



An ethologically motivated neurobiology of primate visually-guided reach-to-grasp behavior

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Abstract

The precision of primate visually guided reaching likely evolved to meet the many challenges faced by living in arboreal environments, yet much of what we know about the underlying primate brain organization derives from a set of highly constrained experimental paradigms. Here we review the role of vision to guide natural reach-to-grasp movements in marmoset monkey prey capture to illustrate the breadth and diversity of these behaviors in ethological contexts, the fast predictive nature of these movements [1,2], and the advantages of this particular primate model to investigate the underlying neural mechanisms in more naturalistic contexts [3]. In addition to their amenability to freely-moving neural recording methods for investigating the neural basis of dynamic ethological behaviors [4,5], marmosets have a smooth neocortical surface that facilitates imaging and array recordings [6,7] in all areas in the primate fronto-parietal network [8,9]. Together, this model organism offers novel opportunities to study the real-world interplay between primate vision and reach-to-grasp dynamics using ethologically motivated neuroscientific experimental designs.

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Introduction

Binocular vision and precise manual dexterity are inextricably linked in the evolution of primate brains and behaviors. Not only does vision routinely guide complex movements, such as reaching, in tasks ranging from foraging and prey capture to object manipulation and diverse tool use [10–12], but the fronto-parietal networks that support these actions show marked expansion in primates relative to other mammals [8,13]. Parietal and premotor brain areas in primates are organized into sub-networks where each has a node that integrates visual and postural information and interacts with a corresponding node involved in movement planning (Figure 1a). The expansion of parieto-frontal networks in primates [8,14] supports a diversity of visually-guided reaching behaviors, including subnetworks that drive specific components of ethologically relevant behaviors [15–19], such as moving the eyes to a target [20], the transport of the hand during a reach [21], and the shaping of the hand for a grasp [22], as well as complex responses across multiple effectors, such as defensive movements to block a looming target at the head [15,16]. While the neural basis of reach-to-grasp movements has been extensively studied in primates [23,24], the range of actions studied to date represents a very small portion of the ethological behaviors evident in primates.

Primate neuroscience has traditionally relied on paradigms in which subjects are head-restrained and positioned in a body-constraining chair that limits their behavior to relatively simple, low-dimensional reaching tasks (Figure 1b). For example, in “center-out” reach tasks, a macaque uses a fixed upper arm posture to move their hand from a central point to a target in 2D [25–27] or in 3D [28]. The obvious advantage of these reductionist approaches is precisely quantifying neural firing with respect to task variables (like 2D target position), but they come at the cost of a more representative understanding of the neural mechanisms that underlie the diversity of primate approaches and reach actions observed in the wild (Figure 1c–e). For example, they do not address grasping for moving objects in 3D space, such as moving prey [1]. The advent of marmosets as a model organism in neuroscience at last enables a fuller

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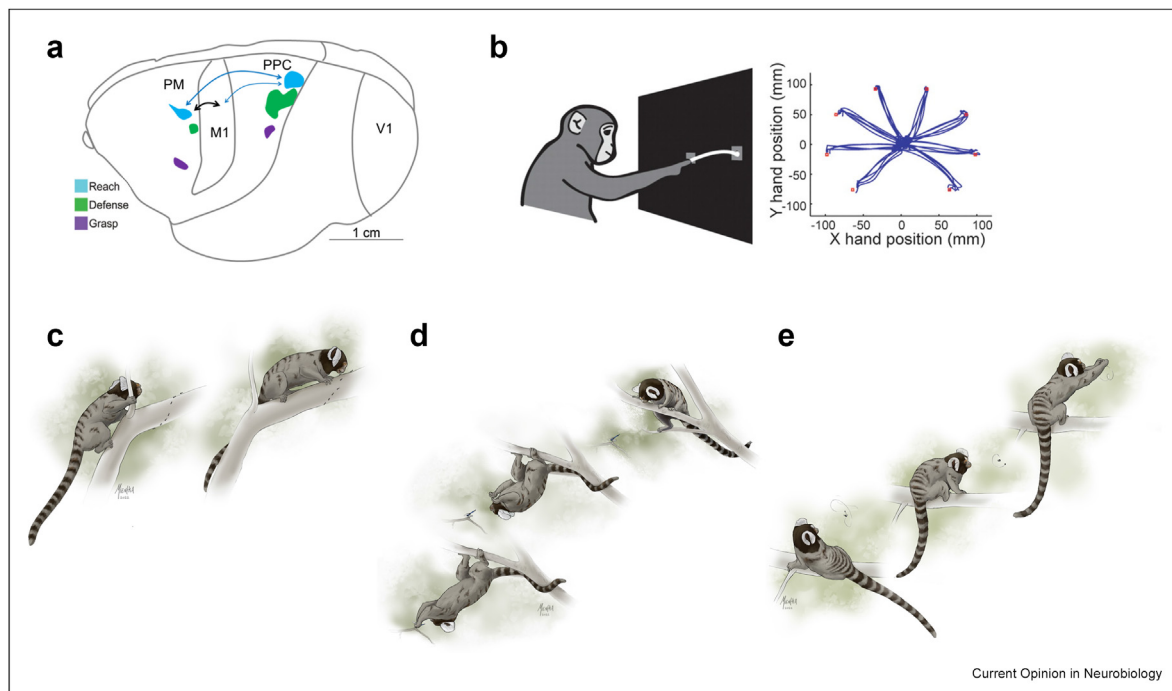
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Figure 1



The neural mechanisms of reach-to-grasp movements in constrained and natural task contexts. **a:** Parieto-frontal subnetworks control ethologically relevant movement behaviors. For example, reaching (in light blue) involves a parietal hub that integrates visual and somatosensory information and makes feedforward projections to a premotor area counterpart, which in turn feeds back to the parietal area. Other subnetworks specialize in different behaviors, such as grasping (in purple). Figure adapted from Ref. [8]. **b:** Traditional reductionist behavioral paradigms reduce the complexity of reaching tasks. In a center-out reaching task, a macaque first points to a central point on a video screen and then makes a rapid reach to an indicated peripheral point. Reach trajectories reflect roughly linear movement of the hand to the endpoint. Figure adapted from Ref. [27]. **c–e:** Reaching in natural contexts imposes a variety of more challenging task constraints. Marmosets employ distinct positional strategies during the capture of different prey. **C:** ‘Mouth Capture’. The marmoset stands over the prey and captures multiple insects with their mouth. The strategy is typically used for small insects found in groups that lack rapid evasive behaviors, such as ants and termites. **d:** ‘Stalk/Pause and Lunge’. The animal identifies the prey, gets into position, and pauses before initiating the prey capture. This strategy is typically implemented with hunting insects that will exhibit quick evasive behaviors when predators are identified, such as dragonflies and stick bugs. **e:** ‘Capture in Flight’. The monkey identifies and tracks the flying insect prey before capturing it with a visually guided grasp. **c, d, and e** adapted from [1].

understanding of natural reach and grasp behavior. Coupled with recent technological advances such as markerless video tracking, this affords powerful new opportunities to overcome these paradigmatic limitations and quantify natural, ethological behaviors in unrestrained primates in a manner not previously possible [29,30], which, if leveraged appropriately, could be used to investigate the neural mechanisms underlying the diversity of visually guided reaching that occurs in human and nonhuman primates.

Marmoset positional and foraging behaviors

Common marmosets (*Callithrix jacchus*) are a small-bodied (~300–500 g) New World primate endemic to the forest of northeastern Brazil that, like early primates, live an almost entirely arboreal life. Owing to the challenges of life in the trees, the species evolved a dynamic suite of positional behaviors that rely on precise visuo-

motor integration to socialize, travel, forage, hunt prey, and avoid the obvious peril of falling [31]. Callitrichid primates—e.g. tamarins and marmosets—evolved unique flattened nails that function much like claws and enable the animals to cling to arboreal substrates in distinct ways and exploit foraging resources that would otherwise be inaccessible, including insects inhabiting the trunks of trees and exudates such as saps and gums [32]. Their flattened nails also enable them to cling to the vertical trunks of large trees and to vertically leap from one tree trunk to another [33]. While exudates are a staple of the Callitrichid diet [34–36], common marmosets complement their unique clinging-related positional behaviors with more primate-typical quadrupedal locomotion to travel along branches and other vegetation in the forest and exploit other rich food sources, such as fruits and insects [31,37], each of which can present distinct behavioral challenges in arboreal environments as they are often found in precarious locations on small

branches or otherwise difficult to reach locations that require creative, visually guided movements to obtain.

Marmoset prey capture in the wild

Marmosets are voracious hunters. These small monkeys learn to hunt a diversity of prey ranging from small insects, such as ants, to reptiles and small mammals [31,38], with this prey accounting for up to half their diet in some seasons [31,39]. Marmosets are not simply opportunistic hunters but employ visual strategies to actively search for prey [40]. The diversity of prey presents distinct challenges for successful predation. For example, cryptic prey require perceptual mechanisms and color vision to identify [41], while for prey that use rapid escape behaviors, marmosets must slowly stalk them [38,1]. Perhaps the most challenging prey for visually guided-reaching are the flying insects, as marmosets must leverage their high-acuity 3D vision, anticipate the prey's flight trajectory, and modify their grasp in response to changes in a prey animal's flight once a reach has been initiated [1]. The combined idiosyncrasies of the arboreal environment and the prey species themselves require dynamic, creative solutions distinct to each predation event.

Ngo *et al.* [1] quantified the prey-capture behaviors of wild marmosets in northeastern Brazil using both traditional ethological characterizations and markerless pose-estimation [30] to explicate the fine details of these natural visuo-motor actions. Analyses revealed that marmosets employed three broad types of prey-capture behaviors when hunting insects that reflected the optimal strategy for the specific species being pursued (Figure 1c–e). Mouth grabs, for example, were used to capture small insects (e.g. ants) found along a branch or tree trunk (Figure 1c). When pursuing prey with more robust, effective escape behaviors, such as dragonflies and stick bugs [42], marmosets employed a stalk/pause and lunge strategy that involved slow, methodical movements towards a prey's position followed by a high-speed two-handed grasp (Figure 1d). To capture flying insects, marmosets visually tracked the prey, presumably predicting its trajectory for successful capture (Figure 1e). Importantly, none of these hunting behaviors were stereotyped, as each instance of prey pursuit and capture required a unique tactic owing to the idiosyncrasies of the context. Given the challenges of arboreal living and the unpredictable nature of prey species, behavioral flexibility and creative problem solving are likely necessary to be an effective predator.

The capture of flying insects is among the notable examples of natural, visually-guided reaching in a primate, as it not only requires stereoscopic vision and estimating the probability of the prey's flight pattern but also rapid adjustments to the hands and arms during the high-speed reach in response to changes in the prey's

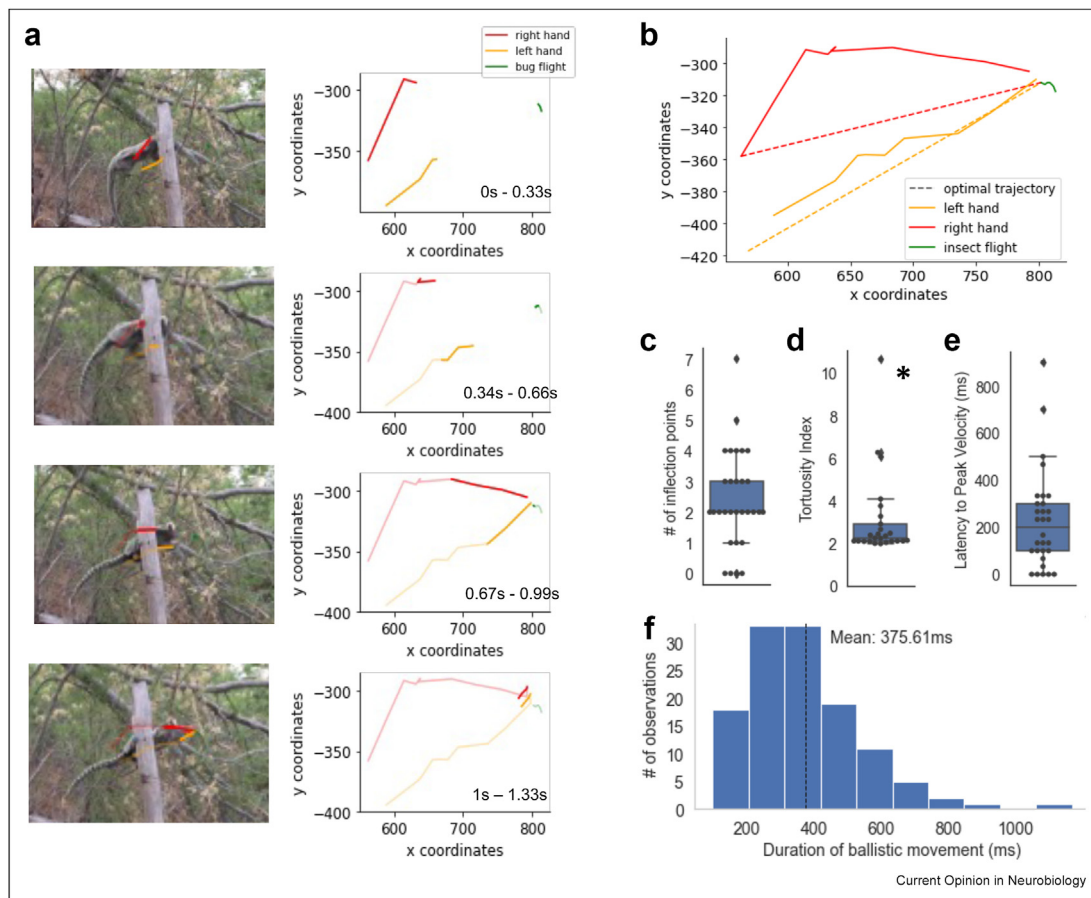
flight trajectory once the grasp is initiated. To quantify this remarkable behavior for the first time in a wild primate, Ngo *et al.* [1] analyzed the relationship between the movement of the flying insect and the marmoset's gaze to better understand how the monkey's tracked their prey in the moments before the capture. Results indicated that the movement between the prey and the monkey's gaze was largely uncorrelated until the final ~ 1.5 s of the capture event. Within ~ 400 ms of the capture, the velocity of the marmoset's head rapidly increased, suggesting the monkey was precisely visually tracking the prey. Figure 2a shows the hand movements of a marmoset and the flight of the prey target in a series of successive frames from a single prey capture event to illustrate the sequence of high-speed precision motor actions involved in the final stages of this behavior. Notably, the hands do not follow a direct optimal strategy (Figure 2b) but rather make several inflection points (Figure 2c) that result in significant tortuosity of the hand movements relative to the target (Figure 2d). Notably, these motor changes happen at remarkably fast speed as the grasp reaches peak velocity in ~ 200 ms (Figure 2e) and are typically 500 ms or less in duration from initiation to capture of the prey (Figure 2f). This suggests that marmosets are making rapid, visually guided adjustments to their hand/arm movements in response to subtle changes in the prey's movements that occur after the rapid grasp is initiated.

Marmoset reach-to-grasp in a laboratory setting

Ethologically motivated experiments in a laboratory setting offer a unique perspective, bridging the highly constrained tasks used in classical neuroscientific experiments and the unconstrained field studies of animal behaviors [43]. Such paradigms can capture ethologically relevant behavioral dynamics that are often missing in highly restrained lab tasks while at the same time maintain the highest spatial-temporal resolution that are possible in a laboratory environment but challenging to achieve in the field. As an example, a recent study [2] used multiple high-speed cameras to examine online adjustments during reaching movements of live crickets (Figure 3a). The use of multiple camera views within the laboratory setting allowed for detailed reconstruction of the 3D kinematics of natural prey capture reach-to-grasp movements, but more so for analyses of the dynamics of reaching for moving targets (i.e. prey; Figure 3b).

Shaw *et al.* [2] found that marmoset reach-to-grasp movements for dynamic prey operate at short visuo-motor delays rivaling oculomotor systems, and that visual prediction helps to compensate for the visuo-motor delays to make online adjustments during reaching. They determined that the marmoset visuo-motor delay was around 80 ms, which is based on

Figure 2



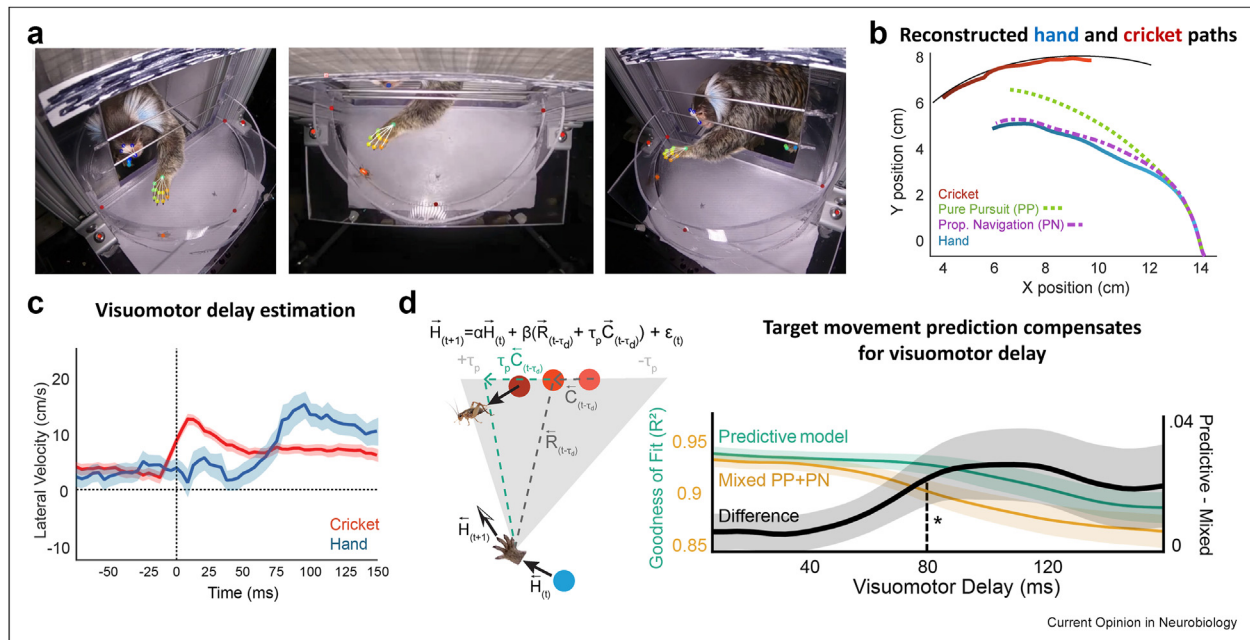
The dynamics of prey capture and active vision among wild marmosets. **a:** Left plots show four continuous time periods during prey capture from an exemplar video of a wild marmoset hunting and the XY coordinates of the marmoset's right (red line) and left (yellow line) hands and insect (green line); right plots show only the XY coordinates. The dark lines show the change in movement during the time interval plotted over that specific time period, while lightly shaded lines indicate the preceding time interval. **b:** The summary of A shows the overall path of both hands and the insect, as well as the optimal trajectory (dashed lines) for each hand. **c:** Number of inflection points during marmoset reaches from all videos analyzed. **d:** The tortuosity index for all marmoset prey-capture reaches. **e:** Latency to peak velocity (ms) during grasps of flying prey by wild marmosets. **f:** Duration of hand movement (ms) from initiation of the motor action to successful grasp of the prey. Figure adapted from [1].

corrective hand movements in response to sudden changes in cricket movements (Figure 3c). This delay is more than twice as fast as that measured in traditional restrained paradigms for macaque monkeys [44,45]. In traditional “double step” tasks, the target jumps instantly between two positions on a computer screen with unpredictable timing during the reach, typically yielding longer estimates of motor delays around 200–300 ms [46–48]. By comparison, faster visuo-motor delays around 100 ms are found during oculomotor pursuit of continuously moving targets in macaques [49], and in marmosets, can be as short as a 75 ms delay [50]. The study by Shaw et al. [2] suggests that continuous prey pursuit with hands can involve fast updating, comparable to oculomotor pursuit in marmosets. The smaller body size of marmosets may reduce visuomotor delay compared to macaques. Moreover,

because natural prey moves in a continuous way, their continuous motion would likely pose specific constraints on the coordination between visual attention and the hand to allow for prediction, which have not been addressed in traditional double-step tasks where targets jump instantaneously from one position to another.

Given the estimated visuo-motor delay, Shaw et al. tested a range of pursuit models to show how visual prediction can help to compensate for such a delay. Several movement control strategies for prey capture have been found in a variety of species, such as pure pursuit and proportional navigation [51–53]. The best fit for any of the reactive pursuit strategies occurs when there is no visuo-motor delay in the system (Figure 3b). However, a system with no delay is, of course, not feasible, biologically or even physically, and contradicts

Figure 3



Behavioral dynamics of marmoset reaching to grasp for a moving prey in a laboratory setting. **a:** High-speed, multi-camera videos show marmoset reaching for a moving cricket. Colored dots indicate DeepLabCut labeling of synchronized video frames from three camera angles. **b:** Reconstructed paths of the hand (blue) and cricket (red) in an example reaching trial. Lighter points indicate the beginning of the reach. A pure pursuit (PP) steering strategy aligns hand velocity with the line of sight (green). Proportional navigation (PN) rotates hand velocity to mirror line-of-sight rotations (purple). Overlaid simulations of PP and PN models show that the PN model best approximates this reach. Both simulations assume no visuo-motor delay in computing their trajectories, whereas the marmoset reach system would have to compensate for delays to achieve the same performance. **c:** Visuo-motor delays in the marmoset reach system are revealed by the delay for increases in the lateral cricket velocity (red), followed by increases in the lateral hand velocity (blue) at a latency of roughly 80 ms. **d:** Cricket velocity can be used to predictively guides hand velocity to compensate for visuo-motor delay. Left: a multivariate linear model used to test the influence of visuomotor delay τ_d and prediction time constant τ_p on the fit of hand velocity. Right: this predictive pursuit model provides a better fit (teal) that degrades more gradually with visuomotor delay than the mixed PP + PN steering model (orange, left vertical axis). The improvement for the predictive vs. steering model (black curve, right vertical).

the experimental estimates a delay of around 80 ms. By configuring an autoregressive model that contains both the visuo-motor delay and a prediction time constant extrapolating the crickets' position to a point in the future, the resulting predictive pursuit model significantly outperforms the reactive pursuit models (Figure 3d). Of note, this predictive formulation is also used in another recent model of pursuit for monkeys controlling a screen cursor with a joystick to capture evading virtual targets [54]. The predictive term there goes beyond 500 ms into the future, consistent with the delays imposed by the joystick control used in that task. By contrast, the natural dynamics of marmoset unfold much faster, and a matching predictive term compensates for the inherent visuo-motor processing delay in the range of 80–150 ms in the future.

Discussion

Like body morphology and other physical traits, a species' ethological behaviors are targets of selection in evolution. Natural behaviors, therefore, reflect evolutionary pressures that have optimized brains to overcome the

challenges each species has faced over their natural history [55]. While this relationship has long been recognized, a significant bottleneck to the neurobiological study of natural behaviors has been accurately quantifying these ethological processes. Recent advances in machine vision, however, now offer the necessary tools to bridge this gap and track complex behaviors with the temporal and spatial precision on par with brains [56]. As highlighted here, marker-less video tracking systems provide a wide range of experimental flexibility critical for expanding experiments beyond more constrained classical approaches, such as the motor control that is required in dynamic conditions with active visual prediction. For example, for an organism to successfully intercept a moving target, it must be able to account for the movement of the target, the movement of its own body, as well as neural conduction and processing delays. Most theoretical frameworks of motor control are based on a predictive model of the future body and target positions, which are incorporated into an update mechanism based on real-time visual information and proprioceptive feedback information [57,58]. However,

previous experimental research in humans and nonhuman primates has largely focused on reductionist paradigms that involve stereotypic movements in constrained positions [59–65]. These highly constrained experimental conditions reduce behavioral patterns to a smaller parameter space that is easier to quantify, but much remains unknown about the control mechanisms in dynamic conditions typical of natural movements [66].

Reaching for dynamic moving targets highlights how a more ethologically motivated behavior, like insect predation, could be valuable towards understanding the underlying neural circuitry of visually guided reaching. While the role of visual prediction in movement planning is generally acknowledged, traditional nonhuman primate neuroscience paradigms have not examined it in depth. Much evidence supports that motor commands in frontal motor areas provide feedback to the parietal visual cortex to facilitate comparison of expected and actual sensory outcomes necessary for on-line movement guidance [57,67] and rapid adjustment of reaching [18]. Areas in the intraparietal sulcus are a likely hub of reach planning that could mediate visual prediction for targets given the convergence of premotor feedback and sensory inputs [19,68–70]. However, the parietal cortex is likely even more broadly involved in complex tasks than is typically investigated in classical constrained reaching tasks [44,58,71,72]. Thus, a focus on ethologically motivated task designs that more fully sample the space and dynamics of these coordinate systems is likely essential to answering many of the remaining questions.

The marmoset monkey offers distinct advantages for the study of fronto-parietal circuits controlling natural reach-to-grasp movements [3]. First, because of their lissencephalic cortex, nearly all the visual, parietal, and frontal areas involved in reach-to-grasp movements lie accessible at the cortical surface for array recordings [6,7]. Like other primates, the marmoset's fronto-parietal cortex is organized into distinct sub-networks that control specific aspects of the behavior (reaching, grasping, and visual pursuit) [8,9]. And a recent study using chronic wireless recordings has demonstrated the feasibility of recording from the cortex of freely moving animals [4,5]. Thus, the marmoset model is well poised to interrogate the neural correlates of visually guided reaching and movement control using ethologically motivated tasks that include real-world complexity and dynamics.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

This is a review paper and does not report new data.

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