variables related to image expansion of objects approaching on a direct collision course (Rind and Simmons 1999; Sun and Frost 1998). One group of neurons signaled the absolute rate of expansion and a very interesting second group responded systematically when tau attained a particular threshold. Thus this neural information could be used in a timely fashion to trigger a behavioral response to avoid collision with the looming. Therefore very simple nervous systems could process tau and be used to guide the movement in the case of approaching looming stimuli.

The tau theory evolved to a more general form, in which the time-to-close of any gap (whatever the dimension of the gap is: force, distance, angle, etc.) at the current gap close rate is used to guide the movement. This current theory relies strongly on a new concept: tau-coupling that implies maintaining two changing tau values at a constant ratio. The neurophysiological experiments on target interceptions performed in our labora-

tory revealed two fundamental issues regarding the use of time-to-close of gaps to guide the interceptive behavior. First, the parieto-frontal system of primates is engaged in the codification of target time-to-contact in the form of a constant increase in activity as a function of time during the interception of apparent motion targets. These tau-ramps recorded in area 7a and particularly in the motor cortex are a neural representations of target time-to-close which, once they reach a specific magnitude, could be used to trigger the interceptive behavior. The second critical observation is that the nervous system could use spatial or temporal affordances to control the interception movement, depending on the visual properties of the moving target. We found that in the real motion the angular position of the target was the critical variable, whereas in the apparent motion condition it was tau. Thus even if the posterior parietal cortex showed spatial information about the perceptual reconstruction of motion during the path-guided apparent motion illusion, in this situation the motor system used the time-to-contact information to control the interception movement. Overall, the psychophysical and neurophysiological evidence suggest a fundamental framework for interceptive behavior in which the behavioral context, the accuracy requirements, the spatio-temporal target kinematics, and subjective preferences define the strategy adopted to control the effector movement in a predictive fashion.

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