Reflexive Limb Selection and Control of Reach Direction to Moving Targets in Cats, Monkeys, and Humans

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Perfiliev S, Isa T, Johnels B, Steg G, Wessberg J. Reflexive limb selection and control of reach direction to moving targets in cats, monkeys, and humans. J Neurophysiol 104: 2423–2432, 2010. First published September 1, 2010; doi:10.1152/jn.01133.2009. When we reach for an object, we have to decide which arm to use and the direction in which to move. According to the established view, this is voluntarily controlled and programmed in advance in time-consuming and elaborate computations. Here, we systematically tested the motor strategy used by cats, monkeys, and humans when catching an object moving at high velocity to the left or right. In all species, targets moving to the right selectively initiated movement of the right forelimb and vice versa for targets moving to the left. Movements were from the start directed toward a prospective target position. In humans, the earliest onset of electromyographic activity from start of motion of the target ranged from 90 to 110 ms in different subjects. This indicates that the selection of the arm and specification of movement direction did not result from the subject’s voluntary decision, but were determined in a reflex-like manner by the parameters of the target motion. As a whole the data suggest that control of goal-directed arm movement relies largely on an innate neuronal network that, when activated by the visual signal from the target, automatically guides the arm throughout the entire movement toward the target. In the view of the present data, parametric programming of reaching in advance seems to be superfluous.

INTRODUCTION

It has been understood over the last decades that control of various motor responses is based on innate neuronal networks that enable almost automatic generation of the motor act (Grillner and Wallen 2004; Grillner et al. 2005). In contrast to the neural substrates underlying learned behavior, which are assembled and refined by experience, wiring of the innate networks is guided mainly by genetic information and is typically accomplished during early ontogenesis (DeBello and Knudsen 2004; Knudsen 1999; Waldenström et al. 2003). Certain adaptive functional plasticity, however, can be exhibited throughout the lifetime (Wolpaw 2007; Zehr 2006). The vital value of such innate networks is that a fairly accurate blueprint of the motor response is inherently imbedded in the nervous system and need not be established by learning or planning. Such basic circuitries were shown even for rather complex motor behavior like orienting of the head toward an external stimulus or control of finger movement during grip formation (Genter and Classen 2006; Johansson and Westling 1984). However, a plausible innate mechanism that can automatically guide the arm toward a target has never been described and even the theoretical possibility seems to be incompatible with the long-standing tradition to view arm reaching as a typical case of voluntary behavior. Indeed, taking an object is generally recognized as a voluntarily controlled act that is planned and programmed parametrically before movement onset (Desmurget et al. 1998; Favilla et al. 1990; Ghez et al. 1997; Glover 2004). This notion is largely based on the observation that our arm is a complex biomechanical device with redundant degrees of freedom admitting an infinite number of trajectories in space and that, in spite of such redundancy, the same movement made repeatedly will follow a similar trajectory (Bernstein 1967). How is this optimal movement path selected? It is assumed that in analogy with a robotic arm, the required coordination is provided by a central program that specifies the metrics of forthcoming movement (Desmurget et al. 1998).

In contrast to such engineering-inspired notions, recent findings in neurobiology suggest that coordination required for reaching may result from the evolutionary wiring of the brain and therefore that its control is reflexive. A number of observations indicate that the problem of redundant degrees of freedom might have been solved at the earlier stages of phylogeny of the nervous system. It was recently found that purposeful target-directed movement of the forelimb emerged already in amphibians (Gray et al. 1997; Iwaniuk and Whishaw 2000). When isolated from the rest of the body, the hyperredundant octopus arm or the spinal frog’s hindlimb can produce well-coordinated movements controlled by local neuronal circuits (Fukson et al. 1980; Sumbre et al. 2001) and in monkeys purposeful-like arm movement can be produced by microstimulation of the motor cortical areas (Graziano et al. 2002). Such findings suggest that the evolution of reaching involved elaboration and refinement of innate mechanisms that produce fast and coordinated acts in response to a visual target.

It should be realized that the study of such reflexive mechanisms would require experimental paradigms with direct spatial relationship between target and movement. However, in many previous studies this relationship was disrupted so that, typically, a target was presented on a screen and the response required movement toward a target, for example a button, located elsewhere. The data obtained in such spatially incompatible conditions led to the conclusion that reaction time of visuomotor response (RT), i.e., the time between stimulus presentation and the onset of the movement reflects the speed of movement preparation. Indeed, it was consistently shown that RT is prolonged when the parameters of forthcoming movement are not defined in advance and that RT will grow.
progressively with increased uncertainty about the movement parameters, such as an increased number of targets. This choice effect, also known as Hick’s law, is generally considered as strong evidence for motor programming and remains one of the fundamentals of motor control theory (Ghez and Krakauer 2000; Schmidt and Lee 2005). Limb selection and specification of movement direction are acknowledged as the most time-consuming stages of planning, requiring ≥350 ms (Lépine et al. 1989; Possami et al. 2002; Rosenbaum 1980; Ulrich et al. 1998; Wild-Wall et al. 2003).

Here, in contrast to previous studies we sought to test parameters of arm movement in a paradigm that maintained the natural direct link between the cue and the response. We show that under these conditions, selective goal-directed arm movement is initiated with such short delay in cats, monkeys, and healthy human subjects that it is not possible to regard the response as voluntarily planned or programmed in advance. Our data strongly suggest that arm reaching can be guided automatically by an innate mechanism that was obstructed and thus overlooked in previously used paradigms with spatial separation between the target and the movement.

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Human experiments

In all, 19 healthy right-handed volunteers (age 18–48 yr; 13 female, 6 male) participated in the study. Human experiments were done according to the Declaration of Helsinki and the local ethics committee approved the study. Informed consent was obtained from the participants. The participants sat in front of a stationary chair, with both arms resting comfortably on a table (Fig. 1). The mechanical system designed to move the target was made of a string stretched around four wheels on ball bearings in a vertically oriented rectangle (3.5 × 1.3 m). The target was fixed at the middle of the lower side of the rectangle and motion was achieved by moving the vertical side of the string hidden from the subject’s vision. The ball was suddenly shifted to the left or right 25–40 cm, with 1.5–3 m/s peak velocity (0.5 m/s within 10–20 ms). Ear protectors or plugs were used to attenuate any noise made by the displacement of the ball.

The subjects were instructed to concentrate exclusively on the target, to feel free to catch it with any strategy that they felt was the most natural, and to catch it as soon as possible when it started to move. After 5–8 training trials each participant performed 120–150 trials in one session. The trajectories of the ball and both hands were recorded in three dimensions using two optoelectronic tracking cameras (Prorflex; Qualysis Medical, Göteborg, Sweden; 500-Hz sampling rate) and passive reflective markers attached to the ball target and to the first phalanx of both index fingers. In five subjects, surface electromyography (EMG) was recorded from both shoulders (m. pectoralis major and m. infraspinatus; sampling rate 2,048 Hz, filtered 30–350 Hz). EMG from additional multiple shoulder and arm muscles (anterior and lateral aspects of the deltoid, m. biceps, and the wrist extensors) were recorded in three subjects. The latency of EMG onset in these muscles was similar to and not shorter than that in pectoralis or infraspinatus. In addition, experiments were recorded on videotape using a conventional digital video camera. In control experiments, we tested a 4-cm red ball target displayed on a computer monitor (refresh rate: 85 Hz), moving with a constant speed of 2 m/s. The protocol was otherwise identical to the real ball target experiments.

Animal experiments

We tested 6 adult cats, 20 kittens (age 7–11 wk), and 5 monkeys (3 Macaca mulata and 2 Macaca fascata). The local Animal Care and Use Committees in Sweden and Japan approved the studies. Targets attached to a string were a toy “mouse” for cats and a piece of sweet potato for monkeys. The horizontal visual field of the animals was restricted, for the cats, by the walls of the cage, or by horizontal panels placed on both sides of a primate chair. Small round holes (50-mm diameter) were made on each wall/panel, allowing presentation of the target without any sound cue indicating direction. Before each trial the experimenter hid the target in one hand and simultaneously imitated with both arms the positioning of the target behind each wall, so that the animals were unaware of the target’s initial location. Movement of the target was initiated by the experimenter when the animal’s posture and gaze were oriented at right angles to the movement path of the target. The target normally appeared at a speed of 1 m/s, although the target could be accelerated ≤4 m/s, depending on the individual reactivity of the animals. The motion of the target was accompanied by a hissing noise produced by the four ball bearings symmetrically.

FIG. 1. A target moving sideways induced similar stereo-  

typed short-latency target-intercepting forelimb movements  

from rest in human subjects (A), cats (B), and monkeys (C).  

Time zero is onset of target motion. Animals and naïve humans  

spontaneously moved the left forelimb in response to a target  

moving to the left and vice versa for a target moving to the  

right. The catching movements were initially directed to the  

anticipated future location of the moving target, resulting in  

a temporary overshoot of the movement trajectory when the  

target stopped moving.
located on both sides of the animal. The noise therefore could not be used as a cue about the direction of the target motion, but being initiated about 100 ms ahead of the target appearance it could be used to facilitate response. To eliminate this possibility the animals first were habituated to the sound produced by the motion of the string. In addition, during the entire experiment after each set of one to two trials, the string was moved a few times in different directions to ensure that animals paid no attention to it. Finally, the hissing noise produced by the string was partly masked by a similar constant noise presented from speakers on both sides of the animal. Each animal performed from 100 to 200 trials per session. Digital video was used to record the animals' behavior.

In experiments with kittens, the animals were placed on a box measuring 50 × 40 × 40 cm (width, depth, height). A 3-cm ball on a string was swayed in front of the animal as a pendulum. The speed was adjusted manually so that the kitten could reach for but not catch the target; peak velocity reached 2.5 m/s. Each kitten was tested during 5–10 min with 5–10 presentations of the pendulum. Typical motion of the targets was recorded by Proreflex cameras in a separate session.

Data analysis

Data were analyzed using programs written in MATLAB (The MathWorks, Natick, MA) by the authors. Velocity was calculated by numerical differentiation after low-pass filtering with 125-Hz cutoff frequency. However, unfiltered velocity trajectories were used to estimate movement onset, detected by the program as lateral (ball) or protraction (hand) velocity exceeding 7 cm/s (recording noise and small movements at rest did not exceed 5 cm/s). All trials were verified by visual inspection of the data records. Figure 2 shows that by using this approach we could identify the onset of target and hand movements with a precision of 2 ms.

Methodological considerations

It is common for motor control studies to use a laboratory surrogate of the real target, such as a flat, noise-free, and precisely controlled image on a computer monitor. In contrast, we preferred a manually controlled real physical target. This choice was dictated by our initial behavioral observations that a real target had a tendency to generate

![Target velocity](image1)

**FIG. 2.** Identification of onset of target and arm movement. *Left column shows typical examples of sideway velocity profile for the target (A), arm (C), and electromyographic (EMG, E) activation during catching. Panels on the right (B, D, and F) depict the same trials at high resolution. Points accepted as the onset of the events are marked by the asterisks. The high-resolution unfiltered plots show data points plotted every 2 ms; onset of target and arm movement was identified as the first point above the background noise.*
fast arm movements in animals and humans. We therefore aimed to ensure the optimal operational condition of any presumed central mechanisms for automatic control of the arm by the target. If such a mechanism exists it must be based on direct transformation of the sensory signal from the target into motor output and we assume that there is a significant dependence of the produced motor response on the quality and strength of the sensory stimulus.

We also deliberately avoided a computer monitor for the main experiments since it substantially restricts spatial domain of the motor task and thus may impose significant constraints on the natural automatic movement generation. In contrast, our natural conditions ensured generation of the movement, with the parameters determined mostly by the genuine properties of the underlying circuitry.

The question arises, however, whether our paradigm was technically precise to ensure the collection of reliable data. The mechanical system used to control the target motion was made stiff enough to produce abrupt shifts of the target without any delay between movement of the handle and the target. Figure 2 shows the abrupt increase in target velocity, with higher acceleration than that of the catching arm. Figure 2 also shows that the onset of target motion could be determined from the motion tracking system with a precision of 2 ms. This substantially exceeds the precision of a conventional computer monitor, which typically has a refresh rate <100 Hz.

As indicated earlier, all the mechanical components generating the noise were symmetrically located on both sides of the animal or human subject; thus this sound could not be used as a clue to facilitate arm selection. In principle, weak symmetrical noise could have been used by the animals for nonspecific preactivation of both arms before arm selection, but this was never observed. In the human studies, there was no noise before the onset of movement of the target.

RESULTS

Characteristics of naturally expressed catching movements

In this study, 12 healthy human volunteers were seated with both arms symmetrically placed on a table in front of a stationary red ball target attached to a string at the subject’s midline (Fig. 1A). The ball was abruptly shifted 25–40 cm to the left or right at 1.5–3.0 m/s peak velocity (Fig. 3D). The subjects were instructed to catch the ball as quickly as possible in target velocity, with higher acceleration than that of the catching arm. The ball was abruptly shifted 25–40 cm to the left or right at 1.5–3.0 m/s peak velocity (Fig. 3D). The subjects were instructed to catch the ball as quickly as possible in target velocity, with higher acceleration than that of the catching arm. The ball was abruptly shifted 25–40 cm to the left or right at 1.5–3.0 m/s peak velocity (Fig. 3D). The subjects were instructed not to strive for the fastest catch, but to make a fast reaching movement in a manner that felt natural and to “let the ball drive the hand.” Average reaction time was 165 ms (SD 20 ms). The correlation between peak ball velocity and peak reaching speed was r = 0.59–0.78 (Pearson’s r; P < 0.001).

The finding that the movements from the onset were directed prospectively to a future target position can be explained by the fact that in most of the trials the motion of the ball was accomplished within 150–210 ms (Fig. 3D). Thus the command for reaching was generated before the target stopped moving and movements were initially directed to the target’s presumed future position derived from its current speed. Such prospective trajectories were observed in all subjects during the reach if it continued to move. We will refer to this pattern as the Interceptive strategy, which we define as an acquisition of the target by a movement leading and aimed ahead of the target. The mean group reaction time, judged from the onset of hand velocity, was 165 ms (SD 20 ms) for the left and 163 ms (SD 20) for the right arm (Fig. 4C). Onset of surface EMG recorded from m. infraspinatus (Fig. 4A) and m. pectoralis major had a group mean latency of 144 ms (SD 20), with earliest onsets occurring at 90–110 ms in different subjects. Analysis of movement trajectories showed that Interceptive movements in all subjects were initiated in the direction of the target, along a straight movement path (Fig. 3A). The sideways velocity profile was single-peaked, with peak velocity ranging between 1.2 and 4.0 m/s in all subjects (Fig. 3C). Subjects reported a distinct feeling that a faster ball triggered arm movement with higher velocity. This was investigated more thoroughly in three subjects where the ball speed was varied, ranging from 0.5 to 4.5 m/s (Fig. 5). To minimize any factors that could influence performance, the subjects used only the right arm and the ball was shifted only to the right. In this test, the subjects were instructed not to strive for the fastest catch, but to make a fast reaching movement in a manner that felt natural and to “let the ball drive the hand.” Average reaction time was 163 ms (SD 19 ms). The correlation between peak ball velocity and peak reaching speed was r = 0.59–0.78 (Pearson’s r; P < 0.001).

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first 15–30 trials. During further training, five subjects directed the movements from the start toward the actual projected endpoint of the target, whereas prospective initial movement direction persisted throughout the session in seven subjects. No movements of the opposing limb were detected during Interceptive reaching movements, but brief weak EMG activity with longer latency was recorded in different subjects in 10–30% of the trials. When specifically asked after the experiment, all subjects reported that they were not aware of deliberately using the Interceptive strategy and found that the selection of the arm to move came naturally.

Instructed reversal of the naturally expressed strategy

These short latencies suggest that reaching may be controlled by hard-wired mechanisms and it may be assumed that intentional reversal of the pattern would be difficult and time-consuming. To test this assumption, seven subjects from the same group and seven naïve participants were instructed to use the opposite arm selection strategy, that is, to strive to use the right arm to reach for targets moving to the left and vice versa. We will refer to this as the Pursuit strategy, which we define as target acquisition by following and catching up with the target (Fig. 3B). All subjects spontaneously reported that this task was demanding and required constant concentration. The subjects were successful in selecting the arm to move according to the specified rule in 80% of the trials (grand mean: 69–91% in individual subjects), whereas in the remaining trials they erroneously used the Interceptive strategy. Average movement onset in the Pursuit task had a mean latency of 234 ms (SD 45 ms; see Fig. 4D). Mean EMG latency was 190 ms (SD 40 ms). Thus RT was prolonged by 69 ms compared with the Interceptive strategy (mean difference in 12 subjects tested in both tasks, 59 ms, SD 11; t-test P < 0.001). Furthermore, RT was more variable in the Pursuit task (coefficient of variation, 0.19; during the Interceptive strategy, 0.12). In the contralateral arm, small movements were observed with similar latency (mean 239 ms, SD 51 ms). Weak EMG activity was detected in 52% of the trials, with a mean latency of 174 ms (SD 33), which is significantly shorter than EMG latency in the arm used for reaching (t-test, P < 0.001). Three of the subjects were additionally trained in the Pursuit task in three daily sessions and, in total, performed 450 trials each. No improvement in performance was observed during the repeated sessions.

The kinematics of the Pursuit movements exhibited larger intra- and intersubject variability compared with Interception. In five subjects, a curved trajectory pattern with an undulating velocity profile dominated, where the movement was initiated roughly toward the starting position of the target and then redirected toward the endpoint (Fig. 3, B and E). In the other nine subjects, the movement path was directed toward the endpoint of the target already from movement onset, with the velocity profile varying between single and double peaked. Maximum sideways velocity ranged from 0.8 to 2.9 m/s. Thus in spite of the longer reaction times compared with Interception, Pursuit movements were not as well optimized for successful and fast catching. Tested immediately after the Pursuit task, all subjects could perform the Interceptive strategy with reaction times and trajectories as described earlier. This was also true for the group of subjects (n = 7) who had started the experiment session with instructed Pursuit. These observations indicate that the Pursuit task may require constant active suppression of Interceptive movements, which would support the idea of an innate mechanism underlying control of the latter.

As a control, we also tested the Interceptive versus Pursuit strategy with a target (red ball, 4-cm diameter) displayed on a computer monitor (refresh rate: 85 Hz). The protocol was otherwise identical to the real ball target experiments. The target moved with a constant speed of 2 m/s. Pilot experiments revealed that a target moving on a monitor did not have the same driving influence on the arm as the real one (cf. METHODS, Methodological considerations). Thus in this test the subjects (n = 4) were explicitly instructed to use the Interceptive strategy in the Interceptive trials. However, after the test, the subjects reported that only the Pursuit task required active use.
Comparison with monkeys and cats

The existence of a phylogenetically old mechanism would imply that the Interceptive strategy for catching moving targets should exist in other species as well. We tested six cats and five monkeys (three Macaca mulata and two Macaca fuscata). The animals were presented with a moving target suddenly appearing on the left or right side through holes in the cage walls. Movements were analyzed using video recording. In all six cats the Interceptive strategy (that is, the left arm was used for targets moving to the left and vice versa) was observed from the first trial and throughout four daily sessions in 96–98% of the trials (Fig. 1B). Reaction time was 160–200 ms. Movements were directed toward the prospective location of the target (Fig. 1B), similar to the Interceptive strategy used by human subjects (Fig. 1A).

In three monkeys, Interceptive responses were observed from the beginning of the session and, on average, in 95% of all the trials (Fig. 1C). Two monkeys had previously been trained for more than a year in experiments requiring the use of the right arm and these animals used the right limb regardless of the direction of the target motion in the first 15–20 trials. This was followed by a brief period (10–15 trials) of bilateral reaching with both limbs when the target was moved from right to the left, but not left to right, and after that the animals adopted the Interceptive strategy in 92–95% of the trials. Video analysis revealed that movements were initiated within 120–200 ms and were initially directed ahead of the current target position (Fig. 1C).

Innate nature of Interceptive movement

Further, to confirm the innate nature of the Interceptive strategy, we tested 20 kittens, aged 7–11 wk. Maturation of the motor cortex in kittens takes place between postnatal day 40 and 90 (Chakrabarty and Martin 2000) and the presence of an Interceptive strategy in the beginning of this period would provide further support for the notion of an innate mechanism for guiding the arm toward the target. The kitten was placed on a box, restricting its mobility, and a ball on the end of a string was moved by hand in pendulum fashion in front of the animal. In 19 kittens the oscillatory motion of the ball induced alternating goal-directed movements of the limbs that was identical to the Interceptive strategy, that is, the left forelimb was used to reach for the ball when it moved to the left and vice versa. The animals could maintain these movements for ≤20 s, during which 20–26 alternating reaches in phase with the target were made (Fig. 6A, Supplemental Movies S1 and S2). The strong innate preference for this strategy was revealed in trials when a kitten, by chance, was holding the limb closest to the target raised as the target was approaching (Fig. 6B, Supplemental Movie S3). In spite of this initial body posture, reaching was still initiated with the opposite limb, corresponding to the Interceptive strategy.

Reaching to stationary targets

Previous studies have indicated that motor responses triggered by moving visual stimuli may be controlled by neural circuitries distinct from those used for reaching to a stationary target (Day and Brown 2001; Fabre-Thorpe et al. 1994; Van Thiel et al. 2002; von Hofsten and Lindhagen 1979; Wentworth et al. 2000). Thus our final question was whether preference of the Interceptive strategy can be observed when fast reaching is made to a stationary visual target. Six naïve subjects were instructed to reach for a red disk randomly presented on a monitor 12 cm to the left or right of the subject’s midline. Similar to the experiments with moving targets, the subjects were first tested with the arm on the side of the target, corresponding to the Interceptive strategy described earlier.

The online version of this article contains supplemental data.
Next, they were instructed to use the contralateral arm, similar to the Pursuit strategy. For the Interceptive strategy, mean group RT was 198 ms (SD 27 ms) for the left arm and 206 ms (SD 26 ms) for the right arm. During instructed Pursuit, RT was 245 ms (SD 41 ms) for the left and 249 ms (SD 45 ms) for the right arm. RT was prolonged for the left arm by 47 ms (SD 20, \( P < 0.001 \)) and for the right arm by 43 ms (SD 22, \( P < 0.002 \)) when using instructed Pursuit compared with the Interceptive strategy. Thus the Interceptive strategy was substantially facilitated compared with Pursuit in response to a stationary cue as well.

**DISCUSSION**

The present study demonstrates that two fundamental steps in the preparation for a reaching movement—arm selection and specification of direction—can in fact be controlled reflexively. The core criterion of a reflex is that the parameters of the stimulus, but not the subject’s voluntary decisions, define and automatically release the response. Here, we have shown that there exists a highly automatic and stereotyped strategy for reaching toward a moving target in different mammalian species, including kittens in early development.

Arm selection is generally regarded as an act of conscious choice between alternatives; volitional control of this behavior was never in doubt. Psychophysical studies have suggested that arm selection is achieved via programming where motor dominance (handedness), spatial attentional information, and biomechanical advantage are used as major determinants (Gabbard and Helbig 2004; Gabbard and Rabb 2000). A number of reaction time studies have concluded that computations of arm selection take 350–450 ms (Lépine et al. 1989; Possami et al. 2002; Rosenbaum 1980; Ulrich et al. 1998; Wild-Wall et al. 2003). In our experiments the subjects voluntarily prepared both arms for potential action, but the shortest latency of selective EMG activity in the muscles of the moving arm ranged from 90 to 110 ms, which is well below the time required for a voluntary response. We conclude that the selection of the correct arm for the action execution was determined automatically by the direction of target motion, but not by the subject’s voluntary decisions. We also demonstrated that speed of reaching was adjusted in response to variations in the target’s speed. This has been shown in previous studies using computer-based models, although with inconsistent results (Bairstow 1987; Brenner et al. 1998; Brouwer et al. 2000). One should take into account that even though the target velocity may have a direct influence on the arm net motor output, this effect will be substantially modified by the current state of the implied neuronal network: this can be affected by an experimental setup that indirectly introduces constraints on the movement (for example, a computer screen that restricts movement direction and amplitude), by explicit instruction to perform fast movements, or by the parameters of the previously made trial (de Lussanet et al. 2001). Our paradigm was relatively free of typical laboratory constraints: we allowed as natural movement as possible and, importantly, we used a natural object to trigger reaching. These conditions seem to be prerequisites for uncovering the influence of the target on the course of the movement.

Furthermore, we observed a clear trend to initiate reaching in a direction ahead of the target, presumably toward the...
target’s future position. Such prospective movements have been observed before in tasks allowing much longer reaction times and have usually been explained to be the result of planning based on previous experience (Eggert et al. 2005; Tresilian 2005; von Hofsten et al. 1998). In contrast, our data suggest that prospective movement can be realized automatically. It is interesting to note that the hand was directed ahead of the farthest possible position of the target, in spite of the fact that the participants were aware about the distribution of the endpoints of the targets. Thus assuming that the theory of prior planning of the movement is correct, they should have been able to prepare default responses toward this region. This observation strongly indicates that reach direction was automatically determined by the speed of the target. Nevertheless, in our present paradigm, target motion was limited to one dimension and a rather narrow velocity range: this issue needs to be addressed in studies where the speed and location of the presented targets are more variable between trials.

Innate nature of the Interceptive strategy

Although an ultimate proof of the innate nature of certain behavior requires genetic studies, the present data suggest that the interceptive strategy is inborn and belongs to a class of species-typical behavior. The fact that movements bearing all the features of voluntary programmed responses can be generated within such a short timeframe suggests the existence of innate and presumably hard-wired link between the circuits that are activated by the target motion and those that control the limbs. This was corroborated by the observations that adult human subjects showed difficulties in reversing the spontaneous Interceptive pattern, even after extensive training, and that automated reaching movements could be induced in naïve kittens at postnatal days 35–40 (recent finding). This is as early as they were able to walk and because maturation of the motor cortex in cats takes place at postnatal days 40–90 (Chakrabarty and Martin 2000), the observed pattern is most likely controlled by dedicated subcortical mechanisms (see also Supplemental Movie S1). It can be noted that behavior similar to the Interceptive strategy reported in the present study has previously been observed during reaching to a fast moving target in human infants already at the age of 5 months (Robin et al. 1996). Presumably these mechanisms may be similar to computational maps described in the optic tectum and superior colliculus for control of orienting movements of the head and the eyes (du Lac and Knudsen 1990; Knudsen et al. 1987; Sparks 1999). Some data have also indicated that the superior colliculus is involved in control of forelimb movement in extrapersonal space (Courjon et al. 2004; Werner et al. 1997).

It has previously been described that regardless of handedness, when the target is presented off-midline, human subjects prefer to reach and also perform more efficiently in ipsilateral fashion compared with when reaching across the midline (Gabbard and Helbig 2004; Gabbard and Rabb 2000). However, these data were obtained in experiments allowing for long reaction times and, correspondingly, the interpretations have been centered on the role of spatial attention and interhemispheric asymmetry in movement planning. Our data show that stationary targets trigger Interceptive, that is ipsilateral, responses with a latency that instead suggests that the ipsilateral advantage may be due to a hard-wired link between circuitries receiving the visual information and those that control the movements of the limb. This would indicate that the brain possesses a smart mechanism that secures the use of the ipsilateral limb for catching both stationary and moving targets. A stationary target presented laterally initiates ipsilateral reaching, whereas a moving target appearing at the same location would initiate movement of the opposite limb, that is, the one that will be ipsilateral to the target by the time of catching. The brain therefore seems to be able to predict the future location of the target and automatically produce the optimal response.

Biological advantage of the Interceptive strategy

There are several reasons why the movement pattern of the Interceptive strategy would have been selected during evolution and fixed in innate and presumably hard-wired circuits. Movements that try to intercept rather than pursue the target can reach farther and, as our data show, can be made with higher velocity. For animals chasing a prey that is swinging from side to side it is highly advantageous to be equipped with a mechanism that automatically directs the proper limb toward the future location of the moving target. However, there are additional potential functions for an innate mechanism that facilitates reaching toward a target in response to a retinal motion signal. The subject’s own motion near stationary targets would elicit a visual stimulus similar to that of a moving target. This could trigger automatic arm movements enabling, for example, arboreal primates to automatically grasp branches when climbing or moving through trees; the same is true when reaching for other stationary objects during motion. Directionally selective deviation of the arm trajectory in response to a retinal motion signal has been recently demonstrated (Saijo et al. 2005).

Why the reflexive nature of reaching was previously overlooked

The main feature of reflexive mechanism is that the arm is driven automatically toward the target, although this does not seem to have been appreciated previously. Many studies have used experimental paradigms in which the natural movements either were reduced to simple muscle contractions or were obstructed and bound to response keys or handheld devices such as a joystick. As a result, the location of the target and the endpoint of reaching were spatially separated (Favilla 1997; Gordon et al. 1994; Khan et al. 2006, 2008; Pellizzer et al. 2006; Schmidt and Lee 2005). We propose that such conditions, which require a transformation between different frames of reference of the visual target and the motor response, will obstruct the direct link between target and limb and reflexive mechanisms will not be revealed. In contrast, our present data demonstrate that when reaching is triggered by natural stimuli and is unobstructed by experimental constraints it emerges as a reflexive, rather than a voluntary planned, act.

There have been a few studies that show that when the experimental paradigm more closely resembles a natural task, RT of reaching is not affected by an increasing number of alternative choices as stipulated by Hick’s law (Favilla 1996; Goodman and Kelso 1980). Current knowledge offers an alternative explanation to the prolongation of RT observed in
tasks with incompatible stimulus–response conditions. It has been suggested that cortically generated motor and cognitive functions are shaped via the competition between functionally related neural circuits (Clark 1996; Houghton and Tipper 1996). Such competition results from the potent interconnections between pyramidal cortical cells, where any undesired coactivation has to be reduced by active and thus time-consuming inhibition. We propose that in the performance of artificial paradigms requiring complex transformations between stimulus and response, the CNS is required to sustain neuronal activity in extensive and multiple cortical circuits, which would substantially augment such undesirable coactivation. Therefore the significant increase in RT observed in such conditions is not due to the response programming per se, but is caused by pronounced undesirable coactivation that required active inhibition. In contrast, during a natural reaching task, which relies on innate circuits, the number of possible targets has no effect on RT because each target selectively and directly triggers the proper network that automatically brings the arm toward the target.

**Concluding remarks**

Innate neuronal circuits underlying automatic generation of motor behavior appears to be an universal tool developed during evolution to control the variety of motor reactions. This has been revealed in studies where the structure and function of the underlying mechanisms could be directly uncovered (cf. *INTRODUCTION*). In contrast, current theories for reaching have been based on ideas borrowed from robotics and control theory and, as a result, reaching has been regarded as a response controlled via advanced parametric programming based on multistep engineering-like computations. This became a dominant concept and has strongly influenced later theoretical and experimental approaches. Nevertheless, other studies have indicated that the engineering analogy should not be literally applied to neuroscience and that more biologically realistic theories for control of the arm are needed (Kalaska 2009). The present findings appear to contradict the basic principles of parametric programming and suggest that reaching may be controlled by innate neural networks that automatically guide the arm toward the target.

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**DISCLOSURES**

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