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RESEARCH ARTICLE

Control of Movement

Anticipatory weight shift between arms when reaching from a crouched posture

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Abstract

Reaching movements performed from a crouched body posture require a shift of body weight from both arms to one arm. This situation has remained unexamined despite the analogous load requirements during step initiation and the many studies of reaching from a seated or standing posture. To determine whether the body weight shift involves anticipatory or exclusively reactive control, we obtained force plate records, hand kinematics, and arm muscle activity from 11 healthy right-handed participants. They performed reaching movements with their left and right arm in two speed contexts, "comfortable" and "as fast as possible," and two postural contexts, a less stable knees-together posture and a more stable knees-apart posture. Weight-shifts involved anticipatory postural actions (APAs) by the reaching and stance arms that were opposing in the vertical axis and aligned in the side-to-side axis similar to APAs by the legs for step initiation. Weight-shift APAs were correlated in time and magnitude, present in both speed contexts, more vigorous with the knees placed together, and similar when reaching with the dominant and nondominant arm. The initial weight-shift was preceded by bursts of muscle activity in the shoulder and elbow extensors (posterior deltoid and triceps lateral) of the reach arm and shoulder flexor (pectoralis major) of the stance arm, which indicates their causal role; leg muscles may have indirectly contributed but were not recorded. The strong functional similarity of weight-shift APAs during crouched reaching to human stepping and cat reaching suggests that they are a core feature of posture-movement coordination.

NEW & NOTEWORTHY This work demonstrates that reaching from a crouched posture is preceded by bimanual anticipatory postural adjustments (APAs) that shift the body weight to the stance limb. Weight-shift APAs are more robust in an unstable body posture (knees together) and involve the shoulder and elbow extensors of the reach arm and shoulder flexor of the stance arm. This pattern mirrors the forelimb coordination of cats reaching and humans initiating a step.

anticipatory postural action; bimanual; crawling; reaching

INTRODUCTION

Reaching movements have been extensively studied in human subjects while they adopt a seated posture (1–10) or a standing posture (11–17). In contrast, we are aware of just one study (18) that examined humans reaching from a crouched posture, where both the knees and hands are placed on the ground. This inattention is striking when a quadrupedal posture is typical of terrestrial vertebrates excepting birds, humans, and some nonhuman primates. Moreover, human infants adopt a crouched posture as one of their movement milestones, and adults utilize a crouched posture for a number of tasks such as accessing power outlets beneath one's desk, gardening, sexual intercourse, and particular trades (e.g., carpentry and mining).

Reaching from a crouched posture creates a demand not present when either sitting or standing: the need to transition the weight of the upper body from both arms to one arm. An analogous situation occurs during step initiation (19–22) and leg lifting (23–25) as the weight support is transitioned from both legs to one leg. Healthy individuals typically use both legs to anticipatorily shift their body weight at the beginning of the motor sequence. The leg to be raised exerts a transient increase in downward force concurrent with a transient decrease in downward force by the stance leg. The two legs also exert side-to-side forces in the same external direction, lateral for the stepping leg and medial for the stance leg, though smaller in magnitude. The ground reaction forces (GRFs) acting opposite these anticipatory

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postural adjustments (APAs) move the body's center of mass from a position midway between the two legs to a position under the stance leg. If the center of mass were not shifted toward the stance leg before it bears the body's weight, then one would quickly fall toward the side of the raised leg. In fact, small and variable weight-shift APAs can result from brain disease and damage, most notably Parkinson's disease (26, 27), and this results in poor gait initiation and fall-prone ambulation.

It is unclear whether human subjects exhibit the same pattern when reaching from a crouched posture. That is, do they generate an APA with their reaching arm that induces upward and medial reaction forces before lift-off along with an APA from the stance arm inducing downward and lateral reaction forces before it accepts the weight of the upper body? Alternatively, APAs may be generated by just one arm (either the reaching arm or stance arm), or parallel APAs may be generated for upward reaction forces in both arms (though greater in the reaching arm) or downward reaction forces in both arms (though greater in the stance arm). A parallel strategy is not observed for the lower limbs but may be adopted here since in-phase coordination is more robust than antiphase coordination when moving the upper limbs in free space (Ref. 28, for review see Ref. 29). Finally, participants may not exhibit any anticipatory change in the arms but rather reactive control of the arm, trunk, and legs since their knees and feet contact the floor. This would not be efficient but is realizable owing to the smaller load of supporting the upper body (versus the entire body) and the greater number of solutions for quadrupedal versus bipedal posture. Distinguishing between these possibilities is a straightforward exercise, but the one previous study that examined humans reaching from a crouched posture focused on the details of hand motion and grasp and the similarities of this behavior between rats and humans; the authors did not record any ground reaction forces (18).

Testing whether weight shifts during crouching include anticipatory control and determining its form (if so) are important to understand coordination of one of our most basic behaviors. Such information will help us contrast weight-shift abilities across different effector systems to identify generalized or specialized control mechanisms. Previous evidence suggests that anticipatory control is present in this behavior. Cats and dogs reaching from their natural quadruped posture (30, 31) exhibit weight-shift APAs in the forelimbs (with corresponding vertical and lateral ground reaction forces), indicating that this capability is not unique to human bipedalism. Moreover, healthy humans express bimanual APAs in other tasks. A well-studied example is supporting an object with one arm and then lifting it away with the contralateral arm (32–36). When object removal is self-initiated the support arm remains relatively immobile by preemptively decreasing its upward force, whereas unexpected removal by the experimenter results in the upward acceleration of the support arm due to it generating an excessive vertical force. Healthy individuals are also adept at stabilizing one arm against spring-loads imposed by the contralateral arm as it reaches in different directions (37), although it is uncertain whether this involves APAs or upregulated feedback processing.

Two secondary issues for the present study are whether the upper limb weight-shift patterns exhibit differences between the left and right arm and whether there are changes with the biomechanical context. Laterality in upper limb control is legion and exemplified by the spring-load experiment mentioned above: participants were better at stabilizing their left arm against loads resulting from the reaching right arm than stabilizing their left arm against loads imposed by the reaching left arm (37). Likewise, weight-shift APAs in the upper limbs may be more pronounced when reaching with the right arm than when reaching with the left arm. APAs are also known to be powerfully modulated with the stability context (14, 23, 38); for example, gripping a fixed handle results in smaller weight-weight APA during leg lifting. Hence, we examined whether upper limb weight-shift APAs were more pronounced during an unstable posture (knees placed together, forming a tripod with the hands) than during a stable posture (knee spaced apart, forming a quadruped posture with the hands).

METHODS

Participants

Twelve right-handed individuals from the university population (aged 23–28 yr; 9 male, 3 female) participated in the experiment. Exclusion criteria included a history of neurological or neuromuscular disorder and shoulder, wrist, knee, or back injury. All procedures were approved by the local Institutional Review Board at New York Institute of Technology, and written informed consent was obtained from all participants before participation. Compensation for the single session lasting between 60 and 90 min was provided.

Experimental Setup and Protocol

Participants performed a reaching task from a crouched body posture (Fig. 1). They kneeled on a thin cushion for comfort, with hands placed directly under their shoulders and onto separate force platforms mounted flush with the floor (AMTI OR6-7). On alternating blocks of trials, the participants adopted a knees-apart posture (knees directly under their hips, creating a stable base of support) or a knees-together posture (complete adduction of the knees, creating a less stable tripodlike posture). Note that they did not sit back on their heels but had their thighs erect and their backs parallel to the ground. Knee and hand placements were kept consistent between trials by marking the position of the hands and knees with tape.

A 4 × 4-cm rubber cube was placed on the floor at the participant's midline and near the limit of their forward reach. Participants reached, grasped, and lifted the cube. Neither the hand's trajectory nor the lifting height was specified. They were simply asked to reach naturally with their left or right arm. The "go" cue, illumination of the left or right LED attached to the cube, was manually controlled by the experimenter, followed a random right-left sequence, and occurred in ~3- to 6-s intervals in random order. The voltage signal to the LED was collected.

The first set of blocks used a "reach at a comfortable speed" instruction, whereas the final blocks used a "reach

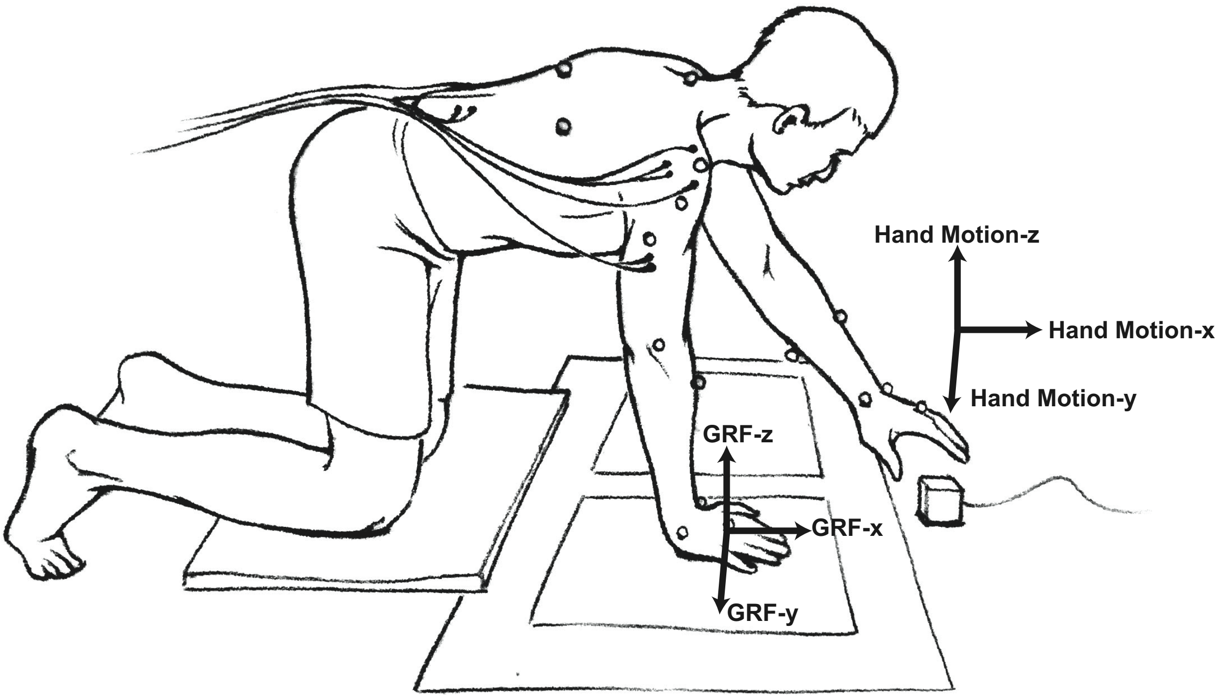

Figure 1. Cartoon of behavior and experimental arrangement. The participant adopts a crouched posture with each hand placed on its own force plate and the knees placed on a soft mat. A small cube with LEDs is located within the subject's reach at midline. Surface electrodes and reflective markers are secured to the subject's arm and trunk to detect muscle activity and body motion. Ground reaction forces (GRFs) under the 2 hands were recorded in the 3 directions of external space: *z* (vertical)-axis (upward is positive), *x* (depth)-axis (forward is positive), and *y* (horizontal)-axis (rightward is positive).

fast" instruction. The protocol consisted of four blocks of 10 reaches at a comfortable speed followed by two blocks of 10 reaches at a fast speed for a total of 20 reaches. Subjects adopted a consistent body posture during a given block (knees apart vs. knees together) and reached equally often with their right and left arm.

Participants were provided a short (1 min) rest period between blocks. At the end of the experiment we recorded their whole body weight on each force plate and on a separate mechanical scale. We also gave a brief survey to nine of the participants.

Motion Capture

A nine-camera motion capture system recorded kinematic data at 100 Hz (Vicon Nexus 2.0, Vicon Motion Systems Ltd.). A custom template used 26 retroreflective markers placed on the upper limbs and trunk (C_7, jugular notch, sternum, and T_{10}) and bilaterally on the acromion, upper arm, lateral epicondyles, midforearm, radial styloid processes, and third metacarpophalangeal joint (MCP). Force plate data were collected at 1,000 Hz.

Electromyography

We employed a 16-channel wireless system (Telemyo 2400 G2, Noraxon USA Inc.) to obtain surface electrical activity from muscles of the left and right arm and trunk: anterior deltoid, posterior deltoid, biceps brachii, triceps lateral, and erector spinae (level of T_{12}). Signals from the bipolar electrodes were gain amplified by 8,000 and collected at 1,000 Hz.

Analyses

Kinematic signals were low-pass filtered at 20 Hz (Butterworth, 6th order). All kinematic analyses focused on the left and right wrist motion. The primary reach was considered bounded by 10% of the peak tangential velocity in the *x-y* plane. From this we obtained the movement time of the reach, the peak wrist velocity, and the start and end positions in all three axes. We also examined the peak lift height after the subject acquired the cube.

Force plate signals were low-pass filtered at 30 Hz (Butterworth, 6th order). Kinetic analyses focused on the vertical and horizontal components (Fig. 1). The beginning of the hand lifting from the force plate was defined as a decrease in vertical force to 90% of its value measured at the "go" cue. The maximum vertical ground reaction force (GRF) under the reaching arm was measured between cue onset and lift-start and subtracted from the maximum vertical GRF in a baseline 300-ms window before the "go cue." This difference was considered the vertical APA of the reach arm. The minimum vertical GRF under the stance arm was measured between cue onset and lift-start and subtracted from the minimum vertical GRF in the baseline period. This difference was considered the vertical APA of the stance arm. A similar approach was used to examine the smaller lateral loading APAs as the arms generated rightward and leftward GRFs. Note that the GRFs were normalized to the subject's body weight. Average force traces were used to determine the participant's APA onset and peak time, since single trials with small force changes can lead to spurious values. Start time was determined as 10% of the peak vertical APA in the averaged knees-together posture. Lift-off by the reaching hand (when the vertical GRF decreased to 0) was estimated by a linear regression of the force trajectory 50 ms before the set dead zone (below 25 N) in the vertical axis; note that the clipping was well below the unloading APAs of the stance arm.

Surface electromyographic (EMG) signals were band-pass filtered between 25 and 250 Hz (Butterworth, 6th order) and rectified. For each trial, a muscle's maximum value for a 150-ms sliding window over the entire behavioral sequence was determined. These single-trial maximums were then averaged within a given condition (e.g., right reach with knees together). From these within-condition maximums we selected the largest to normalize all trials. This approach was designed to avoid outliers and normalize to a task-relevant level (including the different action phases and contexts), although the time-varying signal has transient peaks above this value.

Each muscle's baseline activity was considered the mean value in a 100-ms window before the "go" cue. The muscular APA period was 150 ms wide and ended 50 ms before the

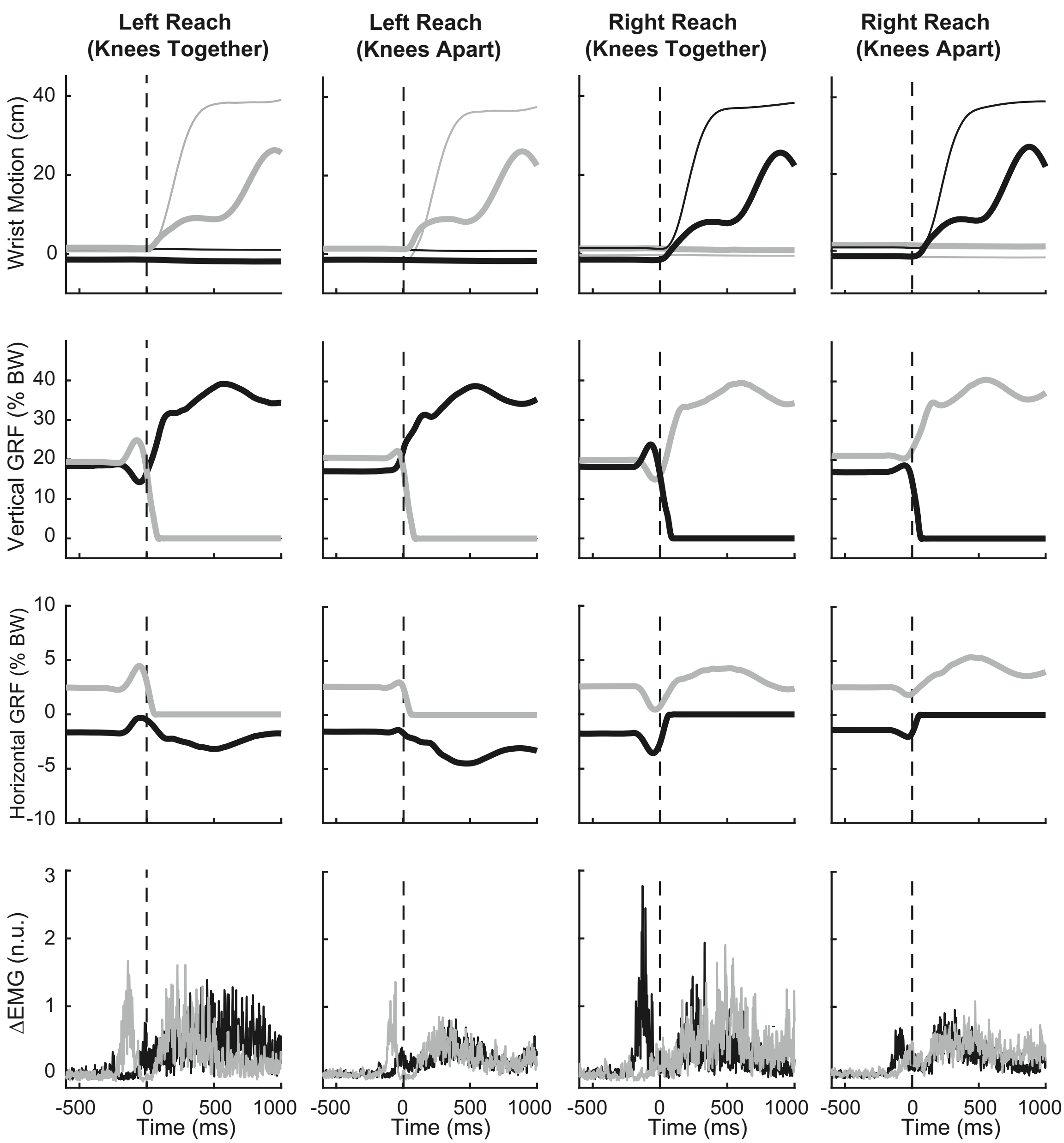

Figure 2. Time course of hand motion, hand force, and arm muscle activity of a representative subject. Data when reaching at a "comfortable" speed are presented in 4 columns: left reach during knees together, left reach during knees apart, right reach during knees together, and right reach during knees apart. All data are time-aligned to the decrease in ground reaction force (GRF) under the reaching arm to 90% of baseline. The 1st row presents the average motion of the left and right wrist in gray and black, respectively. Vertical motion is depicted with a thick solid line, whereas forward motion is depicted with a thin solid line. The 2nd row shows the average vertical GRF under the left and right hand in gray and black, respectively; the GRF is normalized to the participant's body weight (BW). The 3rd row shows the average horizontal GRF under the left and right hand, again in gray and black, respectively. The 4th row presents activity of the subject's left and right posterior deltoid in gray and black, respectively. EMG, electromyograph; n.u., normalized units.

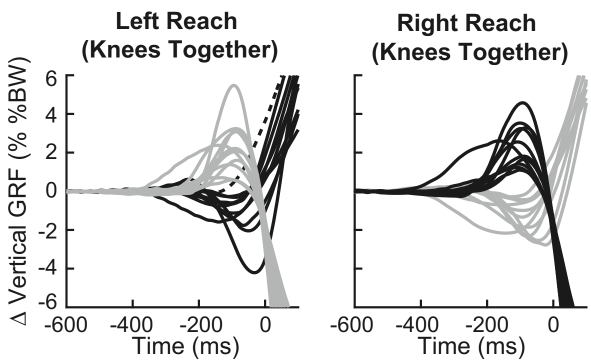

Figure 3. Time course of vertical anticipatory postural adjustments (APAs) from all subjects. Average vertical ground reaction force (GRF) under each participant's left and right arm shown with gray and black lines, respectively, when reaching from a knees-together posture and at a "comfortable" speed (n = 11 subjects). Data normalized to the participant's body weight (BW) and steady-state force are removed to highlight the APAs that precede the reaching hand beginning its lift-start at 0 ms. Note that 1 participant did not exhibit an APA in his stance arm (black dashed line, *left*).

subject's mean time of peak vertical GRF (for the reach arm) or minimum vertical GRF (for the stance arm) during the knees-together posture. The difference in EMG in the muscle APA period and baseline period was considered linked to the weight-shift APA, as it (partly) accounts for the delay between muscle activity and GRF. We also determined the onset of muscle activity on a subject-by-subject basis for the knees-together context, as that involved the largest prereach burst: *1*) the mean traces from the left and right arm were averaged; *2*) the mean and standard deviation (SD) were determined for the baseline period; and *3*) onset was defined as the EMG exceeding its mean + 3 SDs for >5 ms and adjoining a sustained burst, i.e., not an isolated burst. On some samples (<10%) a lower threshold of mean + 2 SDs was adopted to accommodate a noisier signal. We did not determine the onset of EMG for single trials owing to the variable and sometimes small signal.

Statistical analyses were applied to the kinetic and EMG data. Significance was set at $P < 0.05$, and all tests are two-tailed. Two-factor repeated-measures ANOVAs were conducted on the vertical and horizontal GRFs in the baseline period and the peak GRFS comprising the APAs of the reach and stance arm; each individual provided one datum per composite condition (e.g., right arm peak vertical GRF in the knees-together posture), which was the average of repeated trials in that composite condition. These ANOVAs tested for a main effect of arm (right vs. left, an indication of laterality), a main effect of postural context (knees together vs. knees apart, an indication of modifiability), and arm-posture interaction. If no main effect of arm was observed, then the corresponding data of the right and left arm (itself an average) were averaged together for use in a paired t test of postural context; larger APAs may be expected in the knees-together posture to create a larger shift of the center of mass over a narrower base of support. This approach was chosen to separately examine the various force events and conduct fewer specific tests.

Approximately 10% of the GRF sets (5 of 48) were flagged as significantly different from a normal distribution according to a Shapiro–Wilk test ($P < 0.05$), so we also employed a boot-strapped ANOVA and Wilcoxon signed-rank tests as adjuncts. Each boot-strapped test involved 1,000 ANOVAs of randomly sampled (with replacement) data. If F values from the boot-strapped distributions were larger than original F value <50 of 1,000 times ($P < 0.05$), then the result was deemed statistically significant. Additional tests included a nonparametric correlation of the trial-by-trial magnitude of the APAs of the reach and stance arm and linear correlation of the times of peak APA from the reaching and stance arm to assess interlimb coordination.

The EMG analysis was conducted on the "comfortable speed" set, as it had the most trials; one participant was excluded because of poor signal quality. EMG signals from the right and left arm were combined, since no arm differences were observed in the corresponding kinetic analyses. Separate paired t tests were conducted in the reaching and stance arm for postural context. Thirty-five percent of the EMG sets (7/20) were flagged as significantly different from a normal distribution according to a Shapiro–Wilk test, so we employed a Wilcoxon signed-rank test as an adjunct.

One participant was not analyzed because of missing data. Two of the remaining eleven participants performed the task at just the "comfortable" speed.

RESULTS

The general pattern of results is present in the exemplar participant's data. When reaching to obtain the small cube he brought his wrist forward 10s of centimeters, whereas his opposing stance arm remained relatively immobile (Fig. 2, *top* row). Furthermore, the vertical path of his reaching arm first increased when lifting the arm from the floor and then increased again when lifting the grasped cube from the floor. The group average for the forward, lateral, and vertical wrist motions before lifting the cube (combined across conditions,

Table 1. *Time course of vertical APA from the reaching and stance arm*

	Arm–Role	APA Start, ms	APA Peak, ms	Hand Lift-off, ms
"Comfortable" hand speed	Right arm—reach	−256 (68 SD)	−113 (38 SD)	142 (59 SD)
	Left arm—reach	−234 (56 SD)	−104 (27 SD)	131 (55 SD)
	Right arm—stance	−215 (57 SD)	−98 (46 SD)	
	Left arm—stance	−223 (75 SD)	−98 (41 SD)	
"Fast" hand speed	Right arm—reach	−161 (41 SD)	−66 (23 SD)	77 (16 SD)
	Left arm—reach	−160 (39 SD)	−60 (18 SD)	76 (18 SD)
	Right arm—stance	−140 (47 SD)	−43 (35 SD)	
	Left arm—stance	121 (38 SD)	−54 (30 SD)	

APA, anticipatory postural adjustment.

arms, and speeds) was 34.1 cm (5.1 SD), 20.0 cm (4.7 SD), and 8.2 cm (2.7 SD), which are relatively large amplitudes for reaching actions. During the "fast" instruction the tangential wrist velocity was ~40% greater than that observed during the "comfortable" speed instruction: mean = 170.36 cm/s (22.9 SD) versus mean = 120.4 cm/s (28.6 SD), indicating a substantial difference in the overall speed.

His reaching movements were preceded by a characteristic pattern of vertical forces under the two arms (Fig. 2, second row). During the hold period, the exemplar subject steadily bore 15–20% of his body weight on each arm, with a slight bias to greater support on the left arm. Before lifting his (right or left) arm from the floor to execute the reach, where the GRF necessarily drops to zero, he exerted a transient increase in vertical GRF under that arm. Likewise, he exerted a transient decrease in GRF under the stance arm before it bore all the weight of the upper body. This general pattern was not unique to this exemplar participant. Rather, every participant demonstrated the same pattern in the knees-together posture as shown in Fig. 3; baseline GRFs are removed to highlight the transient APAs. The one exception was an absent vertical APA under the right stance arm by one participant when they reached with the left arm (see dashed line in Fig. 3, *left*). Note that the timing of peak reach and stance APAs during the "comfortable speed" instruction was correlated on a subject-by-subject basis whether reaching with the left arm (r = 0.77) or the right arm (r = 0.67). Start and peak times of these APAs and those from "fast"-instructed trials are presented in Table 1 along with the associated lift-off times. APAs and lift-offs were hastened with the "reach as fast as possible" instruction. Interestingly, the timing of peak APAs from the reach and stance arm during the "fast" instruction (knees-together posture) was correlated on a subject-by-subject basis when reaching with the right arm (r = 0.79) but not the left arm (r = 0.01). Finally, the trial-by-trial consistency of the APA timing is evident in the standard deviation of the reaching arm's peak APA: "comfortable" group average = 32 ms; "fast" group average = 10 ms.

The exemplar participant (Fig. 2) exhibited several other patterns reflective of the group trends. During the baseline period, he generated horizontal/side-to-side GRFs directed toward the midline, i.e., a leftward GRF under the right arm and a rightward GRF for the left arm (Fig. 2, third row) and horizontal APAs in the same direction of external space. Furthermore, the vertical and horizontal APAs were more pronounced in a knees-together posture than a knees-apart posture, which is consistent with a greater demand to laterally shift the center of mass underneath the narrow tripod configuration. And finally, the distinct APAs of the reach and stance arm were associated with distinct patterns of muscle activity (Fig. 2, *bottom* row). Posterior deltoid exhibited the clearest relation, with a burst in the reaching arm starting well before lift-start, and this was notably larger during the knees-together posture. The activity of posterior deltoid in the stance was relatively little prior to lift-start but grew after lift-start as that arm increasingly bore the weight of the entire upper body.

Figure 4 presents each participant's vertical GRFs during baseline and APA along with the group mean. The group average of baseline vertical GRF (combined across conditions and speeds) was 17.6% body wt (3.3 SD) for the left arm and 16.2% body wt (2.6 SD) for the right arm. This translates to the two arms supporting ~1/3 of the body weight with an 8% greater contribution by the left arm. Two-way ANOVAs indicate a main effect of laterality on baseline vertical GRF for the "comfortable" speed instruction and the "fast" speed instruction but no main effect of knee posture or interaction between knee posture and arm for either speed instruction (see Table 2).

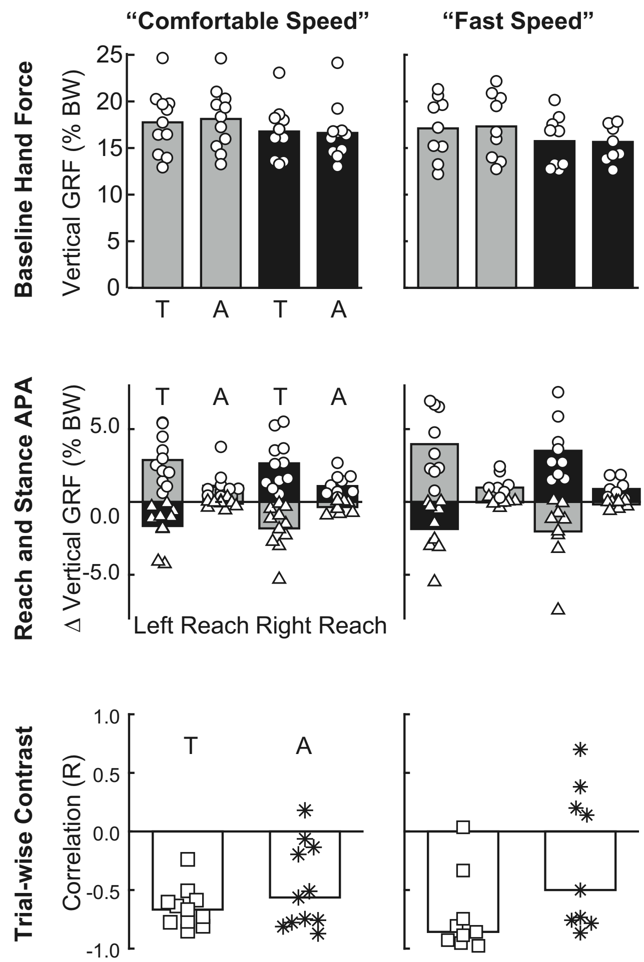

Figure 4. Summary of anticipatory postural adjustments (APAs) and vertical ground reaction force (GRF). *Left* and *right*: data from "comfortable" (n = 11 subjects) and "fast" (n = 9 subjects) speed conditions, respectively. Group means for the left and right arms are depicted with gray and black bars, respectively, whereas individual data are shown by small icons offset to improve visibility. Positive values reflect the upward GRF normalized to the participant's full body weight (BW). *Top*: the steady-state vertical GRF under the 2 arms prior to the "go" cue. T, knees-together condition; A, knees-apart condition. *Middle*: the vertical APAs of the 2 arms: a transient increase in GRF under the reaching arm (circles for individual data) and transient decrease in vertical GRF force under the stance arm (triangles for individual data). *Bottom*: the trial-by-trial correlation of the increase and decrease in vertical GRF under the reaching and stance arm. Open bars show the median correlation, and squares and asterisks depict data from individuals.

The grand mean of the vertical APA by the reaching arm was 1.65% body wt. This transient increase preceded the complete decrease in vertical force as the hand lifted from the surface. Two-way ANOVAs indicated a significant main effect of knee posture for both the "comfortable speed" instruction and the "fast" speed instruction but no

Table 2. *Statistical tests for vertical baseline GRFs and APAs for the reaching arm and stance arm*

		Effect	*F* Statistics	*t* Value	*P* Value	η^2	Cohen's *d*
		"Comfortable" speed					
Steady state	Two-way repeated-measures ANOVA	**Arm**	$F(1,10) = 7.3$		0.023	0.33	
		Knee posture	$F(1,10) = 0.1$		0.71	<0.01	
		Interaction	$F(1,10) = 2.2$		0.14	0.013	
Reach arm APA	Two-way repeated-measures ANOVA	Arm	$F(1,10) = 0.7$		0.41	<0.01	
		Knee posture	$F(1,10) = 29.9$		<0.001	0.64	
		Interaction	$F(1,10) = 0.4$		0.52	<0.01	
	Paired *t* test	**Knee posture**		$t(10) = 4.5$	0.0012		1.34
Stance arm APA	Two-way repeated-measures ANOVA	Arm	$F(1,10) = 1.4$		0.27	<0.01	
		Knee posture	$F(1,10) = 19.4$		0.001	0.58	
		Interaction	$F(1,10) = 0.7$		0.87	<0.01	
	Paired *t* test	Knee posture		$t(10) = -3.9$	0.003		−1.17
		"Fast" speed					
Steady state	Two-way repeated-measures ANOVA	**Arm**	$F(1,8) = 11.8$		0.009	0.46	
		Knee posture	$F(1,8) = 0.6$		0.80	<0.01	
		Interaction	$F(1,8) = 0.3$		0.62	<0.01	
Reach arm APA	Two-way repeated-measures ANOVA	Arm	$F(1,8) = 0.4$		0.55	0.01	
		Knee posture	$F(1,8) = 44.7$		<0.001	0.58	
		Interaction	$F(1,8) = 0.6$		0.45	0.006	
	Paired *t* test	**Knee posture**		$t(8) = 5.4$	<0.001		−1.01
Stance arm APA	Two-way repeated-measures ANOVA	Arm	$F(1,8) < 0.1$		0.78	<0.01	
		Knee posture	$F(1,8) = 12.3$		0.008	0.47	
		Interaction	$F(1,8) < 0.1$		0.86	<0.01	
	Paired *t* test	**Knee posture**		$t(8) = -3.0$	0.016		−1.01

APA, anticipatory postural adjustment; GRF, ground reaction force.

main effect for reaching arm or significant interaction (see Table 2). Averaging the left reach and right reach data of each subject allowed a focused contrast of APA modulation with knee posture. *t* Tests indicated that the downward APA by the reach arm was significantly greater in the knees-together than the knees-apart posture whether reaching at a "comfortable" speed or a "fast" speed (see Table 2).

A similar analysis was conducted for the vertical APAs of the stance arm. Its grand mean across all conditions was −1.0% body wt. Two-way ANOVAs indicated a significant main effect of knee posture but no main effect for the arm providing stance support or significant interaction (see Table 2). *t* Tests on the averaged left and right changes indicate significantly greater vertical APAs in stance arm during the knees-together posture whether reaching at a "comfortable" speed or a "fast" speed (see Table 2).

To examine whether vertical APAs of the reach and stance arm covaried from trial to trial, we determined their correlation for each participant for a given knee posture and reach speed. The set of correlations for the group was then evaluated with a signed-rank test. This analysis revealed a significant negative correlation of the transient forces during the knees-together posture: "comfortable" speed median rho = −0.67, signed rank = 0, *P* = 0.001; "fast" speed median rho = −0.86, signed rank = 1, *P* = 0.008. Larger (smaller) APAs by the reach arm occurred on trials with larger (smaller) APAs by the stance arm. With the knees apart, this coupling tended to be weaker and did not reach significance for the fast speed: "comfortable" speed rho = −0.79, signed rank = 3; *P* = 0.027; "fast" speed median rho = −0.5, signed rank = 11, *P* = 0.20.

The preceding material focused on the vertical baseline forces and APAs. Participants also produced horizontal GRFs during the baseline period along with horizontal APAs appropriate to shift their body weight to the stance arm (Fig. 2 for an exemplar participant and Fig. 5 for all participants). The group average of baseline lateral force was 1.1% body wt (1.1 SD) for the left arm and −0.8% body wt (1.1 SD) for the right arm such that they were <10% of the baseline vertical GRFs. Similarly, the horizontal APAs were ~50% of the magnitude of the vertical APAs since the reaching arm exerted medial directed GRF with a grand mean of 0.83% body wt and the stance arm exerted a lateral directed GRF with a grand mean of 0.62% body wt. Note that the external direction of the horizontal APAs was the same for the reaching and stance arm, in contrast to the reciprocal changes in their vertical APAs.

The statistical results for horizontal APAs were similar to those reported for the vertical APAs and are reported in Table 3. Two-way ANOVAs indicated a significant main effect of knee posture (greater with the knees together) but no main effect for reaching arm or significant interaction for the lateral loading APA with either speed instruction. As with the vertical APAs, we combined data from the left and right arm and conducted paired *t* tests. These indicated that horizontal APAs by the reach arm were significantly greater in the knees-together than the knees-apart posture as were the horizontal APAs of the stance arm. In a final set of analyses we examined the pattern of arm and trunk activity associated with the weight-shift APAs. All six muscles were robustly engaged in the motor sequence, though with their own distinctive trajectory. The muscle that most consistently exhibited activity related to the weight-shift was posterior deltoid (a shoulder extensor) (see Fig. 2, *bottom* row, for an exemplar subject and Fig. 6, *top* row, for the group. The first and second columns of Fig. 6 present EMG signals aligned to the beginning of the lift, as in Figs. 2 and 3. Posterior deltoid exhibits a large burst in the reaching arm that ends around the lift-start. A more sustained second burst occurs as the

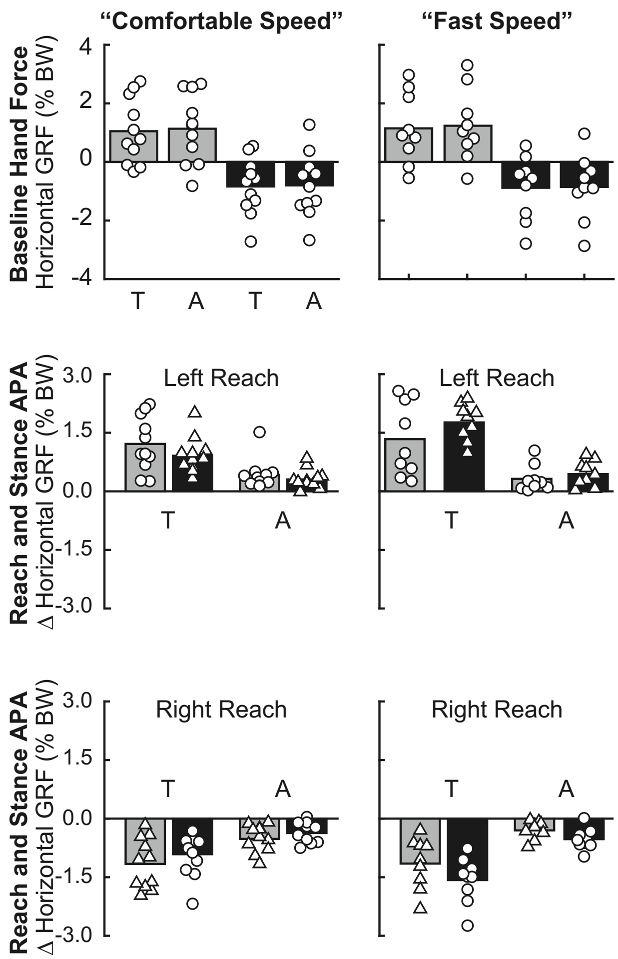

Figure 5. Summary of anticipatory postural adjustments (APAs) and horizontal ground reaction force (GRF). *Left* and *right*: data during the "comfortable" (n = 11 subjects) and "fast" (n = 9 subjects) speed conditions, respectively. Group means for the left and right arms are depicted with gray and black bars, respectively, and individual data are shown by small icons. *Top*: positive and negative values reflect the rightward and leftward GRF normalized to the participant's full body weight (BW). T, knees-together condition; A, knees-apart condition. *Middle*: the transient rightward GRF under both arms when reaching with the left arm. Circles, reach arm; triangles, stance arm. *Bottom*: the transient leftward GRF under both arms when reaching with the right arm. Circles, reach arm; triangles, stance arm.

participants bring their hand to the target ahead of the body. In the stance arm, the posterior deltoid's activity rises before the lift-start, followed by a larger, more sustained burst.

Relating these bursts and modulation with knee posture to the weight-shift APA requires aligning each participant's EMG to their own APA (rather than a fixed time) and bracketing the relevant relative time window. This format is used in the panel of the third and fourth columns of Fig. 6 and shows a robust burst in the reaching arm's posterior deltoid before the peak APA and very little activity in the stance arm's posterior deltoid preceding its weight-shift APA.

Figure 7 presents the individual and group patterns of the average EMG within these APA-aligned windows of Fig. 6; the corresponding statistical results are presented in Table 4. Weight-shift-associated EMG of the reaching arm's posterior deltoid was moderate with the knees together, 28.7% (17.1 SD), as was the posture-dependent modulation, 16.0% (14.5 SD), which obtained statistical significance. Activity of posterior deltoid in the stance arm was very low with knees together, 0.4% (2.2 SD), and posture dependence was smaller but also less variable, −1.6% (0.9 SD), which yielded a statistically significant effect.

Anterior deltoid (a shoulder flexor) showed a quite different pattern (Figs. 6 and 7). In the reach arm, it had a small increase then decrease in activity before the lift-start, which was followed by a burst and sustained activity appropriate to flex the shoulder forward. In the stance arm, the muscle exhibited larger and earlier increases in activity that were sustained throughout the trial. Aligning the signals to the peak APAs confirmed some activity linked to the weight-shift for the reach arm with knees together, 3.9% (8.4 SD), but greater activity in the stance arm, 22% (14 SD). The modulation with posture in the stance arm, 5.1% (7.5 SD), did not reach significance (Table 5).

Triceps lateral showed a pattern resembling posterior deltoid (Figs. 6 and 7). In the reaching arm there was a clear burst starting before the lift-start followed by relatively low activity during the reach itself. In contrast, the increased activity in the stance arm started later and was sustained thereafter. The peak-aligned signal reveals a small burst in the reach arm with knees together of 11.9% (7.1 SD). The elbow extensor's burst was significantly modulated with knee posture, 6.1% (4.9 SD). The muscle's EMG in the stance arm was weak, 0.4% (7.0 SD), and not significantly modulated with posture (Table 5).

Biceps brachii showed small increases in both the reaching and stance arm before lift-start, followed by a large burst in the reaching arm and smaller sustained activity in the stance arm (Figs. 6 and 7). The peak-aligned signals were 8.1% (7.2 SD) in the reach arm with knees together. Activity in the reaching arm was significantly modulated with knee posture, 4.1% (3.7 SD). The muscle's EMG in the stance arm was similar, 7.4% (8.8 SD), but not significantly modulated with posture, 3.9% (7.0 SD).

Erector spinae of the trunk showed largely parallel changes in activity in the reach arm's side and the stance arm's side (Figs. 6 and 7). Bursts were expressed before lift-start, followed by sustained activity though the reach. There was almost no activity for most of the APA period, as the measured onsets followed the APA's start in both the reaching and stance arm. However, the bursts were quite steep, leading to 3.7% (6.4) in the reaching side and significant modulation with posture, along with 8.5% (11.9) on the trunk side and no significant modulation with posture. The boot-strapped ANOVAs and Wilcoxon signed-rank tests did not yield different conclusions with the force plate signals. No GRF conclusion switched from above to below the alpha level of $P < 0.05$, or vice versa. A few changes occurred with the EMG signals. Posture-dependent modulation of the anterior deltoid during stance was deemed significant along with the triceps lateral during the reach. Table 5 shows that these values hovered just above threshold with paired t tests (P = 0.058 and P = 0.056). With the signed-rank tests they hovered just below (P = 0.049 and P = 0.049). At no point did a nonparametric test lead to acceptance of a null hypothesis that was rejected though a parametric test.

Table 3. *Statistical tests for horizontal baseline GRFs and APAs for the reaching arm and stance arm*

		Effect	*F* Statistics	*t* Value	*P* Value	η^2	Cohen's *d*
		"Comfortable" speed					
Steady state	Two-way repeated-measures ANOVA	**Arm**	*F*(1,10) = 8.9		0.014	0.47	
		Knee posture	*F*(1,10) = 8.0		0.018	<0.01	
		Interaction	*F*(1,10) < 0.1		0.79	<0.01	
Reach arm APA	Two-way repeated-measures ANOVA	Arm	*F*(1,10) < 0.1		0.79	<0.01	
		Knee posture	*F*(1,10) = 25.3		<0.001	0.64	
		Interaction	*F*(1,10) = 0.3		0.10	<0.01	
	Paired *t* test	**Knee posture**		*t*(10) = 5.1	0.0012		1.52
Stance arm APA	Two-way repeated-measures ANOVA	Arm	*F*(1,10) = 0.1		0.72	<0.01	
		Knee posture	*F*(1,10) = 33.3		<0.001	0.61	
		Interaction	*F*(1,10) = 0.4		0.57	<0.01	
	Paired *t* test	Knee posture		*t*(10) = −5.8	<0.001		1.74
		"Fast" speed					
Steady state	Two-way repeated-measures ANOVA	**Arm**	*F*(1,8) = 7.5		0.025	0.48	
		Knee posture	*F*(1,8) = 1.2		0.30	<0.01	
		Interaction	*F*(1,8) > 0.1		0.83	<0.01	
Reach arm APA	Two-way repeated-measures ANOVA	Arm	*F*(1,8) = 0.3		0.60	<0.01	
		Knee posture	*F*(1,8) = 24.7		0.001	0.56	
		Interaction	*F*(1,8) = 0.6		0.48	<0.01	
	Paired *t* test	**Knee posture**		*t*(8) = 5.0	0.001		1.67
Stance arm APA	Two-way repeated-measures ANOVA	Arm	*F*(1,8) < 0.1		0.79	<0.01	
		Knee posture	*F*(1,8) = 156		<0.001	0.76	
		Interaction	*F*(1,8) = 1.9		0.20	0.01	
	Paired *t* test	**Knee posture**		*t*(8) = −12.6	<0.001		4.20

APA, anticipatory postural adjustment; GRF, ground reaction force.

A further analysis was undertaken to relate the onset of the EMG to the onset of the APA (see *Analyses* and Table 5). Posterior deltoid and triceps lateral of the reaching arm began their bursts—46 ms (34 SD) and 26 ms (24 SD), respectively—before the start of the reach APA. The activity increase by the stance arm's anterior deltoid also preceded the stance APA by 56 ms (13 SD). All other muscle onsets followed the APA start and/or were highly variable, though they often preceded the peak APA.

A final set of observations are the survey results of the young healthy individuals. We were concerned that repeated kneeling and bearing weight on the hands may cause discomfort or fatigue despite our efforts to avoid this. Three of nine participants indicated "some" discomfort toward the end; the others indicated "none." All participants except one indicated an ability to perform "many more" blocks, and seven participants indicated "no conscious strategy." One said "most often no," whereas the other commented that his reaching speed could improve with weight shifting since he wrestled in high school.

DISCUSSION

The present study has provided the first detailed examination of ground reaction forces at the hands and associated arm muscle activity of humans as they reach from a crouched posture. This behavior occurs in a wide variety of settings and allows a direct comparison between the motor patterns of humans and quadruped models of reaching as well as between upper limb and lower limb control, i.e., with step initiation. Our primary observation is that young and healthy individuals produce vertical and horizontal GRFs under their reach arm before lifting, along with complementary vertical and horizontal GRFs under their stance arm before accepting the weight of the upper body. These transient forces are clear evidence of an anticipatory weight-shift involving both arms that mirrors those exhibited by cats reaching from a quadrupedal posture and humans during step initiation and leg lifting. Other possibilities, such as APAs restricted to one limb, semiparallel APAs, or even purely reactive control, were credible, if unfavored, possibilities owing (in part) to the legs contacting the floor and providing a mechanical resource. Instead, our results exemplify the generality of weight-shift APAs. Several secondary observations are important for understanding the organization of this anticipatory control. First, weight-shift APAs occurred whether participants reached at a "comfortable" speed or "as fast as possible." This expression across a range of temporal demands is similar to how weight-shifts during stepping are robust to low and high reaction time pressure (22) as well as normal cuing or hastening by a loud sound (20) and indicates that it is a general feature of reaching from a crouched posture. It should also be noted that instructing the participants to "reach as fast as possible" resulted in hastened APAs like the hastened reach as if energizing all components of the motor sequence, a healthy complement to Parkinson's disease and its blunting of APAs and bradykinesia of the intended movement. To be clear, this does not indicate that the APA and reach are organized hierarchically, but rather an increase in speed appears to be a natural default and this preference highlights the typical integration of posture and movement. Note that this issue remains unresolved, with behavioral evidence tending to support a parallel organization (38, 39) whereas physiological evidence points to a parallel and hierarchical mixture (see below).

The next important observation is that weight-shift APAs (both reach and stance components) were greater in the unstable knees-together posture than the more stable knees-apart posture. This makes functional sense since the need to shift weight to the stance arm is less pressing with the knees spaced

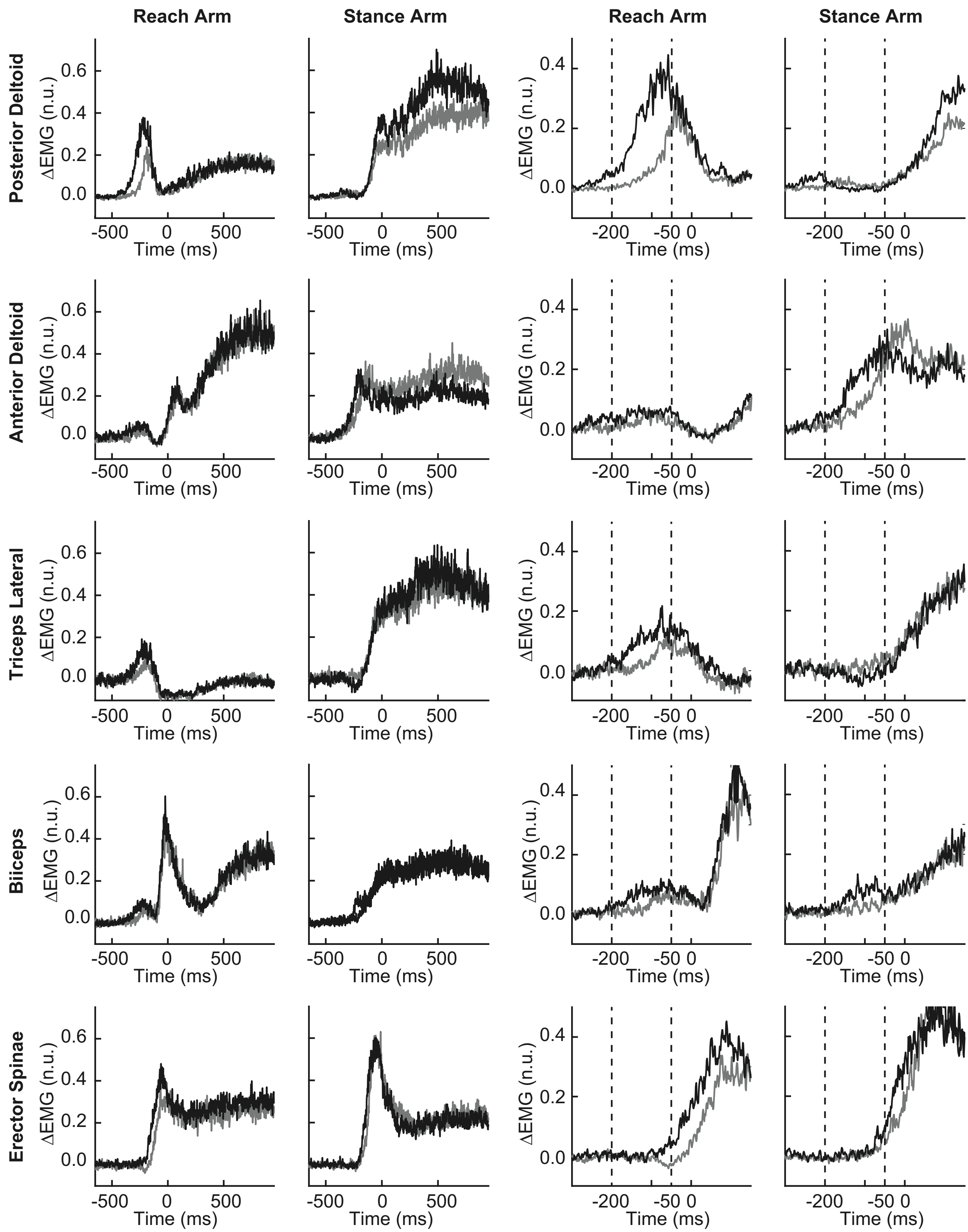

Figure 6. Muscle activity in the reaching and stance arm throughout the motor sequence. Traces in the 1st column depict the group mean activity of muscles in the reaching arm and the same side of the trunk. Traces in the 2nd column depict the group mean activity of muscles in the stance arm and the same side of the trunk. Black and gray traces indicate activity during the knees-together posture and knees-apart posture, respectively. For both columns the data are time-aligned to the decrease in vertical ground reaction force (GRF) under the reaching arm to 90% of baseline, as in Figs. 2 and 3. The 3rd and 4th columns present the same data, now aligned to each participant's peak anticipatory postural adjustment (APA). The dashed lines bracket the preceding 150-ms window (shifted by 50 ms) to analyze muscle activity related to the weight-shift APA. All electromyographic activity (EMG) is during the "comfortable" speed instruction. n.u., Normalized units.

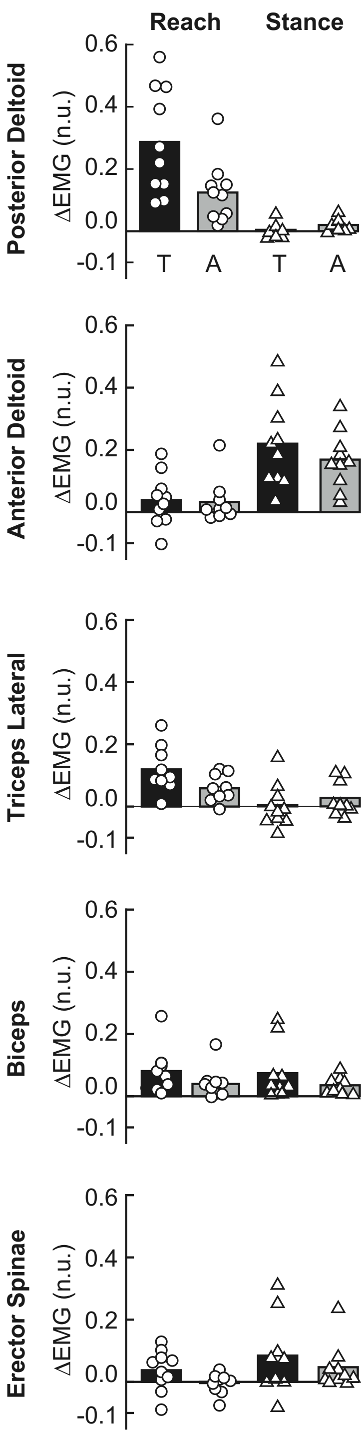

Figure 7. Change in muscle activity linked to anticipatory postural adjustment (APA). Data show normalized muscle activity in the period associated with the weight-shift APA (during the "comfortable" speed instruction); see *Analyses* and Fig. 6. Vertical axis is the normalized change in activity from baseline. Black and gray bars show the group mean activity for the arm during knees-together (T) and knees-apart (A) postures. Muscle activity in the reaching arm is presented on *left* (with white circles for individual data), whereas muscle activity in the stance arm is presented on *right* (with white triangles for individual data). *n* = 8 subjects. EMG, electromyograph; n.u., normalized units.

apart, as the center of gravity is closer to the base of support compared to the knees placed together in a tripodlike posture. Other authors have also observed the attenuation of APAs when they no longer aid mechanical stability [e.g., blocking the mechanical interactions between effectors (14, 38)] or when a secondary source of stability is provided [e.g., holding a fixed handle during leg lifting (23)]. There are many further examples of contextual modulation of weight-shift APAs such as step height for obstacles (22), floor translation as a triggering stimulus (40), and fear of falling (41). Furthermore, systematic differences in APAs are present between different populations, e.g., males and females (42) and healthy weight and obese (43). All these may have analogs to upper limb weight-shift APAs, although no apparent differences were evident between males and females with our small sample.

Laterality of the crouched reach was another topic of interest. Participants bore more body weight accepted by the left than the right arm in the steady baseline period. Yet there was no consistent laterality effect in the weight-shift pattern, e.g., larger APAs when reaching with the right/dominant arm (note that all participants were right arm dominant). The lack of an apparent difference contrasts with other studies. Superior stabilization is found when the dominant arm reaches and the spring-linked nondominant/left arm is instructed to remain still than vice versa (37). Trunk APAs also occur at an earlier time when reaching with the dominant versus nondominant arm while sitting (44) or standing (45), and these APAs contribute to the greater terminal accuracy of the reach. Superior weight-shift APAs (in both size and effectiveness) have also been observed when people lift their dominant versus nondominant leg (46), and hastened stepping may be biased to the dominant leg (20). Accordingly, laterality effects may become evident under more demanding or complex circumstances. And, in fact, the one example we observed was when subjects reached with the left arm with the "fast" instruction. Here the timing of peak APAs from the left reaching arm and the right stance arm were uncorrelated (across subjects), whereas correlated timing was seen when they reached at the "comfortable" speed with the left arm or reached with the right arm with either speed instruction. APA magnitude had a positive correlation between limbs (within subjects) at "comfortable" speed, but the low number of repeats during the "fast" speed precluded a right reach versus left reach comparison.

The basic pattern of forelimb forces that we observed in humans parallels the behavior exhibited by cats reaching from their quadrupedal posture. The similarity further extends to the patterns of muscle activity (31). The upward and medial GRF from the reaching limb was preceded by a burst of activity in the ipsilateral posterior deltoid and triceps lateral in humans, and the homologous muscles of the cat, spinodeltoideus and triceps lateral, are similarly active. These extensor muscles also showed little activity in the APA period when reaching with the contralateral limb, i.e., when the ipsilateral limb provided unilateral support. The two recorded axial muscles—erector spinae in humans and biventer cervicis in cats—had a later onset and symmetrical activity for reaching with the ipsilateral and contralateral limb. So although these muscles did not generate the weight-shift, they helped stabilize the trunk during this motor sequence. Finally, ispilateral biceps brachii is clearly

Table 4. *Statistical tests for vertical baseline GRFs and APAs for the reaching arm and stance arm*

			Effect	*t* Value	*P* Value	Cohen's *d*
Posterior deltoid	Reach arm	Paired *t* test	**Knee posture**	$t(9) = 4.5$	0.002	1.41
	Stance arm	Paired *t* test	**Knee posture**	$t(9) = -5.5$	<0.001	−1.74
Anterior deltoid	Reach arm	Paired *t* test	Knee posture	$t(9) = 0.38$	0.71	0.12
	Stance arm	Paired *t* test	Knee posture	$t(9) = 2.2$	0.058	0.69
Triceps lateral	Reach arm	Paired *t* test	Knee posture	$t(9) = 3.9$	0.004	1.23
	Stance arm	Paired *t* test	Knee posture	$t(9) = -2.2$	0.056	−0.69
Biceps brachii	Reach arm	Paired *t* test	Knee posture	$t(9) = 4.5$	0.001	1.43
	Stance arm	Paired *t* test	Knee posture	$t(9) = 1.8$	0.11	0.54
Erector spinae	Reach arm	Paired *t* test	Knee posture	$t(9) = 2.5$	0.037	0.78
	Stance arm	Paired *t* test	Knee posture	$t(9) = 1.8$	0.11	0.57

APA, anticipatory postural adjustment; GRF, ground reaction force.

linked to raising the reaching limb in both humans and cats. We also found a small burst in the APA period, though later than the posterior deltoid and triceps, and since it is a flexor at both the elbow and shoulder, it is unclear what function this activity met.

Our results complement other demonstrated parallels of human and nonhuman quadrupedal behavior. Locomotion has been the most thoroughly explored behavior (see Refs. 47 and 48 for review). Some exemplars of commonalities include a diagonal gait when ambulating on all four limbs (49) and phase-dependent cutaneous reflex activity of the upper limbs (50) and lower limbs (51). Humans and cats also express a common strategy of postural stabilization to a translating floor (52); compensatory responses are dominated by shear forces that are generated by the hindlimb. And in the most extreme case, humans with the rare genetic disorder of Uner Tan syndrome do not express bipedalism but instead ambulate on all four limbs (53, 54). Given our common evolutionary heritage, these behavioral similarities likely reflect similar neural processing by quadrupeds and humans.

The physiological basis of APAs has been explored with animal models, healthy human participants, and clinical populations. Collectively, this work has revealed parallel and hierarchical processing among cortical, subcortical, and spinal centers for APAs. Motor cortex is a key player for this, as many limb-related neurons from behaving cats exhibit responses time-locked to the APA of given limb (55) and damage to medial motor cortex in humans leads to poorly formed APAs (56). Animal studies indicate that ponto-medullary reticular formation—a region well established for tonic postural control and locomotion (reviewed in Ref. 57)—is also key for APAs. A large number of limb-related neurons in this region exhibit responses time-locked to a limb's APA (58–60), and local application of cholinergic agonists to reticular formation results in altered APAs to cortical-evoked movements (61). Unfortunately, the only studies of ponto-medullary reticular formation in humans are indirect and hinge on loud/startling sound cues that lead to shortened reaction time for prepared movement compared to slower reaction times with a moderate sound cue (62, 63). The hastened responses, which include weight-shift APAs during prepared stepping (20), have been argued to reflect the engagement of a faster recticulospinal pathway, but this paradigm also appears to engage a fast corticospinal process (64), which would conflate the results. Another complication that should be emphasized is that APA-associated neurons in motor cortex and reticular formation often exhibit complex relations to the subsequent reach task and across limbs (55, 58–60), implying a reconfiguration of downstream spinal networks and precluding a simple function being attributed to any area. Clinical studies also reveal that the basal ganglia are critical for properly formed APAs. Individuals with Parkinson's disease exhibit reduced interarm APAs (65). In addition, their weight-shift APAs during stepping are attenuated (26, 66–69), prolonged in duration (66–69), and more variable trial to trial (27).

Although the present study provided valuable information on upper limb coordination in humans, it also possessed several limitations that should be mentioned. First, we focused on a relatively homogeneous population of healthy young adults. Given the changes in APAs with different age, sex, and body weight, further studies on a broader range of individuals are needed to understand the generality of these motor patterns. For example, do human infants express these weight-shift APAs concurrent with their crawling skills between 6–12 mo (49), around 18 mo when reaching from a seated posture (70), or 2 yr and older like for coordinating grip and lift of an object (71)? Second, the present study focused on movements of the upper limbs and forces transmitted through them. We did not record the ground forces applied by the legs or their muscle activity. They could have a substantial effect in weight-shifts seen at the hand given their greater leverage and strength. Research on cats and dogs shows that hindlimb and forelimb loading is coordinated: the hindlimb ipsilateral to the reaching forelimb exerts a sustained increase in downward force while the contralateral hindlimb has a sustained decrease in upward force (30, 31). This force redistribution creates a stable platform among the remaining contact points. We expect that a similar force change would be expressed by human participants in the knees-apart posture, though not in the knees-together posture, which is already tripodlike.

Table 5. *Onset of muscle activity on the reaching and stance side during knees-together posture*

	Reach Side, ms	Stance Side, ms
Posterior deltoid	−46 (34 SD) 10/10 subjects*	124 (74 SD) 3/10 subjects
Anterior deltoid	−8 (118 SD) 6/10 subjects	−56 (13 SD) 10/10 subjects
Triceps lateral	−26 (24 SD) 9/10 subjects	113 (87 SD) 3/10 subjects
Biceps brachii	32 (91 SD) 7/10 subjects	47 (71 SD) 8/10 subjects
Erector spinae	89 (56 SD) 9/10 subjects	74 (50 SD) 8/10 subjects

*Number of subjects with muscle onsets before peak anticipatory postural adjustment (APA).

Relatedly, we only obtained a single sample of trunk musculature, erector spinae, when there are many different trunk muscles and these support a wide number of actions. Reciprocal APAs may occur in other trunk muscles or the same muscles in a different movement context. Finally, we only examined movements in a single direction, distance, and precision requirement. This focus was a reasonable starting point but likely underestimates the flexibility of weight-shift APAs and associated stabilizing responses and may even obscure their role. For example, a recent study using many different reach directions concluded that preparatory postural responses are best described as promoting movement within the base of support (72). These issues are left to future study.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

R.G. and I.K. conceived and designed research; R.G., S.P., and D.D. performed experiments; I.K. analyzed data; R.G. and I.K. interpreted results of experiments; I.K. prepared figures; R.G. and I.K. drafted manuscript; R.G. and I.K. edited and revised manuscript; R.G. and I.K. approved final version of manuscript.

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