MUSCLES THAT SEE
Early Muscle Activations are Time-Locked to the Onset of Visual Targets

by

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Abstract

The visual grasp reflex provides automatic orienting of gaze (the visual axis in space) to novel visual stimuli. Previous studies have demonstrated activation of neck muscles of awake monkeys appearing at a short fixed latency (55 to 95 ms) after visual target presentation, regardless of whether or when saccades are made. The purpose of these early visually-driven muscle activations may be to prime head rotation required as a part of the coordinated eye-head movement to the target. Similar orienting responses might be found for visually guided reaching. Here, we explore early visually-driven muscle activations of the human upper limb immediately preceding planar reaching movements. Subjects performed reaches towards small visual peripheral targets while upper limb kinematics were recorded and intramuscular electromyography was collected from four shoulder and elbow muscles. Subjects maintained their right hand at a central fixation marker that was extinguished for a gap period (200 ms) prior to appearance of a peripheral target. Subjects were instructed to reach to the target as quickly as possible. Some subjects exhibited a short burst of muscle activity (about 20 ms duration) time-locked to visual target onset. This burst occurred around 85 ms to 105 ms after target onset and preceded the onset of muscle activity associated with volitional arm motion by about 100 ms. Notably, this burst was dependent on target location: visually-driven muscle activity occurred in right shoulder extensor muscles for rightward targets and was absent for leftward targets. In order to better dissociate the visual burst from volitional motor activity, we employed a delay paradigm. No time-locked muscle activity was present in the delay task either after the target appeared or after the fixation marker was extinguished. This suggests that the visual burst is dependent on the imminence of voluntary movement and the laterality of the target. We conclude that the appearance of a visual target can result in short-latency activity on the arm musculature that is appropriate for orienting the arm to the target.

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Ad Majorem Dei Gloriam

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List of Acronyms and Abbreviations

Br	brachioradialis muscle
cm	centimetres
CNS	central nervous system
DP	deltoid muscle (posterior fibres)
EMG	electromyography
Hz	Hertz
KINARM	Kinesiological Instrument for Normal and Altered Reaching Movements
MRF	mesencephalic reticular formation
ms	milliseconds
μV	microvolts
PM	pectoralis major muscle
PPC	posterior parietal cortex
RT	reaction time
SC	superior colliculus
TLat	triceps brachii muscle (lateral head)

Chapter 1

Introduction

Imagine a goalie in a hockey game trying to watch the puck in play. At first, his vision is blocked by other players. Suddenly, another player hits the puck, and the goalie spots it as it zooms towards himself. If he is to defend his net, the goalie will need to rapidly adjust the position of his stick to block the oncoming shot. In other words, his central nervous system needs to coordinate his eyes, head, and arm to orient him towards a novel visual stimulus. While hockey is not strictly an activity necessary for survival, the ability of the nervous system to coordinate responses to novel visual stimuli is essential for humans and other animals.

1.1 Reflexes

Reflexes are an important example of how the nervous system is able to respond to various stimuli. Reflex is defined as the fastest and simplest transformation of some sensory signal into a motor response (Prochazka et al., 2000). The classic example of a reflex is the stretch reflex (Liddell and Sherrington, 1924), colloquially known as the knee-jerk reflex. When a muscle is stretched by some force, the nervous system transforms the stretch into a involuntary contraction of the same muscle.

Another classic reflex is the grasp reflex, where pressure on the palm results in flexion of the fingers and thumb (Seyffarth and Denny-Brown, 1948). This reflex, although present in newborns, is suppressed in adults except in certain disease states (Schott and Rossor, 2003). Even so, this reflex demonstrates how the nervous system can automatically produce a useful action, such as grasping, when presented with a relevant stimulus, such as pressure on the palm.

Going back to the hockey goalie example, it could be useful if the nervous system could provide an automatic orienting response of the hand to novel visual stimuli. Using visual stimuli rather than somatosensory stimuli to evoke reflexive responses does have precedence. For example, several clinical cases have been documented where patients were unable to suppress automatic groping and grasping of novel visual stimuli (Magnani et al., 1987). Another example, explored in detail below, is that the hand can be automatically oriented to changes in target location during reaching movements (Pélisson et al., 1986). Such an automatic response could then be useful when attempting to reach an object in a changing environment. It is therefore possible that a functional automatic reaching response to novel visual stimuli exists. Such a response might parallel the visual grasp reflex, which involves orienting to novel visual stimuli.

1.2 The Visual Grasp Reflex

The visual grasp reflex refers to the automatic orienting of gaze to foveate a novel visual stimulus in the periphery (Hess et al., 1946). Gaze is determined by the position of the eye in space, and so shifts of gaze can involve movement of the eye, the head, and even the body (McCluskey and Cullen, 2007). The visual grasp reflex is useful for animals because they are required to vigilantly monitor novel visual stimuli in their environment for survival. It should be noted that while the direction of gaze is changing, vision is blurred and the animal is unable to monitor its environment. Therefore, the movements of the eye, head, and body would need to be coordinated to minimize the time when gaze is not stable.

The example of the hockey goalie above demonstrates the necessity of rapidly coordinating gaze and hand movement. In such fast-paced scenarios, it would be optimal to adjust both gaze and hand position simultaneously to respond to the change in the visual environment. Therefore, it is conceivable that the visual grasp reflex could be extended to orient the hand as well as gaze.

1.3 The Eye and the Visual Grasp Reflex

Perhaps the best understood component of the visual grasp reflex is the movement of the eye. The eye is capable of rapid, ballistic movements known as saccades. Such movements can be automatically elicited by novel visual stimuli, thus forming the eye component of the visual grasp reflex (Hess et al., 1946; Ingle, 1973). However, it is possible for animals to suppress this reflex and even look away from visual stimuli to the opposite direction (Hallett, 1978). Nonetheless, it should be noted that saccades made in response to visual stimuli can have latencies that approach the minimum conduction time of nerve impulses from the visual system to the oculomotor system; these saccades are known as express saccades (Fischer and Boch, 1983; Paré and Munoz, 1996). In monkeys, normal visually-guided saccades have a reaction time around 140 ms after target onset, whereas express saccades have a reaction time of 70 to 80 ms (Fischer and Boch, 1983). In humans, on the other hand, the range of normal visually-guided saccades spans 140 to 180 ms, and express saccades span the interval around 100 to 135 ms (Fischer et al., 1993; Munoz et al., 1998). It is these express saccades which make up the eye movement component of the visual grasp reflex, and their short latency demonstrates the automatic nature of the visual grasp reflex.

One particular structure of the brain implicated in the production of automatic eye movements in response to visual stimuli is the superior colliculus. The SC receives input from the retina and other visual areas, and it has neurons whose discharge is associated with maintaining fixation or initiating saccadic movement (Munoz and Fecteau, 2002). Visuomotor neurons in the deeper layers of the SC show a “visual burst”, that is, a sudden increase in activity 40 to 50 ms after target onset (Wurtz and Goldberg, 1972). This burst is thought to trigger the production of express saccades if the visuomotor system is sufficiently disinhibited (Dorris et al., 1997). In addition, the production of express saccades is also contingent on advanced motor preparation and thus on the probability of the appearance of a target (Paré and Munoz, 1996).

Experimentally, the gap paradigm has been used to study express saccades because it is thought to disinhibit the visuomotor system (Dorris and Munoz, 1995). A gap period is inserted between the disappearance of a fixation marker and the appearance of a visual target which results in a reduction in saccadic reaction time (Saslow, 1967). The gap effect is thought to be associated with changes in activity in the SC: during the gap period, the activity of neurons in the SC responsible for maintaining fixation is diminished, while the activity of neurons in the SC responsible for initiating saccades increases (Dorris et al., 1997). Thus activity in the SC correlates with the production of express saccades, highlighting the role of the SC in the visual grasp reflex.

1.4 The Head and the Visual Grasp Reflex

Head movement plays an important role in the visual grasp reflex. As such, the proper coordination of the head and other aspects of the visual grasp reflex is necessary for maintaining stable gaze. The head has much greater inertia than the eye and therefore takes longer to move (Zangemeister and Stark, 1982), so activating the neck muscles to move the head before moving the eye increases the contribution of head motion to the gaze shift. Indeed, it has been shown in cats that head movements are smoothly coordinated with eye movements when shifting gaze to novel visual targets, and that head movements precede eye movements (Guitton et al., 1984). Humans also show activation of neck muscles before the eye begins to move (Biguer et al., 1982). Other studies have confirmed that the head is commanded to move before the eyes, indicating that the central nervous system plans around the greater inertia of the head when preparing to shift gaze (Corneil and Elsley, 2005). Also, since gaze can remain stable during head movements because of the vestibulo-ocular reflex (Zangemeister and Stark, 1982), the CNS might use the advance planning of head movement while still deciding whether to orient the eye.

Neck muscles can be recruited before gaze shifts even when the head is fixated and can be activated at a very short and constant latency after visual target appearance (55 to 95 ms), regardless of when the saccade began (Corneil et al., 2004). These muscle activities consist of a short burst of activity about 20 ms in duration. Notably, these activities are directionally specific, that is, the neck muscles recruited are specific for turning the head in the same direction as the target. Some muscles responsible for turning the head in the opposite direction also show an inhibition of activity that is time-locked to the target onset. The directional specificity of these responses indicate that this effect is different from startle. In the case of acoustic startle, for example, early muscle responses on the neck can be elicited, but these responses are bilateral, not directional (Siegmund et al., 2001). Were the effect of the visual target onset on the neck muscles a startle effect, the neck muscles ought to have be activated bilaterally. However, since only the muscles responsible for turning the head in the direction of the stimulus are activated, this effect must not be a startle response. These results show that the CNS can prepare head movements before the decision to shift gaze is made by priming the neck musculature.

As with eye movements, the SC is also thought to be involved in the production of head movements related to visually-guided gaze shifts. Studies in the cat (Guitton et al., 1980; Roucoux et al., 1980) and monkey (Corneil et al., 2002a;

Corneil et al., 2002b) have shown that stimulation of the SC can evoke gaze shifts with coordinated eye-head movements. In addition, research has shown that activity in the deeper SC commands for gaze-shift rather than the individual eye and head components (Freedman and Sparks, 1997a). The SC can therefore be seen as an important structure for synergistic eye and head orienting movements in the visual grasp reflex.

1.5 The Hand and the Visual Grasp Reflex

1.5.1 Eye-Hand Coordination

In order to understand the role of the hand in the visual grasp reflex, it is important to understand the coordination of the eye and hand in reaching tasks. When both the hand and eye are used to orient to a novel visual stimulus, the movement of the eyes precedes the movement of the hand (Biguer et al., 1982). The onset of muscle activity from a primary agonist of the arm, however, can precede saccadic eye movements in coordinated eye-hand movements (Gribble et al., 2002). In both of these studies, it was also shown that the onset of eye movement was correlated with the onset of hand movement and the onset of limb muscle activity, suggesting coordinated control of these components.

Another link between the eye and hand is the gap effect. Studies have demonstrated that the use of a gap period in a reaching can reduce manual reaction times (Bekkering et al., 1996; Gribble et al., 2002). This fact shows that changes in the visual environment can affect the movement of the hand and is further evidence of the coordination of the eye and the hand.

Behavioural studies have also shown that, while the hand is reaching to a visual target, the subject's gaze is fixed on the visual target and cannot be changed to a new target until the reach is finished (Neggers and Bekkering, 2000). This inhibition of new saccades is present regardless of whether the hand is visible during the reach, suggesting that this effect was controlled by a non-visual signal in the CNS (Neggers and Bekkering, 2001). Control of the eye during a hand movement by this non-visual signal demonstrates how the CNS is able to coordinate eye and hand movements by keeping gaze stable until the movement is finished.

Not only does the CNS control whether or when eye and hand movements are made, but it can also respond to changes in vision by modifying an ongoing arm movement. Research has shown that subjects are capable of correcting reaches to a visual target when there is no vision of the hand, suggesting that the CNS is able to perform such corrections by comparing visual input with the position of the hand calculated from efference copy (Prablanc et al., 1986). Consequently, when the location of the visual target is displaced during a saccade, subjects are able to modify their reaches to the new target position, even though they cannot see their hands while reaching (Pélisson et al., 1986). Such corrections to hand position are automatic and unconscious; the subjects did not even notice the change in target position. Thus the CNS not only coordinates the planning of eye and hand movements but can also modify an ongoing hand movement in response to changes in the visual environment. Additional research indicates that it takes the CNS a minimum of about 125 ms after a visual perturbation to cause a responding change in hand motion, and these responses are highly automatic and difficult to voluntarily suppress (Day and Lyon, 2000).

Since hand movement can affect eye movement and visual information can affect hand movement, it is obvious that the CNS can transform information from the visual system into commands for the motor systems of the hand and eye. One particular part of the CNS that is involved in visually guided reaching is the posterior parietal cortex. The PPC is situated between visual and motor cortex and has activity related both to reaching and eye movements (Goodale and Milner, 1992). For example, Snyder et al. (1997) have demonstrated that neurons in the PPC can encode intended movements of the arm and eye. Also, MacKay (1992), Rushworth et al. (1998), and Grafton et al. (1992) have shown that neurons in the PPC are active during reaching as well. Additional research had indicated that the specific areas of PPC that have activity related to either eye or hand movements do overlap, implying that the PPC is an important structure for their coordination (Levy et al., 2007). It is important to note that the PPC plays an important role in online correction: patients with lesions of the PPC are unable to produce the automatic rapid corrections to target perturbations which normal subjects are capable of (Pisella et al., 2000); this suggests that the PPC is involved in direct visuomotor transformations (Rossetti et al., 2005). The PPC, therefore, is likely an important structure in coordinating movement of the eye and hand.

The SC could also play a role in visuomotor transformations for reaching. As mentioned above, the SC is involved in the production of saccades and the coordination of the eye and head in gaze shifts. Research in monkeys has also demonstrated that neurons in the SC can modulate their activity during reaching to visual targets (Werner et al., 1997a). Cells of the deep SC and the underlying mesencephalic reticular formation as well have activities that are correlated to the activities of muscles of the arm (Stuphorn et al., 1999). These correlations were found mostly for the musculature of the shoulder, and the activity in the SC and MRF preceded the activity in the muscles by about 52 ms. Other neurons in the SC had responses which were tuned to arm movements in particular directions away from the centre of gaze (Stuphorn et al., 2000). Gaze shifts involving eye and head movement are also coded in gaze-related coordinates (Freedman and Sparks, 1997b), and so hand and gaze shifts could potentially be coordinated in the SC as well.

1.5.2 A Possible Visual Orienting Response of the Hand

So far we have described several links between the eye and the hand and the coordination of their movements. These links suggest that the hand may have a visual orienting response which is analogous and complementary to the visual grasp reflex. Going back to the example of the goalie, it would be advantageous if he could adjust the position of his stick as soon as he saw the change in the puck's trajectory, allowing him to better defend his net. Thus rapid manual responses to novel visual stimuli could be very beneficial.

There are several reasons why the hand could have a visual orienting response. As stated above, changes in vision can lead to automatic changes in hand trajectory during ongoing movements. This is similar to how the appearance of visual stimuli can result in automatic saccades with the visual grasp reflex. The visual grasp reflex can be suppressed by fixation-mediated inhibition in the superior colliculus (Munoz and Wurtz, 1993; Dorris and Munoz, 1995), and, as mentioned above, the use of a gap period can result in disinhibition of arm and eye movements (Bekkering et al., 1996; Gribble et al., 2002). Therefore it is possible that, in a reaching task using a gap period, the appearance of a novel visual stimulus might result in a reflexive activation of the muscles of the arm. Such activity might be similar to the early neck muscle responses time-locked to visual stimuli found in monkeys described above. One reason for this is that both the neck and arm are used for orienting to visual targets in a reaching task. Another reason is that the muscles of the neck and the muscles of the arm are both responsible for moving structures that have substantial inertia compared to the eye and might benefit from early activation. Also, in the case of quadrupeds, the musculature of the forelimbs could be involved in moving the body to orient gaze to novel visual stimuli and could benefit from an early orienting response of the forelimb. We therefore predict that short-latency muscle activity time-locked to the appearance of visual stimuli can be found on the musculature of the arm.

1.6 Study Objectives

The purpose of this study is to examine if the muscles of the human arm demonstrate an early visual orienting response. The first objective is to determine if short-latency visual responses are present on the musculature of the arm. These responses should be distinguishable from activity related to the initiation of hand motion and so should occur before it. Also, if these responses are related to the appearance of the visual stimuli and not to the onset of hand movement, they ought to occur at a fixed latency after the appearance of the visual stimuli, regardless of when the hand begins to move. If these responses are distinct from startle, these responses should be directionally appropriate, that is, the muscles that show the response ought to be those used for initiating hand movement towards the visual stimuli. On the other hand, if the responses were a startle effect, the muscles that show the response should have no relationship to the direction of the visual stimulus. Instead, all the muscles should be activated simultaneously, regardless of where their action moves the hand.

Another objective of this study is to see which particular muscles show time-locked responses to visual stimuli. It is possible that the responses would appear more often on the muscles responsible for moving the shoulder than those responsible for moving the elbow because the known components of visual grasp reflex are axial, and the shoulder is closer to body axis than the elbow.

The third objective of this study is to see if time-locked responses can still be elicited on the arm musculature if the appearance of the visual stimulus was separated from the signal to reach. We use the disappearance of the fixation marker after a random period of time for the signal to reach. In this paradigm, the appearance of the target might not elicit a response because the subjects don't need to move yet. Early activity would then be wasteful. Also, with a randomized delay period, no prediction could be made as to when the target could appear, and so there might not be sufficient motor preparation in the nervous system to elicit a time-locked response. After the signal to reach, there might be a time-locked response on the musculature of the arm as the subjects orient their gaze and arm to the target. Without the gap period, however, there might be inhibition in the nervous system to elicit a time-locked response. Also, since the signal to reach is not directionally specific, there might only be a startle response preceding volitional muscle activity related to the movement itself. However, there might be no response at all before the volitional activity.

Chapter 2

Methods

2.1 Subjects

All experiments were approved by the Health Sciences Research Ethics Board at Queen's University, Kingston, ON. The experiments were performed by 8 healthy participants (2 male, 6 female, ages 23 to 26, right-handed). Subjects were required to sign a consent form, were remunerated for their time, and could withdraw from the study at any time.

2.2 Equipment

Arm kinematics were recorded using KINARM (BKIN Technologies, Kingston, ON), a robotic exoskeleton which records shoulder and elbow joint kinematics in the horizontal plane (Figure 2.1, Scott, 1999). Hand position and visual targets were projected above the arm on a semi-silvered mirror in the horizontal plane.

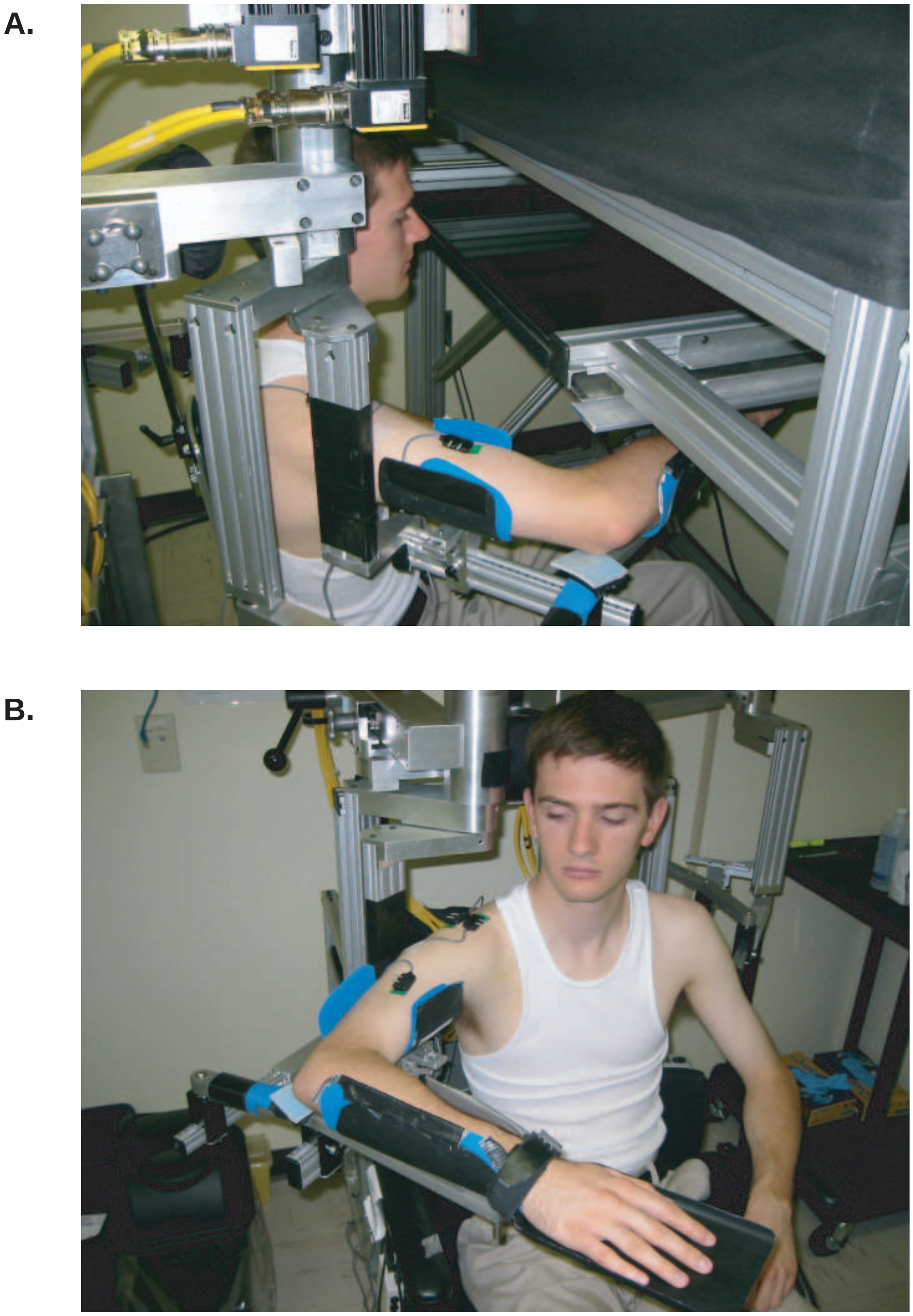

Figure 2.1: **KINARM.** This figure shows the author in KINARM with intramuscular electrodes inserted. KINARM is shown both inside (A) and outside (B) the workspace.

To account for delays in the projector, visual target appearance was detected using a photodiode. Auditory feedback was presented via generic PC speakers. Tasks were developed and executed using the Dexterit-E software interface included with KINARM. Muscle activities were collected using a DELSYS Bagnoli 16-channel EMG amplifier and were digitally sampled at 1000 Hz. Intramuscular recordings were done with sterile fine-wire electrodes (Motion Lab Systems, Baton Rouge, LA; Parts # 000-318-30 and 000-318-50).

2.3 Experimental Procedure

Previous studies have shown that neck muscles show short-latency responses following the sudden appearance of visual stimuli that are appropriate for orienting gaze to the stimulus (Corneil et al., 2004). In the present study our aim was to determine if similar responses could be identified on the musculature of the human arm. Preliminary experiments were conducted to select appropriate muscles to record (Table 2.1), the optimal target locations, and the best technique to record muscle activities. We chose to record from the brachioradialis, triceps brachii (lateral head), pectoralis major, and deltoid (posterior fibres) muscles for our experiment (Figure 2.2). These muscles were chosen because they are monoarticular extensors and flexors of the shoulder and elbow involved in moving the arm in the horizontal plane, are easy to locate using isometric contractions, and are relatively easy to record with intramuscular electrodes.

The targets that we chose (Figure 2.2) were placed so that the upper-left and lower-right targets were roughly aligned along the axis of the forearm, the lower-left and upper-right targets were perpendicular to this axis, and the fixation

Table 2.1: **Muscles recorded in preliminary experiments.** Note that this table shows only the actions that produced movements in the horizontal plane with the hand pronated. However, when the extensor carpi muscles were recorded, the wrist was rotated so that the palm was facing the midline of the body.

Muscle	*Joint*	*Action*
Brachioradialis	Elbow	Flexion
Anconeus	Elbow	Extension
Pectoralis major	Shoulder	Flexion
Deltoid (posterior fibres)	Shoulder	Extension
Deltoid (anterior fibres)	Shoulder	Flexion
Triceps brachii (long head)	Shoulder and elbow	Extension
Triceps brachii (lateral head)	Elbow	Extension
Biceps brachii	Shoulder and elbow	Flexion
Extensor carpi radialis	Wrist	Extension
Extensor carpi ulnaris	Wrist	Extension

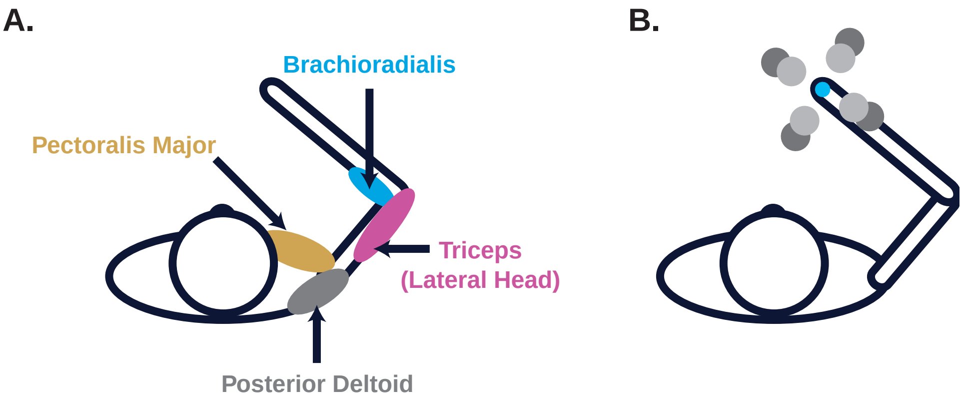

Figure 2.2: **Muscles and targets used in final experiment.** (A) This panel shows the monoarticular extensors and flexors of the elbow and shoulder that were chosen for this study. (B) This panel represents the relative locations of the various targets used in the pro-reaching (10 and 15 cm distances) and delayed reaching (15 cm distance) tasks. The central blue circle represents the fixation marker (r = 1 cm). The light gray circles represent the peripheral targets 10 cm from fixation (r = 3 cm, θ = 60°, 150°, 240°, 320°). The dark gray circles represent the targets 15 cm from fixation. Note that subjects always saw whole circles.

marker was positioned approximately at the subjects' midline. The upper-left and lower-right targets, called the shoulder targets, require largely shoulder muscular torque to be reached, and the lower-left and upper-right targets, called the elbow targets, require largely elbow muscular torque to be reached.

We first recorded muscle activities with surface electrodes, and we were able, in some cases, to find bursts of muscle activity that were time-locked to visual target appearance (Figure 2.3). However, very few subjects showed this effect. Suspecting that these "visual bursts" might be too weak to be recorded from the surface, we continued the preliminary experiments using intramuscular electrodes. We then found these visual bursts on a much greater proportion of subjects, including subjects who had never shown it before with surface electrodes. Therefore, we settled on using intramuscular electrodes for the experiment.

Each experimental session began with setting the subject up with our equipment. For recording muscle activities, the muscles were identified by palpating the muscle site while the subject performed isometric contractions. The skin over the recording site was then scrubbed with gauze soaked in rubbing alcohol. Intramuscular electrodes were inserted into the desired muscles by the experimenter using an aseptic technique (Basmajian and Stecko, 1962). After electrode setup, muscle activities were assessed using an oscilloscope and speakers while subjects performed isometric contractions and free movements. If necessary, electrodes were removed and replaced with fresh ones to obtain a better signal.

After setting up muscle recordings, subjects were calibrated in KINARM according to instruction from Dexterit-E. A metal shield below the projection screen was put in place and a cloth bib was placed on the subject and attached to the

KINARM to prevent subjects from seeing their arm.

2.4 Pro-Reaching Task

The pro-reaching task (Figure 2.4A) was designed to see which targets and muscles robustly elicited the visual burst. It was modelled on the gap pro-saccade paradigm in the oculomotor literature (Munoz et al., 2000) and serves as the basis for the other tasks. A gap period was used because it allows for disengagement of fixation prior to target appearance which disinhibits the saccadic system (Dorris and Munoz, 1995), reduces manual reaction time by possibly disinhibiting arm musculature (Gribble et al., 2002), and therefore facilitating the visual burst on the musculature of the arm.

The pro-reaching task began with the appearance of a central fixation marker on the projection screen in front of the subject. Subjects moved their hand to the central fixation marker and were required to maintain this position for a period of 1 to 2 seconds (randomized). Then, the screen was blanked (including the hand feedback indicator) for a 200 ms gap period, after which a new target appeared in the periphery. Subjects were required to move their right hand to the peripheral target within 500 ms after its appearance. As soon as subject reached the peripheral target, the peripheral target changed colour to indicated success (green) or failure (red) in the task. Also, a buzzer would sound if the target was not reached in time. Note that subjects only had to reach the target and were not required to hold their hand there for any period of time. After a short delay, the screen was blanked and the next trial would begin.

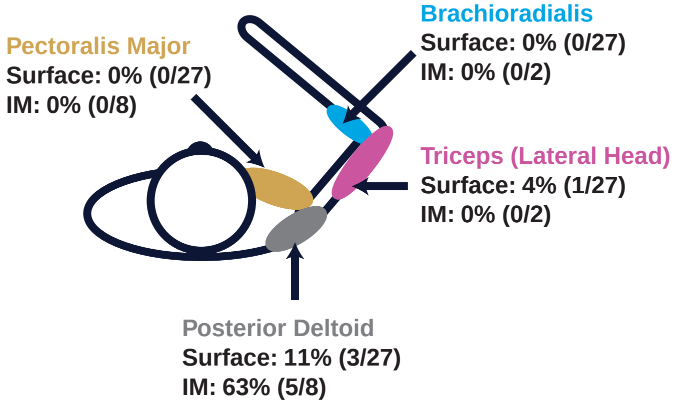

Figure 2.3: **Proportion of subjects who showed the visual burst in the preliminary experiments.** This figure shows a subset of monoarticular extensors and flexors of the elbow and shoulder that were chosen for the preliminary experiments. The label for each muscle indicates the proportion and number of subjects who showed the visual burst on that muscle during preliminary experiments when recording from either surface or intramuscular electrodes.

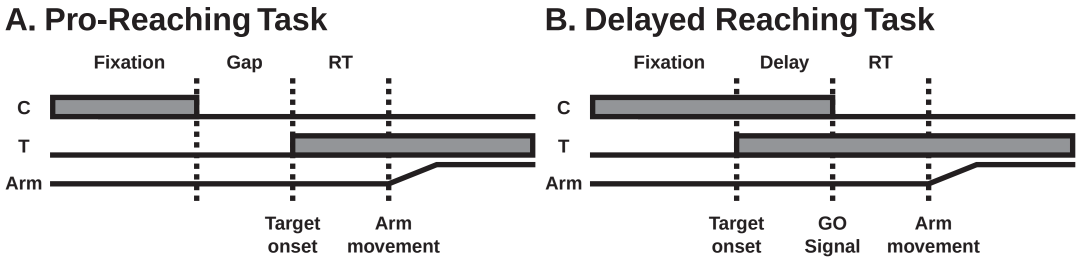

Figure 2.4: **Timelines for different tasks.** Timelines are provided for the two different task types: pro-reaching (A) and delayed reaching (B). *RT* (reaction time) indicates the time from the onset of the ’go’ signal to the onset of hand movement. Note that, for the pro-reaching task, the target onset also acted as the ’go’ signal. Also, *C* refers to the central fixation marker, and *T* refers to the peripheral target. The shaded blocks indicate the times when the marker or target were visible.

Subjects (n = 8) performed this task a block at a time, with each block consisting of 10 reaches to each of the four target directions in random order for a total of 40 trials per block, lasting approximately 4 minutes. Each subject performed eight blocks with short (10 cm distance from fixation marker) targets and eight blocks with long (15 cm distance from fixation marker) targets for a total of 640 trials per subject, taking just over 45 minutes.

2.5 Delayed Reaching Task

The delayed reaching task (Figure 2.4B) was similar to the pro-reaching task but was modified to see if the visual burst could still be elicited if the appearance of the target was separated from the signal to initiate reach. Instead of a gap period, the screen did not blank but the peripheral target appeared following the fixation period. The fixation marker then remained lit for a delay period of 1-2 s (randomized), and its disappearance was the cue to initiate reach. When the fixation marker disappeared, subjects were required to reach to the peripheral target within the aforementioned time limit. If the subject left the fixation marker during the delay period, the peripheral target would turn red, a buzzer would sound, and the trial would end. Each subject (n = 6) completed 8 blocks of this task since only the 15 cm distant targets were used.

It should be noted that, for each experimental session, each subject was run for a block of the pro-reaching task with short targets, then a block of the pro-reaching task with long targets, then a block of the delayed reaching task, and this order was repeated until all the required blocks had been run.

2.6 Post-Processing and Analysis of Data

After each recording session, the collected data were stored in a database and analyzed using custom programs developed with MATLAB (Mathworks, Natick, MA).

2.6.1 Kinematics & Muscle Activity Processing

Muscle activities were filtered using a Butterworth bandpass filter (zero phase shift, 2nd order, 20 to 450 Hz range) and then were full-wave rectified. Note that any trials that included muscle activity exceeding ± 450 μV were considered to be clipped and were rejected from further analysis. Kinematic signals were filtered using a Butterworth lowpass filter (zero phase shift, 6th order, 25 Hz cutoff).

2.6.2 Event Processing

We discovered a variable delay between when Dexterit-E issued a command to draw a target and when the projection system displayed the target. Importantly, if Dexterit-E issued a command to display two targets simultaneously, the projection system would display the two targets simultaneously. We took advantage of this by modifying the tasks to display a second target, called the sync target, at the same time that other important visual updates occurred, such as peripheral target appearance or fixation target disappearance. A photodiode was placed above the subjects' workspace in the position where the sync target would appear, preventing the subject from seeing the sync target. The sync target was determined to have appeared at the time when the photodiode output exceeded 50% of the maximum and to have disappeared at the time when the photodiode output dropped below 50% of the maximum. All data was subsequently aligned to the appearance of the sync target.

2.6.3 Manual Reaction Time Analysis

The manual reaction time for the pro-reaching task was calculated to be the time from target onset to when the tangential hand velocity exceeded 5% of its maximum. The manual reaction time for the delayed reaching task was calculated relative to fixation marker disappearance, which was the GO signal, rather than target onset. The subject was considered to have moved in the correct direction if the difference in the direction of the hand movement at 100 ms after the manual reaction time and the direction from the fixation target to the peripheral target was less than 45°. The latency added to the manual reaction time was needed to compensate for initial curvature of hand movements. We excluded trials from further analysis if the subject began to move in the wrong direction. Also, trials were excluded if subjects made anticipatory movements, that is, if the manual reaction time was less than 125 ms because previous studies have shown that this cutoff is the minimum time needed for visual information to affect arm movement (Day and Lyon, 2000). Any movement made before this time would have to have been the result of guessing where the target would appear.

2.6.4 Visual Burst and Inhibition Analysis

We created plots of the muscle activities aligned on target onset for each individual subject, target, and muscle. We then determined if the visual burst occurred for any of these plots by visual inspection. The visual burst appeared in the raster tracings as a band of muscle activity across most trials whose onset was at a fixed latency after target onset, regardless of the manual reaction time. The visual burst also appeared as a sharp peak or increase on the average muscle activity plot. Likewise, for the antagonist muscles, we determined if a depression of muscle activity time-locked to target onset occurred by visual inspection. This time-locked inhibition appeared in the raster tracings as a band of no muscle activity across most trials whose onset was at a fixed latency after target onset, regardless of manual reaction. The time-locked inhibition also appeared as a sharp decrease followed by little or no activity on the average muscle activity plot.

2.6.5 Burst Window Analysis

We noted that for certain muscles and targets in the pro-reaching task, a burst of muscle activity time-locked to peripheral target presentation occurred. This was found in varying degrees across subjects, and so we developed a statistic to indicate its presence. We analyzed muscle activities from the pro-reaching task to determine whether or not significant activity occurred during the burst window. From visual inspection of our results, we determined that the burst began about 75 ms after target onset at the earliest and ended around 105 ms at the latest, and so we chose these values for the burst window. For each trial, we calculated the average activity of each muscle for the last 100 ms of the gap period (μ_{gap}) as well as the standard deviation over the same window (σ_{gap}). The trial was considered to have had significant activity if at least 3 samples in a row within the burst window were greater than $\mu_{\text{gap}} + 3\sigma_{\text{gap}}$.

We performed the same analysis for the delay task as well. The above procedure was used twice for two different windows: 75 to 105 ms after peripheral target appearance and 75 to 105 ms after fixation marker disappearance.

2.6.6 Correlation of Visual Burst Amplitude with Manual Reaction Time

In order to explore the potential relationship between the visual burst and motor performance, we compared the amplitude of the visual burst with the manual reaction time on a trial by trial basis. We calculated individual average activities during the burst window for all trials for a specific subject, target, and muscle, as well as the manual reaction times for each of these trials. A line of best fit was then calculated using robust linear regression (MATLAB function *robustfit*), a technique which is less sensitive to outliers than normal linear regression.

Chapter 3

Results

3.1 Pro-Reaching Task

3.1.1 Behavioural Data

Overall, subjects performed this task well (see Table 3.1 for a breakdown of reaction and movement times and error rates according to target). Subjects were able to reach the peripheral target before it timed out for most trials (95%) and reached it on average 400±122 ms (value±SD) after its appearance. Hand movements began in the correct direction for most trials (95%) and were qualitatively straight (Figure 3.1). The average manual reaction time was 187±66 ms (see Figure 3.2 for a breakdown according to target), and anticipatory movements were made for 8% of trials.

Table 3.1: **Pro-reaching task statistics.** This table shows statistics from the pro-reaching task broken down according to target. All non-percentage data is given in the value±SD format.

	Short Shoulder	*Short Elbow*	*Long Shoulder*	*Long Elbow*
Reached target in time (% trials)	96	99	87	98
Time to reach target (ms)	414±90	340±48	465±169	372±110
Began to move in correct direction (% trials)	91	97	94	98
Average manual reaction time (ms)	181±48	180±43	194±79	193±41
Anticipatory movement (% trials)	10	9	6	5

Figure 3.1: **Example hand tracings.** Hand tracings from a single subject for all correct trials in a single session for the centre-out reaching with short peripheral targets. Each tracing shows the path of the hand while the subject reached out from the central fixation target to one of the peripheral targets.

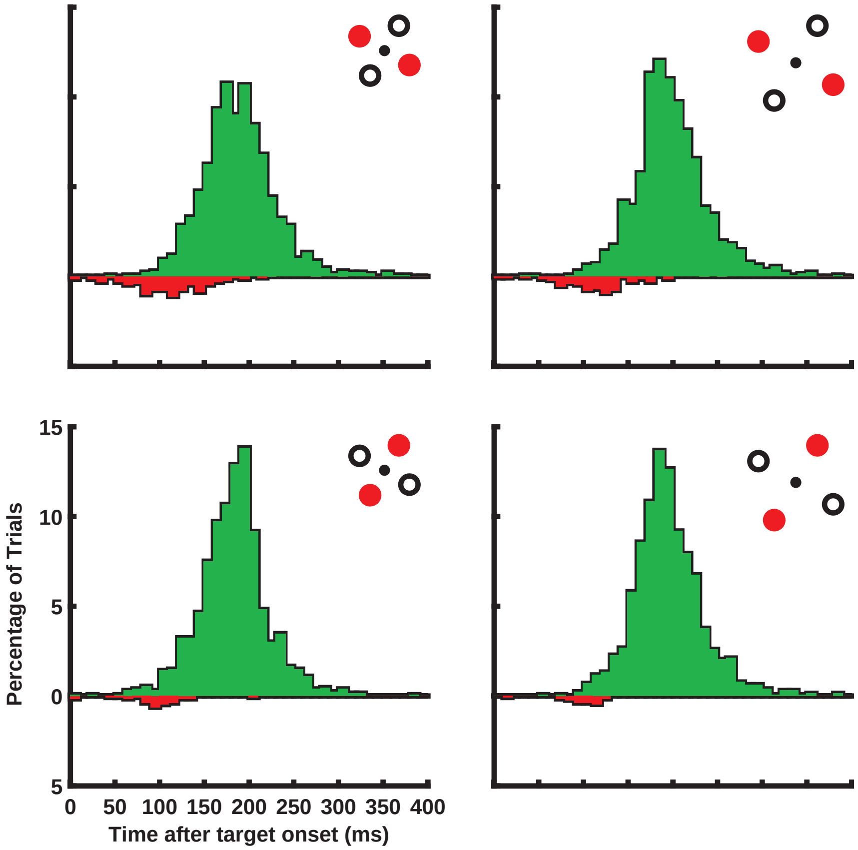

Figure 3.2: **Manual reaction times for pro-reaching task.** Each panel shows a histogram of manual reaction times relative to the appearance of the peripheral target for the pro-reaching task across all subjects. As indicated by the icons, the top row of panels shows histograms for the shoulder targets, the bottom row shows histograms for the elbow targets, the left column of panels shows histograms for the short targets, and the right column shows histograms for the long targets. The green histograms represent the number of trials in the correct direction, while the red histograms represent the number of trials in the incorrect direction.

3.1.2 Muscle Activities

A wide variety of muscle activities were demonstrated in this task. An example from a typical subject is shown in Figure 3.3. For the lower-right target, there appears in the DP tracings a band of activity across all trials over the range of approximately 80 to 100 ms after target onset. The timing of this burst of activity was not dependent on the manual reaction time but was time-locked to target onset; that is, the activity began at the same amount of time after target onset for all trials, regardless of when the hand began to move. DP also showed an inhibition of activity time-locked to target onset (90 ms after target onset) across all trials for the target in the opposite direction (upper-left target) as well as for the lower-left target (80 ms after target onset). No time-locked activity was shown on DP for the upper-right target. PM also showed a band of activity which was time-locked (95 ms after target onset) for the upper-left target and for the lower left target (85 ms after target onset). There also appeared to be a weak time-locked inhibition on PM for the lower-right target (90 ms after target onset). No similar time-locked activity was noted on PM for the upper-right target. TLat and Br showed no activity time-locked to target onset for any target.

A comparison of DP activities for the lower-right target across all subjects is shown in Figure 3.4. Six subjects (75%) were found by visual inspection to show the visual burst on DP for this target over a window of about 80 - 110 ms after target onset, and five subjects (63%) showed time-locked inhibition starting at about 90 ms after target onset. See Tables 3.2 and 3.3 for a cross-subject summary of time-locked activation and inhibition for all muscles and targets and Figure 3.5 for a graphical summary of visual burst and inhibition timing.

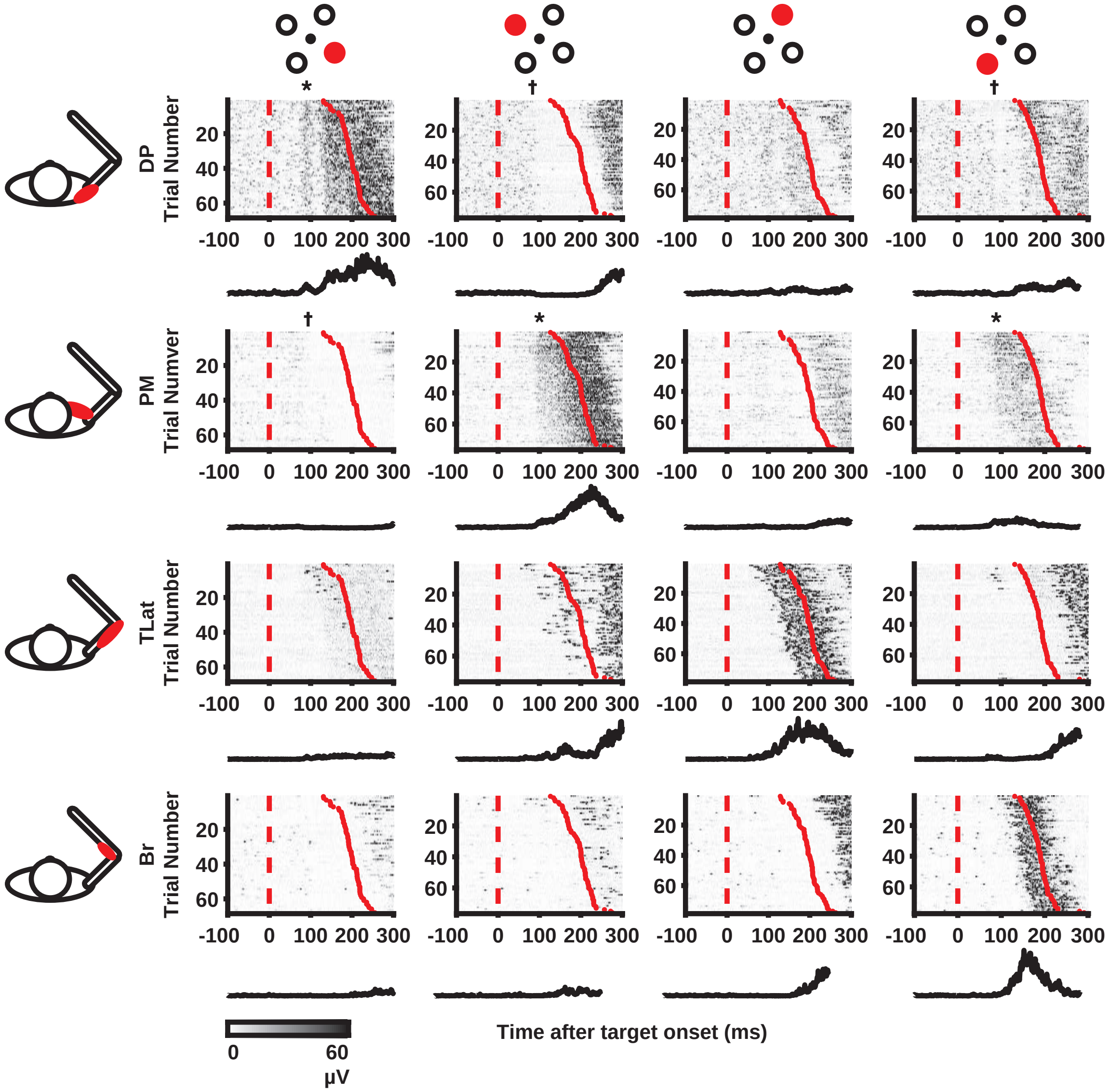

Figure 3.3: **Muscle responses for pro-reaching task.** Example muscle activities for a single subject across all correct trials for all targets (10 cm distance). Each panel shows activities from the four muscles studied on a trial by trial basis (raster tracings) as well as averaged across all trials (line immediately below). The same muscle was recorded for each row of panels and is highlighted in red on the icon to the left. The same target was reached to for each column of panels and is highlighted in red on the icon above. All individual trials were sorted by manual reaction time (indicated by the red dot marker) and were aligned on the onset of the peripheral target (t = 0 ms). Darker tracings indicate stronger activity, as indicated by the gradient bar on the bottom. Note that the muscle activities in the rasters were clipped if they exceeded 65 μV to increase visual contrast. The average activities were scaled from 0 μV to their maximum. An asterisk (*) above the rasters indicates the presence and timing of activity time-locked to target onset. A dagger (†) above the rasters indicates the presence and timing of inhibition of activity time-locked to target onset.

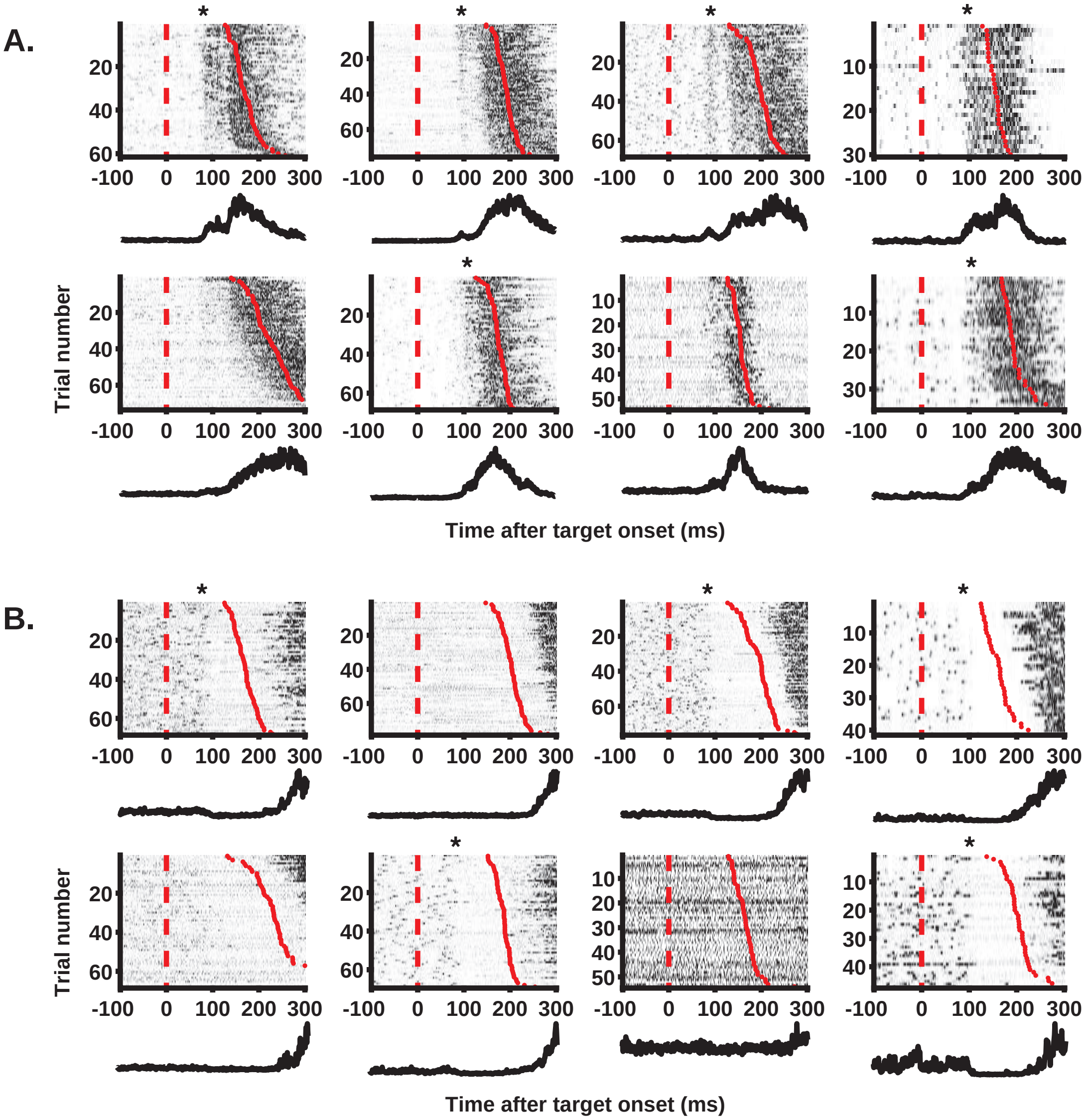

Figure 3.4: **Muscle responses for pro-reaching task (multiple subjects).** (A) This panel shows activities from each subject for DP when reaching to the short lower-right target. An asterisk above the rasters indicates the presence and timing of activity time-locked to target onset. Each raster plot and the plot of its average below it represents a different subject. The average plot ranges from 0 μV to its maximum. The activities shown in the rasters are clipped to the range of the average below for increased contrast.(B) This panel shows activities from each subject for DP when reaching to the short upper-left target. An asterisk above the rasters indicates the presence and timing of inhibition of activity time-locked to target onset. The order of subjects in panels A and B is the same.

Table 3.2: **Cross-subject summary of time-locked activity.** This table indicates the presence of activity time-locked to target onset for each muscle and target across all subjects (n = 8). The number in each column is the number of subjects showing time-locked activation.

Target	*DP*	*PM*	*TLat*	*Br*
Short Lower-Right	6	0	2	0
Short Upper-Left	0	2	0	0
Short Upper-Right	1	0	1	0
Short Lower-Left	0	2	0	1
Long Lower-Right	5	0	1	0
Long Upper-Left	0	2	0	0
Long Upper-Right	0	0	1	0
Long Lower-Left	0	2	0	0

Table 3.3: **Cross-subject summary of time-locked inhibition.** This table indicates the presence of inhibition time-locked to target onset for each muscle and target across all subjects (n = 8). The number in each column is the number of subjects showing time-locked inhibition.

Target	*DP*	*PM*	*TLat*	*Br*
Short Lower-Right	0	2	0	0
Short Upper-Left	5	0	0	0
Short Upper-Right	0	1	0	1
Short Lower-Left	1	0	0	0
Long Lower-Right	0	3	0	0
Long Upper-Left	4	0	0	0
Long Upper-Right	0	1	0	0
Long Lower-Left	1	0	0	0

Burst Window Analysis

A cross-subject comparison of the proportion of trials showing significant activity in the burst window for all targets and muscles is given in Figure 3.6. The primary agonists for the short targets in the pro-reaching task all have a significantly greater mean of the proportion of trials with significant activity during the burst window across all subjects than that for at least one other muscle. This is also true for the long shoulder targets in the pro-reaching task. Notably, for the short lower-left target in the pro-reaching task, PM has a significantly greater mean than DP, and for the long-lower left target in the pro-reaching task, PM has a significantly greater mean than both DP and TLat.

Correlation of Visual Burst Amplitude with Manual Reaction Time

Figure 3.7 shows a series of correlations of visual burst amplitude with manual reaction time for a single subject. As can be seen in this figure, the primary agonist muscle for the shoulder targets had significant slopes for their lines of fit, and TLat had a significant slope for the lower-right target as well. No significant slopes existed for the upper-right target or for the primary agonists for the elbow targets, but DP and PM both had significant slopes for the lower-left target. All the significant slopes were negative except for DP for the lower-left target, indicating that shorter manual reaction times were correlated with greater activity during the burst window. Note that some combinations of target and muscle had large bursts of activity only for short reaction times. A comparison of correlations across multiple subjects is shown in Figure 3.8 and a summary of significant correlations is shown in Table 3.4.

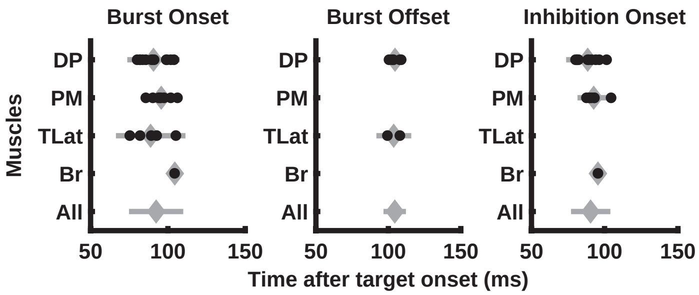

Figure 3.5: **Cross-subject summary of time-locked burst and inhibition timing.** Each point in each panel denotes the timing of visual burst onset, visual burst offset, or inhibition onset for a single subject and muscle across all targets. The gray lozenges give the mean timing for a specific muscle, and the gray horizontal lines represent two times the standard deviation for both directions.

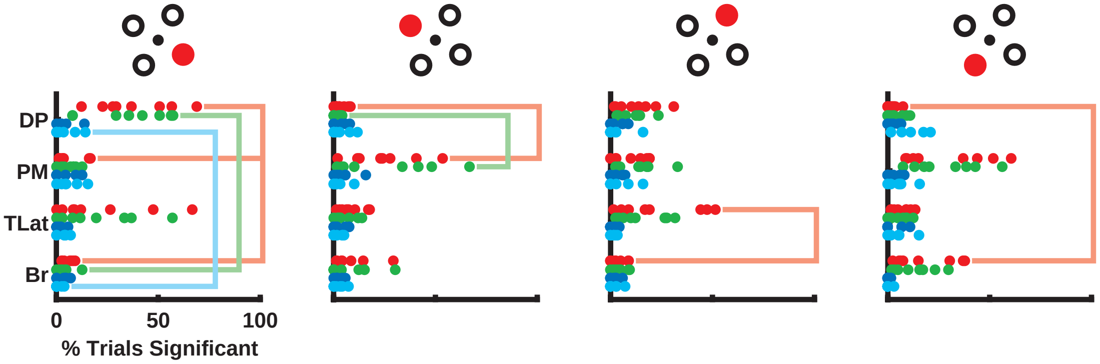

Figure 3.6: **Cross-subject burst window analysis.** Trial significance was calculated as described in Results. Each dot in each column represents the proportion of trials which showed significant activity within the burst window for a single subject. The red dots are for pro-reaching trials where the distance to the peripheral target from the fixation target was 10 cm. The green dots are for pro-reaching trials where the distance to the peripheral target from the fixation target was 15 cm. The dark blue dots are for delayed reaching trials after the peripheral target had appeared. The light blue dots are for delayed reaching trials after the fixation target had disappeared. For each target, if the mean of the proportion of trials with significant activity during the burst window across all subjects for the primary agonist was significantly greater than that for another muscle (Kruskal-Wallis test with Tukey's HSD test for multiple comparisons, $p < 0.05$), this was indicated by a line between the primary agonist and the other muscle. The colour of this line, though slightly lighter, has the same meaning as the colours listed above.

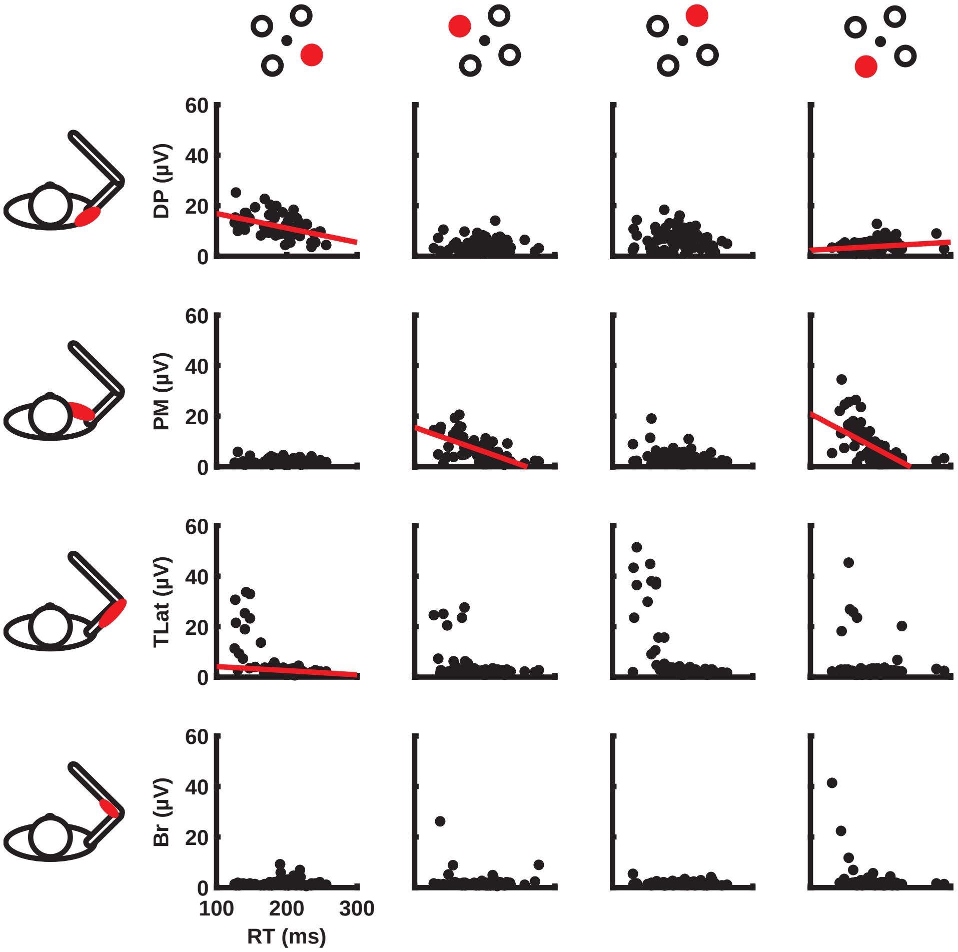

Figure 3.7: **Correlation between manual reaction time and visual burst amplitude.** Each plot compares the average muscle activity in the burst window with manual reaction time across all trials for a single muscle and target. This data was obtained from a single subject performing the reaching task with short targets. The same muscle was recorded for each row of panels and is highlighted in red on the icon to the left. The same target was reached to for each column of panels and is highlighted in red on the icon above. Each point represents the correlation for a single trial. The line of best fit is also shown. If the slope of the line of fit is significantly different from zero (t-test, $p < 0.05$), the line is highlighted in red.

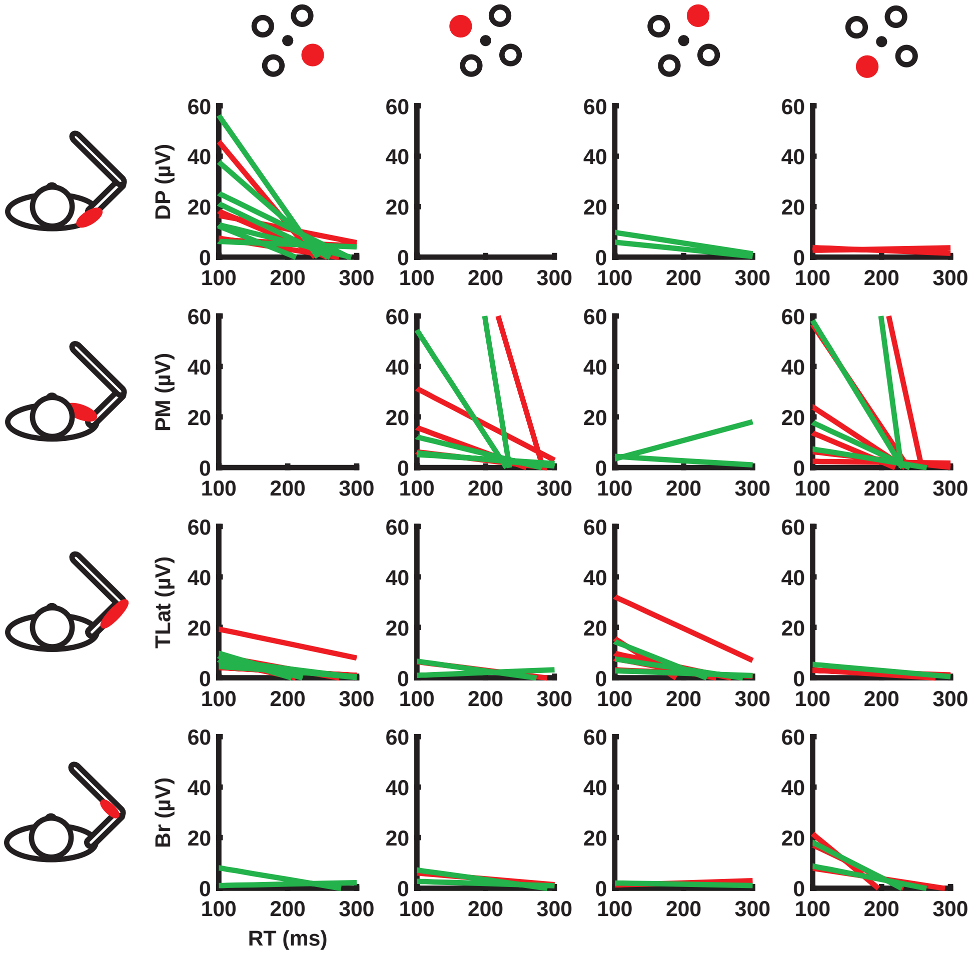

Figure 3.8: **Correlation between manual reaction time and visual burst amplitude across all subjects.** The figure is formatted as in Figure 3.7, except no individual points are plotted, and each panel contains lines of best fit for all subjects. Short targets are represented by red lines and long targets are represented by green lines.

3.2 Delayed Reaching Task

3.2.1 Behavioural Data

Overall, subjects performed this task well (Table 3.5). Subjects were able to reach the peripheral target before it timed out for most trials (82%) and reached it an average of 431±188 ms after its onset, and they were able to reach it before it timed out for most trials (82% of trials). The average manual reaction time was 227±81 ms (Figure 3.9). Also, subjects never began to move in the wrong direction and left the fixation marker during the delay period for 8% of trials. Reaches were qualitatively straight, like in the pro-reaching task.

3.2.2 Muscle Activities

We analyzed muscle activities recorded in the delay task both after the onset of the peripheral target (start of delay period) and after the offset of the fixation target (end of delay period). Muscle activities after the start of the delay period for a typical subject are shown in Figure 3.10. No time-locked activity was observed after peripheral target onset for any muscle or target. This was true also for all subjects.

Muscle activities after the end of the delay period for a typical subject are shown in Figure 3.11. No activity time-locked to the offset of the fixation marker was observed for any muscle or target, although there was activity tied to the movement onset. This was true also for all subjects.

Table 3.4: **Correlation between manual reaction time and visual burst amplitude across all subjects.** Each number indicates the number of subjects (n = 8) whose correlation, for the particular target and muscle, was significant ($p<0.05$) and had a negative slope.

Target	*DP*	*PM*	*TLat*	*Br*
Short Lower-Right	5	0	5	0
Short Upper-Left	0	4	1	1
Short Upper-Right	0	0	5	0
Short Lower-Left	1	6	2	3
Long Lower-Right	7	0	5	1
Long Upper-Left	0	5	1	2
Long Upper-Right	2	1	3	1
Long Lower-Left	0	4	1	2

Table 3.5: **Delayed reaching task statistics.** This table shows statistics from the delayed reaching task broken down according to target. All non-percentage data is given in the value±SD format.

	Shoulder	*Elbow*
Reached target in time (% trials)	78	86
Time to reach target (ms)	456±93	405±246
Began to move in correct direction (% trials)	100	100
Average manual reaction time (ms)	224±9	230±83
Left fixation marker during delay period (% trials)	8	8

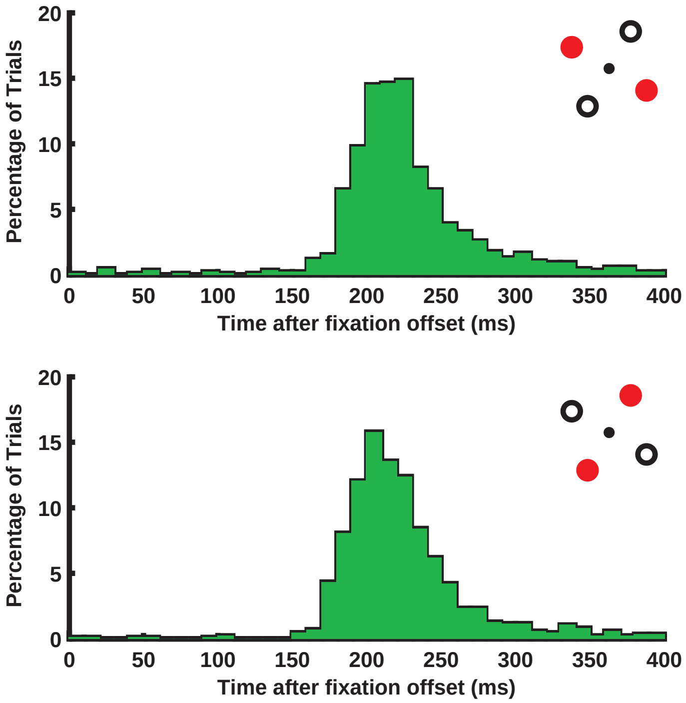

Figure 3.9: **Manual reaction times for delayed reaching task.** A histogram of manual reaction times relative to the offset of the fixation target for the delayed reaching task across all subjects. The format is similar to Figure 3.2, except only long targets are shown.

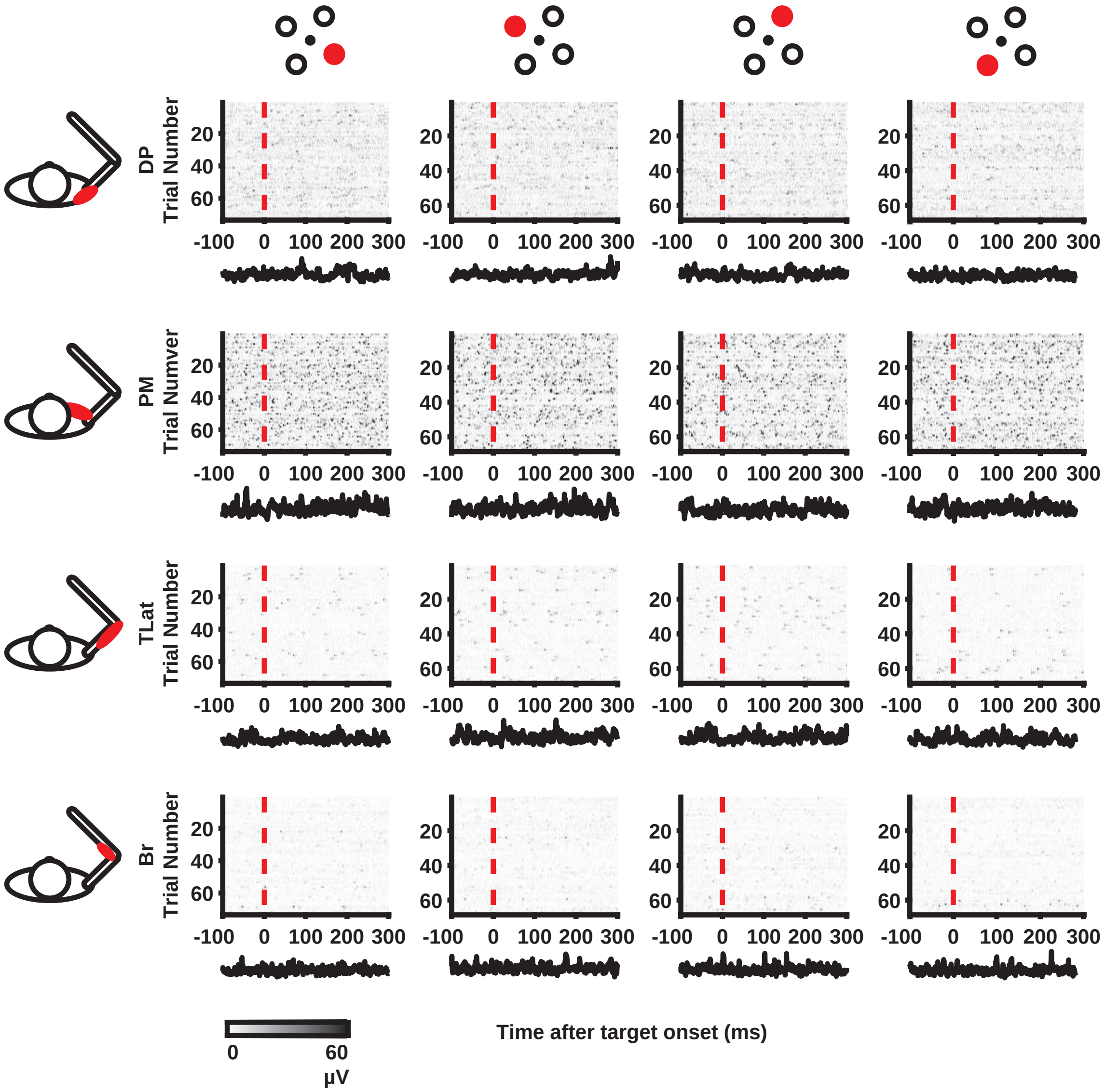

Figure 3.10: **Muscle responses for delayed reaching task after peripheral target onset.** This figure is formatted as in Figure 3.3.

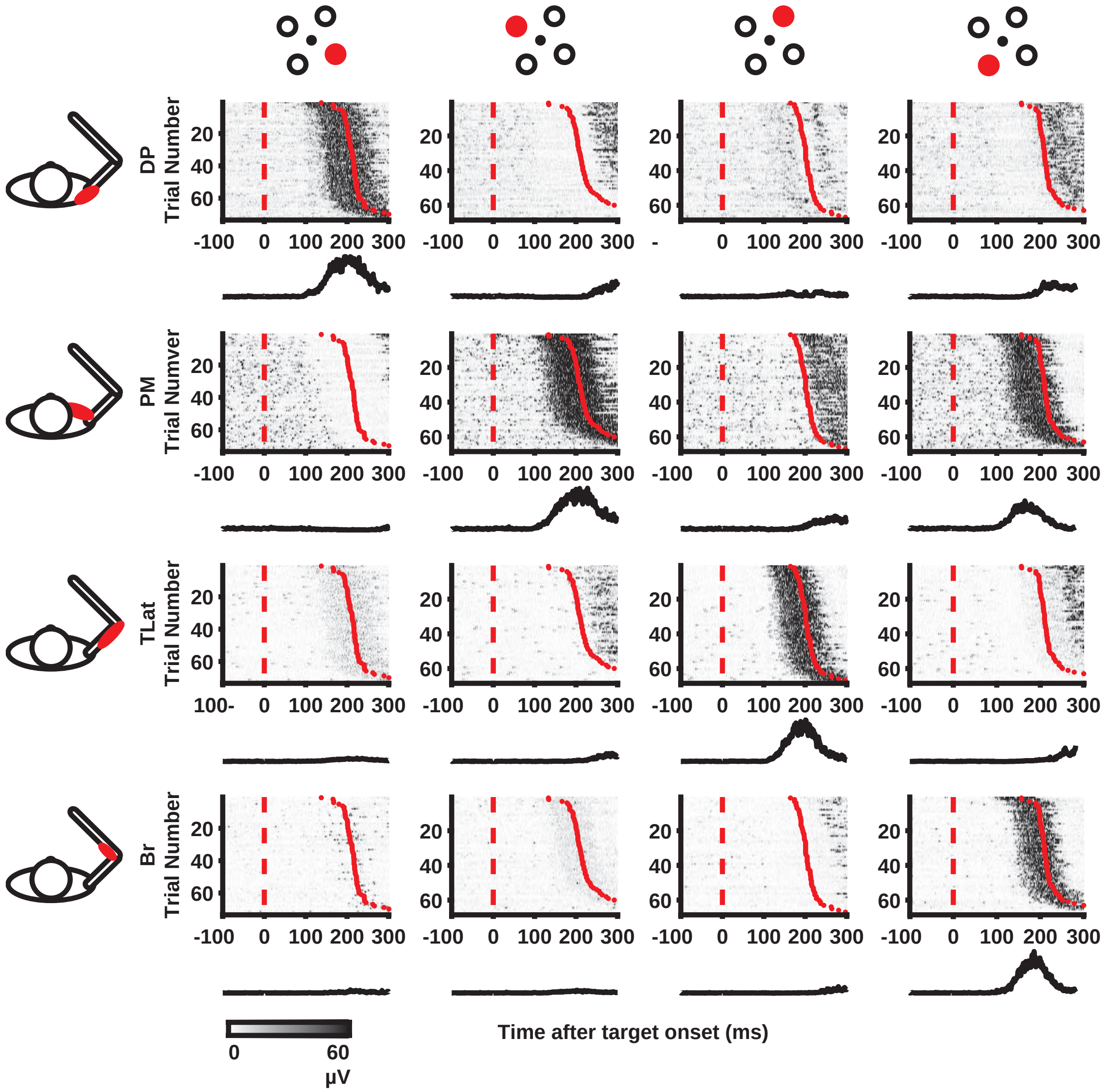

Figure 3.11: **Muscle responses for delayed reaching task after fixation target offset.** This figure is formatted as in Figure 3.3.

Burst Window Analysis

A cross-subject comparison of the proportion of trials with significant activity during the burst window was done for the delayed reaching task, as shown in Figure 3.6. DP had a significantly greater mean of the proportion of trials with significant activity during the burst window across all subjects for the lower-right target after fixation target offset than Br. No other significant differences in means were found.

Chapter 4

Discussion

We have demonstrated that short-latency muscle activity time-locked to the appearance of visual stimuli can be found on the musculature of the human arm. A majority of subjects demonstrated such activity, mostly on the shoulder muscles. This was complemented by short-latency, time-locked inhibition, again mostly on the shoulder muscles. In contrast, no subject ever showed the visual burst or time-locked inhibition during the delayed reaching task, either after target presentation or after fixation marker offset. Therefore, the short-latency visual response was only present during imminent reach.

4.1 The Visual Orienting Response of the Hand

4.1.1 The Occurrence of the Visual Burst

The presence of early activity on the arm musculature that precedes hand movement indicates that there exists a visual orienting response of the hand similar and complementary to the visual grasp reflex. Previous studies have shown that arm muscle activity can precede eye movements (Biguer et al., 1982; Gribble et al., 2002), and we have demonstrated that short-latency responses occurred at a fixed latency after target presentation, regardless of when hand movement began. This indicates that the CNS can activate the muscles of the arm before the decision to move the hand is made. Thus the muscles of the arm are capable of participating in an early orienting response that can complement the oculomotor and head movement components of the visual grasp reflex.

Our work extends the research done by Corneil et al. (2004). The visual burst was shown on neck muscles of monkeys at 55 to 95 ms after target onset; we have demonstrated similar responses on the musculature of the human arm occurring at about 85 to 105 ms after target onset. This difference in timing could be attributed to the fact that monkeys are smaller than humans, and therefore nerve impulse conduction times would be shorter from the brain to the monkey neck musculature than to the human arm musculature. Also, this difference in timing could also be attributed to the fact that the shoulder musculature is further away from the CNS than the neck musculature. Finally, we did not control for target luminance, which could have differed between the two experiments.

The visual burst consisted of a burst of muscle activity whose onset occurred at a fixed latency after target onset. This activity preceded the onset of hand motion and usually preceded, by a variable amount, muscle activity that was correlated with the onset of hand motion. The visual burst was therefore separate from the command to move.

It is important to note that we found the visual burst mostly on the muscles of the shoulder. This confirms our earlier hypothesis that shoulder responses would be more likely than elbow responses. We also noted that the visual burst appeared more often on DP than on PM. The visual burst was rarely found on TLat and virtually never on Br. A similar pattern was observed for time-locked inhibition, except no subjects showed time-locked inhibition on TLat. As mentioned above, no subject ever showed the visual burst during the delayed reaching task on any muscle for any target either after peripheral target onset or after fixation marker offset. It would therefore appear that the presence of the visual burst is dependent on the onset of the peripheral target and the signal to initiate reach coinciding spatially and temporally.

While we saw the visual burst on some muscles for some subjects, we did not see it in all subjects for all muscles. It is possible that, by chance, we had chosen inappropriate sites to insert the electrodes, although each muscle's activity was assessed at the beginning of the experimental session. It should be noted that intramuscular electrodes do not record activity from the entire muscle but only a limited area (Basmajian and De Luca, 1985). It is also known that muscles can be divided into compartments that are differentially recruited by the nervous system according to the desired movement (Brown et al., 2007). Thus it is possible that had we inserted the electrodes into different compartments of the muscles, we may have more reliably observed the visual burst on more subjects or muscles.

Another possibility is that the target positions were not optimal for recruiting the different muscles, although we did try to place the targets so that each muscle would be the primary mover for a single target. It is known, for example, that the intersegmental dynamics of the arm can result in multi-joint motion arising from single-joint torque and vice versa (Kurtzer et al., 2006). If we had placed the targets differently to work with these dynamics, we might have seen the visual burst more often on different muscles and subjects.

Additionally, we did not control for the depth of electrode insertion. It is known that the muscles of the monkey forelimb are composed of different types of muscle fibres with different metabolic capabilities, and the proportion of these types of fibres vary with depth (Singh et al., 2002). If the visual burst selectively recruited a specific type or types of fibre, it is possible that we might have missed these fibres when we inserted the electrodes and therefore could not record the visual burst.

We performed a comparison of the proportion of trials with significant activity during the burst window for all subjects and for each target across all muscles (Figure 3.6). This analysis confirmed that DP had a significantly greater mean proportion of significant trials for all subjects for short and long targets combined when it was the primary agonist than any other muscle for the same target or for when another muscle was the primary agonist for another target. Accordingly this analysis highlights how the visual burst was found mostly on DP and was found most often when DP was the primary agonist for a target.

4.1.2 The Visual Burst and Motor Preparation

The relationship of the visual burst to the ensuing movement of the hand implies that the visual burst is a muscular analogue of preparatory motor activity. Specifically, it seems that at as early as 85 ms after receiving visual information, the CNS is able to produce a response in the muscles of the arm which is appropriate for moving the arm towards the target. In order for some neuronal signal to qualify as preparatory activity, it must occur before the reaction time, it must be related to preparatory information, and it must predict motor performance (Riehle and Requin, 1993). Although we did not record neuronal activity, our results demonstrate that the visual burst may be an analogue of preparatory activity.

The first criterion for preparatory activity is that it must occur before the reaction time. We found that the visual burst occurred about 85 to 105 ms after target onset and preceded the manual reaction time, which was on average 187 ms after target onset. The visual burst did not result in initiating hand movement as we had defined it for this experiment. Instead, the visual burst onset preceded the onset of hand movement by a variable amount of time. Thus it appears that the CNS sends motor commands to the musculature of the arm before it has made the decision to move the hand. Also, because of its timing, the visual burst could occur even before express saccades, which have a reaction time of around 100 to 135 ms for humans (Fischer and Boch, 1983). It is known that muscle activities on the extraocular muscles precede the actual movement by 7 ms (Biguer et al., 1982). Even so, it appears that the CNS can relay motor commands to the arm before the eye. This concurs with Gribble et al. (2002), who found that the muscles of the shoulder can be activated before eye movement. This is also similar to the finding of Corneil and Elsley (2005) in humans that the command sent by the CNS to move the head is sent before the command to move the eyes. In short, the fact that the visual burst precedes overt movement of the arm indicates that the visual burst is related to motor preparation.

The second criterion for preparatory activity is that it must be related to preparatory information. An example of preparatory information would be the location of the target. If the visual burst is related to motor preparation, the visual burst ought to reflect in some way the location of the target. Corneil et al. (2004) observed that the visual burst on the neck was directionally specific, and we observed similar directional correlation on arm musculature. The visual burst was present on a muscle when the position of a target required that the muscle to be activated to begin reaching to the target. Occasionally, the visual burst would occur on the same muscle for another target, but in all of these cases the muscle assisted the primary agonist in producing the movement and the amplitude of the burst was less than the burst when the muscle was itself the primary agonist. As for target distance, there was very little variation in the occurrence of the visual burst between short and long targets. The directional specificity of the visual burst would imply that it is not a startle response because startle responses are not directionally specific (Siegmund et al., 2001).

Time-locked inhibition was also directionally specific. In general, the occurrence of time-locked inhibition was reciprocal to the occurrence of the visual burst (compare Figures 3.4A and 3.4B). Time-locked inhibition was present on a muscle when the position of a target required that the antagonist to that muscle be activated to begin reaching to the target. Time-locked inhibition was rarely found on the same muscle for any other target, but in all of these cases the antagonist to this muscle assisted the primary agonist in producing the movement. Very little variation in the occurrence of time-locked inhibition was observed between the short and long targets. Like the visual burst, time-locked inhibition was directionally specific and thus was not a startle response.

Since the appearance of the visual burst and time-locked inhibition on a particular muscle was specific to target direction, it appears that the visual burst is related to preparatory information.

The final criterion for motor preparatory activity is that it must predict motor performance. We performed a correlation between manual reaction time and visual burst amplitude across all subjects (Figure 3.8) to see if there was any relationship between the magnitude of the visual burst and the latency to initiate reaching. In general, we found a negative correlation between the average activity in the burst window and the manual reaction time, meaning that the trials with the shortest reaction times often had the highest activity in the burst window. This was true mostly for the primary agonists for each target, although similar correlations were found for other muscles, usually those which could assist the primary agonist in reaching the target. Intersegmental dynamics could result in otherwise unforeseen muscle recruitment patterns because multiple muscles could have been recruited to produce the otherwise simple movements (Kurtzer et al., 2006).

We also observed that the trials with the shortest manual reaction times had muscle activities associated with movement onset that could overlap with the burst window. Thus, for some targets and muscles, there was sharp increase in burst window activity for trials with shorter reaction times. Such an increase might be caused one of two things. Since the muscle activities in these early trials are associated with the onset of hand motion, these trials might simply be the result of subjects correctly guessing where the target will appear. In such a case, the subjects could initiate reaching before they could use the target onset to guide hand movement. We anticipated this by dropping trials which had reaction times less than 125 ms. However, this may not have been a sufficient criterion, since erroneous trials were still observed after this time (Figure 3.2). On the other hand, these early trials could represent a synergistic effect between the visual burst and the onset of hand movement. Gribble et al. (2002) stated that, in their reaching experiment, they may have observed a distinct class of arm movements with very short manual reaction times. Trials with overlapping visual burst activity and movement-onset activity might be good candidates for such "express" arm movements because the visual burst might reflect motor preparation of the arm's motor system which was sufficient to cause preprogrammed arm movements to be executed earlier. However, the distribution of manual reaction times in this study was unimodal (Figure 3.2), not the typical bimodal distribution of reaction times that has been found for express saccades (Munoz et al., 2000). Thus it appears that no express arm movements were made in this study. Nevertheless, the amplitude of the visual burst can predict manual reaction time, thus solidifying the relationship between the visual burst and motor preparation.

From these observations, it appears that the visual burst might indeed be a muscular analogue of a motor preparation signal. The visual burst precedes the onset of hand movement as defined by this study, its directionality reflects the target location, and its amplitude is correlated with manual reaction time. It can be concluded from this that the activity of the arm musculature could serve as a window into the motor preparation involved in reaching.

4.2 The Visual Orienting Response of the Arm and Online Correction

Although we did not observe overt movement associated with the visual burst, there is evidence that the visual burst might be related to online correction in reaching, especially if the visual response signals a jump of the target. Online correction refers to smooth changes in the trajectory of ongoing hand movements in response to a change in the position of a visual target (Pélisson et al., 1986). Changes in the motion of the hand can be reliably elicited as early as 125 ms after the perturbation of a visual target (Day and Lyon, 2000), and corresponding changes in shoulder muscle activities can be elicited as early as 90 ms after target perturbation (Soechting and Lacquaniti, 1983). The timing of the change in muscle activities during online correction is similar to the timing of the onset of the visual burst after target presentation. Also, both initiating a reach in the gap paradigm and online correction involve orienting the hand to a visual stimulus. It might then be possible that the visual burst and online corrections share a common mechanism.

4.3 Possible Neural Correlates of the Visual Orienting Response of the Arm

We observed in this study that the visual burst on the arm musculature reflects certain motor preparation parameters, and so the arm may possess a visual orienting response. As such, it is likely that there are shared neural structures that coordinate the movement of the eye, head, and arm.

The PPC is one possible neural correlate of the visual orienting response of the arm. The PPC is involved in sensorimotor transformations for both the eye and hand (Buneo and Andersen, 2006). It is also thought to be an important part of the mechanism responsible for online corrections: if the PPC is damaged, corrections are no longer automatic but become slow and deliberate (Pisella et al., 2000). As such, the PPC is important for eye-hand coordination. Since the visual burst might be related to online correction, it is possible that the visual burst is related to activity in the PPC.

It has also been suggested that subcortical structures may be involved in online correction (Day and Brown, 2001). The role of SC in online correction is also supported by research that has shown reach-related activity in the SC (Lünenburger et al., 2001). Research has also shown that stimulation of the SC in cats during forelimb movement can cause perturbations of the movement (Courjon et al., 2004). This indicates a direct role of the SC in online correction of forelimb movements. Therefore, if there is any relation between the visual burst on the arm musculature demonstrated in our study and online correction, it is possible that they would both involve the SC.

In addition, the role of the SC in planning and executing saccades is well known (Munoz et al., 2000), and there is evidence that the SC may be associated with motor planning for the head and hand as well. Corneil et al. (2007) have demonstrated that neck muscles are primed ahead of the onset of gaze shift, this priming is correlated with low-frequency activity found in the SC during a gap saccade task, and this priming can be replicated by low-frequency stimulation of the SC. This evidence, in combination with the visual burst previously found on neck muscles, indicates a role of the SC in planning head movements for gaze shifts. It is also feasible that the SC could be involved in motor planning for the hand. Research has shown that muscle activities on the arm can be preceded by correlated activities in the SC (Werner et al., 1997a; Stuphorn et al., 1999; Stuphorn et al., 2000). Other studies note that the SC receives input from motor and premotor cortex and may have outputs on the spinal motor system through tectorecticulospinal projections (Werner et al., 1997b). Our study demonstrates visual bursts similar to those found by Corneil et al. (2004). Because the visual bursts on the neck musculature are thought to be relayed through the SC (Corneil et al., 2007), it is therefore possible that the visual responses on the arm musculature are also related to activity in the SC.

We also found that there was a negative correlation between the manual RT and the mean activity during the burst window. It would therefore appear that the trials with the largest activity in the burst window had the shortest reaction times. Since the SC (Werner et al., 1997b) and the arm musculature (Evarts, 1966) both receive input from motor areas of the CNS, this correlation could reflect shared input from the CNS to the SC and arm musculature.

4.4 Future Directions

The discovery that motor preparation of visuomotor transformations can be seen on arm musculature opens the way to further research, including examining cognitive and sensory parameters by recording arm muscle activity in a reaching task. Using a countermanding task, for example, would allow us to see if there is a causal relationship between the appearance of the visual burst and arm movement. Previous studies have indicated that the stop signal reaction time in a reaching task for humans is about 200 ms (Mirabella et al., 2006). Since the visual burst can still be seen on the arm musculature when manual reaction times exceed 200 ms, it might be possible to elicit the visual burst without voluntary movement in a countermanding task. Similarly, it might be of interest to use a reaching version of the anti-saccade task (Everling et al., 1998) to see if the visual burst would still occur even if the subject was prepared to reach in the opposite direction of the target, thus examining the effect of cognitive parameters on the visual burst. Also, for any future study, it would be worthwhile to record gaze during the tasks so that correlations between components of hand shifts and gaze shift could be established.

Because we have discussed the possible role of the PPC and the SC in mediating the visual burst on the arm musculature, it would be advantageous to record from PPC and SC neurons while monkeys perform the pro-reaching and delayed reaching tasks. Such a study could solidify the role of either or both of these areas in coordinating eye and hand movements if activity in these areas and visual burst activity on the arm could be correlated. Also, if similar activities in these areas could be found while the monkey performed a task involving online correction, a link would be forged between the mechanisms responsible for the visual burst and online corrections.

4.5 Conclusions

We have found bursts of activity on the musculature of the arm, primarily on the shoulder, which were time-locked to the onset of the visual target. This visual burst was dependent on the imminence of movement and the directionality of the target, and it was appropriate for orienting the arm to the target. The burst did not cause overt hand movement but preceded hand movement onset by a variable amount of time. We conclude that this is a correlate of the visual grasp reflex for the arm and highlights the possible role of the PPC and SC in preparing arm movements.

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