

## EMG Study of Hand Muscle Recruitment During Hard Hammer Percussion Manufacture of Oldowan Tools

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**KEY WORDS** stone tool-making; electromyography; flexor pollicis longus; fossil hominids

**ABSTRACT** The activity of 17 hand muscles was monitored by electromyography (EMG) in three subjects during hard hammer percussion manufacture of Oldowan tools. Two of the subjects were archaeologists experienced in the replication of prehistoric stone tools. Simultaneous videotapes recorded grips associated with the muscle activities. The purpose of the study was to identify the muscles most likely to have been strongly and repeatedly recruited by early hominids during stone tool-making. This information is fundamental to the identification of skeletal features that may reliably predict tool-making capabilities in early hominids. The muscles most frequently recruited at high force levels for strong precision pinch grips required to control the hammerstone and core are the intrinsic muscles of the fifth finger and the thumb/index finger regions. A productive search for skeletal evidence of habitual Oldowan tool-making behavior will therefore be in the regions of the hand stressed by these intrinsic muscles and in the joint configurations affecting the relative lengths of their moment arms. *Am J Phys Anthropol* 105:315-332, 1998. © 1998 Wiley-Liss, Inc.

Who made Oldowan stone tools? This is a recurring question in paleoanthropology, recently raised again with the discovery of Oldowan stone tools in Ethiopia at a level dating to 2.5-2.6 Ma (Semaw et al., 1997), contemporary with australopithecines and earlier than the most ancient known member of the genus *Homo* reported by Kimbel et al. (1996).

The route to the answer should be through the fossil hominid hands that were capable of making the tools. Several attempts have been made to infer tool-making capabilities from available skeletal features in fossil hand bones such as muscle attachment areas, bone and joint surface configurations, relative metacarpal robusticity, hand segment proportions, and skeletal topography affecting the length of tendon moment arms (Napier, 1962; Ricklan, 1987, 1990; Susman

1988a,b, 1989, 1991, 1994; Susman and Creel, 1979; Susman and Stern, 1979; Susman et al., 1984; Marzke, 1997). However, these inferences have been drawn in the absence of data that indicate 1) which muscles are most heavily recruited during Oldowan tool-making, and 2) which skeletal features may be relied upon as predictors of the relative size and moment arm lengths of these muscles.

In the experiments reported here, we directly sought such data from the perspective of tool-making, as a necessary preparation for detailed examinations of fossil bones. Using electromyography (EMG), we identi-

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fied muscles that are recruited repeatedly at high levels when a hammerstone held by one hand strikes flakes from a core held in the other hand. Our assumption is that the most strongly recruited muscles are likely to have generated recognizable periosteal reactions at their attachment sites which could be identified in hand bones of early hominid tool-makers. This assumption is currently being tested in our laboratory.

In a related kinematics experiment (Marzke et al., submitted), we found that each thumb muscle, with the exception of the transverse adductor pollicis muscle, has a significantly larger dynamical moment arm in humans than in chimpanzees for at least one axis of rotation and one thumb joint. Thus, we now have a potential additional source of evidence in fossil hominid hands for stone tool-making capabilities, namely, the orientations and dimensions of skeletal features that determine the relative lengths of moment arms for the tendons of the muscles that are strongly recruited. A larger moment arm gives a muscle greater mechanical advantage, maximizing the potential of the muscle to exert torque while minimizing the number of muscle fibers needed, thus conserving the energy required for repetitive muscle contraction. Evolutionary increase in moment arm lengths thus would have enhanced habitual, effective, hard hammer percussion manufacture of stone tools, well known by practitioners to make heavy demands on several groups of hand muscles. How large these demands are, and upon which muscle groups, are set forth in the following sections.

## MATERIALS AND METHODS

The experiments were conducted in the gait analysis facility of the Mayo Clinic Orthopedic Biomechanics Research Laboratory in Rochester, Minnesota. The doctors who inserted the electrodes and the staff who coordinated data acquisition are all regular participants in the EMG analysis of clinical disorders of patients who come to the facility, including patients with problems in the hand.

### Subjects

The three authors from Indiana University were the subjects of the experiments.

Toth (Subject 1) was selected because he has been manufacturing Oldowan tools by hard hammer percussion regularly for nearly 20 years. It can be expected that in the course of these years he has settled into grips and hand movements that expedite the production of Oldowan flakes with minimum muscle fatigue and pain-producing stress to the joints. Schick (Subject 2) was selected because she also learned to replicate Oldowan tools and has continued the activity over many years. Because her tool-making activity has been more sporadic, it was anticipated that she might use some muscle recruitment patterns that differ from those of Toth. Hunt (Subject 3) served as the novice tool-maker, whose muscle use we thought might differ still more and might thereby put into relief the patterns in the more experienced subjects, and those most likely to have been arrived at by early hominids that habitually made Oldowan tools.

Toth and Schick are right-handed and Hunt is left-handed. The terms "dominant" and "nondominant" will therefore be applied to the specific hand used by a subject. Dominant hand length and breadth were  $18.7 \times 8.6$  cm in Subject 1,  $17.6 \times 8.2$  cm in Subject 2, and  $19.6 \times 8.3$  cm in Subject 3.

The importance of testing at least three subjects with differing expertise is that muscle recruitment patterns found to be common to all of them are likely to be patterns that are most compatible with human hand morphology. The common patterns suggest to us the grips and associated hand musculoskeletal features that should be targeted for analysis in the development of biomechanical models for the functional interpretation of similar morphology in ancestral hominids.

### Stone tool materials

Stones collected from an Indiana quarry were used for the experiments. They were medium-grained, river-worn cobbles with small crystal inclusions which can be flaked equally well in any direction, closely similar in composition to stones used by the Oldowan tool-makers.

### Muscles and activities monitored

Seventeen muscles were monitored with EMG in the course of the study (Table 1), 16

TABLE 1. *Muscles monitored in the EMG experiments*

Extrinsic muscles	Abbreviation	Intrinsic muscles	Abbreviation
Flexor carpi ulnaris	FCU	Flexor pollicis brevis	FPB
Flexor pollicis longus	FPL	Opponens pollicis	OP
Flexor digitorum profundus 2	FDP2	Adductor pollicis (transverse)	APT
Flexor digitorum profundus 5	FDP5	Dorsal interosseus 1	D1
Extensor digitorum communis 2	EDC2	Palmar interosseus 1	P1
Extensor digitorum communis 5	EDC5	Palmar interosseus 3	P3
Extensor pollicis brevis	EPB	Flexor digiti minimi	FDM
Extensor pollicis longus	EPL	Abductor digiti minimi	ADM
		Opponens digiti minimi	ODM

functioning on the hand and one (flexor carpi ulnaris) exclusively on the wrist. Eight are extrinsic and nine are intrinsic muscles. Ten channels of A/D conversion were used for receiving muscle signals. One set of ten muscles in the dominant hand and a slightly different set of ten muscles in the nondominant hand were monitored in the first experiment. A year later, a third set of muscles was monitored in both hands of Subjects 1 and 2, including four muscles that were not monitored in Subject 3 in the first experiment (flexor digiti minimi, adductor pollicis (transverse portion) and the first and third palmar interosseous muscles), and four muscles that were monitored for only one hand in Subject 3 (the extensor pollicis longus muscle in the dominant hand and the flexor pollicis brevis, first dorsal interosseous, and extensor pollicis brevis muscles in the nondominant hand). Records were obtained from only one hand at a time in each session.

By monitoring a large number of muscles, we were able to identify those muscles that are most consistently recruited at high levels to control stones during hard hammer percussion. This information allows us to concentrate in our biomechanical analyses on those regions of the hand skeleton that are the major foci of stresses associated with stone tool-making and are therefore most likely to reveal traces of this activity in fossils.

Selection of the muscles was based on several criteria. First, muscles known to leave obvious marks of their attachments on bones (including fossils) were preferred (OP, ODM, FPL, D1 (muscle abbreviations are given in Table 1); see Napier, 1959, 1962; Day and Scheuer, 1973; Musgrave, 1971; Trinkaus, 1983; Susman, 1988b, 1989). Second, we targeted those whose moment arms are believed to be enhanced by distinctively

human skeletal configurations (FCU, FPL, FPB, FDM, ODM; see Napier, 1959; Stern and Susman, 1983; Trinkaus, 1983; Ricklan, 1987; Sarmiento, 1988). Third, we focused on muscles of the thumb, index, and fifth finger that seemed to us most likely to be strongly recruited in tool-making, based on frequent grips and hand movements observed in our earlier study of tool-making (Marzke and Shackley, 1986). We were guided in muscle selection (and later in the interpretation of our data) by predictions of muscle interaction in moving and stabilizing link systems of the hand and wrist, based on the detailed functional analysis of hand muscle functions by Brand and Hollister (1993) and on EMG studies which recorded muscle signals during prescribed grips and movements (Forrest and Basmajian, 1965; Hall and Long, 1968; Close and Kidd, 1969; Long et al., 1970; Long, 1981; Cooney et al., 1985; Hepp-Reymond et al., 1996; Maier and Hepp-Reymond, 1995). Fourth, muscles discussed in other functional analyses of hands in connection with grips used in tool-making were included (FCU, FPL; see Ricklan, 1987; Susman, 1988a,b).

Each subject sat on a stool and struck flakes from a core held in the nondominant hand with a hammerstone held in the dominant hand. Flake removal continued until the core was small, allowing for the observation of changes in grip of the core accompanying changes in its size.

All subjects used the same hammerstone for each session and selected cores of roughly the same size and shape for reduction. In the first year's experiment the hammerstone was  $10 \times 8 \times 6$  cm and weighed 605 g. The next year there were two sessions for the dominant hand of both subjects, one with a large hammerstone ( $9 \times 9 \times 7$  cm, 780 g) and the second with a small hammerstone

(7 × 6 × 6 cm, 400 g), but only the small hammerstone was used when the nondominant hand was monitored.

#### Procedures for recording muscle recruitment and tool-making activities

**Electrode placement and signal transmission.** Insulated nichrome intramuscular wire electrodes (0.03 mm in diameter) were inserted into the muscles with a 25 gauge hypodermic needle. Entry points were selected that would not interfere with the grips and hand movements. Electrode placement was verified by isolated muscle function testing. The signals were monitored closely during the activities since there was a potential for electrode displacement because of the nature and forcefulness of the activities. Displacement proved to be rare but was corrected whenever observed and the activities were repeated.

Eleven channels of data were collected at 728.36 samples per second per channel. The EMG signals were amplified by a preamplifier (Motion Lab Systems, Inc., Baton Rouge, LA) worn by the subject in a backpack. From the preamplifier the signals went to an interface unit (Motion Lab Systems) and then to an A/D converter operated from an IBM-compatible personal computer. The A/D converter was controlled through CODAS (computer-based oscillograph and data acquisition system) software. Both the A/D converter and software are products of DATAQ Instruments Inc., Akron, Ohio.

**Hammerstone strike recording.** Ten of the 11 channels carried signals for the muscles. The eleventh channel carried signals from a microphone, placed near the subject and connected to the A/D converter. The microphone detected the sounds produced by strikes of the hammerstone on the core. The pulsed strike waveforms were displayed on the computer screen above the ten muscle channels, enabling observation of muscle signals relative to the time of strike.

**Videotaping.** The subject was videotaped during the activities using a Sony Trinitron video camera recording at a speed of 60 frames/second. The muscle signals and video images were simultaneously transmitted to a screen and displayed side by side. Reflex-

ive markers were placed over the radial and ulnar styloid processes and over the first, second, third, and fifth metacarpal heads, proximal phalanges, and distal phalanges to facilitate qualitative observations of thumb, finger, and wrist movements.

#### Measurement of force potential

Prior to each tool-making session, we measured the maximum force of isometric contraction for all muscles containing electrodes using both the grasp meter and the pinch meter with the NK Hand Assessment System. For each precision grip, the pinch device was enclosed in an insulating pad and placed between a stone and the thumb or fingers (for a table of human precision grips, see Marzke, 1997). The maximum signal for each muscle provided a baseline against which muscle signals from the tool-making activities were compared. When activity signals exceeded the isometric ones, the maximum activity signal was used as the baseline.

#### Data analysis

The signals from muscles recruited during the tool-making activities and the isometric sessions were rectified, filtered, and then analyzed using WINDAQ software. The analysis of muscle signals for each tool-making session was restricted to data collected over a range of 16 strike signals. Each muscle signal at strike and each peak muscle signal in a strike cycle was compared in size with the baseline maximum signal registered for the muscle in the isometric session (or in some cases, reached during the activity) and was assigned to a percentage level of none (0–5%), low (6–30%), moderate (31–55%), marked (56–80%) or maximum (81–100%). These strike and peak levels were then entered into a spreadsheet, along with the time of each signal, for use in the comparison of patterns and levels of muscle recruitment among the three subjects.

Before the comparison, a modal level (representing central tendency) was determined for each series of 16 strike signals and for each series of 16 peak signals for each muscle of both hands in all subjects and sessions. Each series of signals was regarded as a series of 16 trials. Peak signals

for trials varied by two levels in 48% of the series. Variation was by three levels in 27%, while 20% had a single level. Variation was over four levels in 5% of the series.

Results of the comparisons were evaluated and categorized as follows.

Category 1: Muscles that exhibit marked and maximum modal peak levels in all three subjects for one or both hands are considered the most important indicators of habitual muscle recruitment during stone tool-making in early hominids. In some cases, the importance of these muscles is emphasized by their strong recruitment in *multiple* sessions for Subjects 1 and 2. These we feel are the muscles that direct us to the regions of the hand and wrist skeleton that are most likely to reflect tool-making capabilities in early hominids.

Category 2: Muscles that exhibit high modal peak levels in Subjects 1 and 2 also have strong implications for early hominid muscle use during Oldowan tool-making. The category is limited in number, but includes the two experienced subjects.

Category 3: Muscles whose modal peaks are below the marked level in Subject 1, or which dropped below marked/maximum levels in two of the three sessions for Subject 1, are considered less likely potential stressors of fossil hominid hand skeletons than those exhibiting consistently higher levels.

The reason for our emphasis on data from Subject 1 is that his many years of tool-knapping are likely to have led him to muscle recruitment patterns that are most similar to those most effective and economical in early hominid tool-makers who practiced these activities habitually.

The very specific purpose of this study should be kept in mind. The relative importance of muscles was judged on the basis of their potential contribution to stress on the hand bones, since it is the bones that must serve as clues to tool-making capabilities in fossil species. This weighting of muscles in relative importance is different from weighting that might be applied if we were examining their relative roles as prime movers, antagonists, synergists, and fixators in given activities. A muscle that peaks at a low level may be an essential contributor to fixation of a proximal joint during forceful action by

another muscle on a more distal joint, but its role is not likely to be recorded by stress markers at its attachment points. However, its role could be reflected by relatively larger *tendon moment arms* that may have increased in the course of human evolution. The increase would have been advantageous for keeping energy requirements at the lowest possible level for contraction of the full complement of muscles during tool-making and other manipulative activities.

## RESULTS

### Grips

Grips were identified at each of the 16 strikes for all activities and all subjects. There was consistency among subjects in the nature and range of grips. To some extent this is to be expected, because Subjects 2 and 3 had learned some techniques from observing Subject 1. However, the grips are very similar to those used independently by Shackley in a preceding, unrelated experiment (Marzke and Shackley, 1986).

The hammerstone was invariably held by a precision three-jaw chuck grip (Marzke, 1997) or by modifications of this grip. Subject 1 tended to place the index finger near the third finger, where it avoided direct vertical reaction forces of the core. In all subjects, the side of the fourth finger buttressed the side of the hammerstone and the fifth finger buttressed the fourth for all hammerstone grips (Fig. 1).

The core was held primarily by precision cradle grips (Marzke, 1997), involving a variable number of fingers depending on the core's size (Fig. 2). The palmar aspects of the fingers were oriented upward, stabilizing the base of the core against downward blows by the hammerstone. The flaking edge of the core rested on the distal finger pads or slightly overhung them. The larger cores were pressed by the volar aspects of the fingers against the volar aspect of the free thumb and the thenar side of the palm. As the cores became smaller, either the volar pads of the fingers and the opposed free thumb maintained the grip or the core was supported by the volar pads of the fingers against an adducted free thumb and thenar area of the palm. Frequently, the wrist was adducted and flexed, so the flake-removal

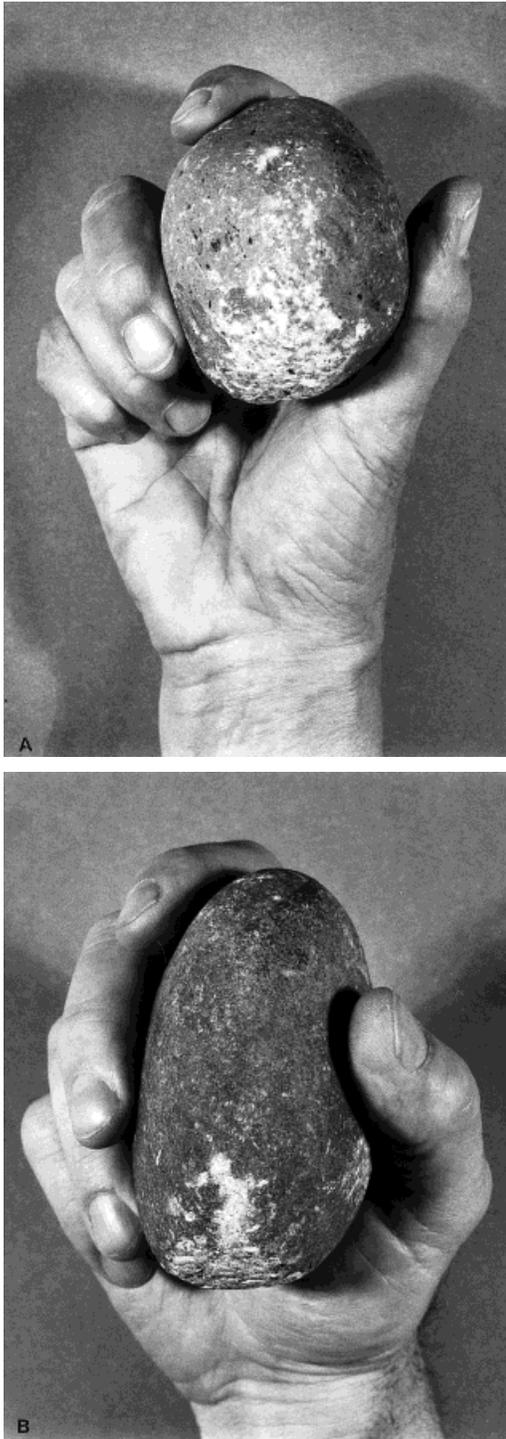


Fig. 1. Grips used for hammerstones. (A) Three-jaw chuck full finger grip of small hammerstone. (B) Three-jaw chuck full finger grip of large hammerstone, with fourth finger buttress. Note the somewhat lateral position of the index finger in (B), typical of the grip by Subject 1.



Fig. 2. (A) Grips used for cores. Cradle five-jaw grip of large core. (B) Cradle three-jaw grip of small core.

surface faced the knapper. The hammerstone strike of larger cores was usually at a position on the core above the third-to-fifth finger distal pads. For smaller cores, the thumb opposed the radial two fingers and flakes were removed above these fingers, while the fourth and fifth fingers were curled out of the way.

The data confirm overwhelmingly an earlier finding of Marzke and Shackley (1986) that the precision grip between the thumb and volar pad of the index finger simply is not recruited during Oldowan stone tool-making.

#### Muscle recruitment

All peak muscle force levels reported below are modal levels, shown for all muscles of the dominant hand in Table 2 and for the nondominant hand in Table 3. The muscles are grouped in their order of importance as indicators of prehistoric muscle recruitment, based on the criteria in the Materials and Methods section on data analysis. It is interesting to note that only three of the ten

TABLE 2. Modal peak levels of all muscles monitored: dominant hand

Subject/ session <sup>1</sup>	Muscle														
	FPB	OP	D1	P1	APT	FDM	ADM	ODM	P3	FCU	FPL	EPL	EPB	FDP2	FDP5
1/1	mrk	mrk	max				max	max		max	mrk		mod	mrk	mrk
1/2	mrk		max	max	low	mrk			low		low	mod	low	max	
1/3	mrk		max	max	low	mrk			mod		low	mod	mod	mod	
2/1	mrk	mrk	mrk				max	low		max	mrk		mrk	max	max
2/2	max		max	mod	max	max			max		max	max	mrk	mrk	
2/3	max		max	mod	max	max			max		max	max	max	max	
3/1	mrk	mod	mrk				mod	max		mrk	mrk		mod	mrk	mrk

<sup>1</sup> Session 1: 1995; session 2: 1996, small hammer; session 3: 1996, large hammer.

muscles that peaked consistently at these high levels were extrinsic muscles (FCU, FDP2, and FDP5).

**Muscles with marked/maximum modal peaks in one or both hands of all subjects (Category 1).** The FPB muscle peaked at marked/maximum levels in the dominant hand of all subjects, including all three sessions for Subjects 1 and 2. All subjects exhibited marked/maximum levels of the FCU in the single sessions for both hands. In the dominant hand, the D1 peak mode was maximum for all three sessions in Subjects 1 and 2 (with the exception of one session of marked for Subject 2), and was marked for Subject 3 in his single session. The FDP2 muscle of the dominant hand was at marked/maximum levels in two of three sessions for Subject 1, in all three sessions for Subject 2, and in the single session for Subject 3. The FDP5 muscle contracted in the dominant hand of all subjects during one session each at marked/maximum levels.

**Muscles with marked/maximum modal peaks in one or both hands of the two experienced subjects (Category 2).** For the sessions in which all three subjects participated, two muscles fall into Category 2. In the dominant hand of the two experienced subjects, the OP peaked at the marked

level while the ADM was recruited at the highest level (peaks for both muscles were moderate in Subject 3). For the sessions in which only the two experienced subjects participated, four muscles have modal peaks at the marked/maximum levels. In the non-dominant hand, the APT and P1 muscles peaked at maximum level and the FPB at marked/maximum levels. The FDM muscle was similarly strongly recruited, in this case for the dominant hand across two sessions and for the nondominant hand in the one session for which it was recorded.

**Muscles with modal peaks below the marked level in Subject 1 (Category 3).** The FPL of the dominant hand in Subject 1 ranged from marked in the first session to low in the next two sessions. In Subject 2 it ranged from marked in the first session to maximum in the next two sessions. It was marked in Subject 3 for the single session in which it was monitored. In the nondominant hand, FPL never reached a maximum level in any subject. It was marked in one session for Subject 2, and otherwise was at a moderate level for Subjects 1 (two sessions), 2 (one session), and 3 (one session).

The EPL, EPB, and P3 muscles were all at moderate/low levels in both hands of Subject 1, compared with marked/maximum levels

TABLE 3. Modal peak levels of all muscles monitored: nondominant hand

Subject/ session <sup>1</sup>	Muscle																
	FPB	OP	D1	P1	APT	FDM	ADM	ODM	P3	FCU	FPL	EPL	EPB	FDP2	EDC2	FDP5	EDC5
1/1		mod					mrk	low		mrk	mod	mod		low	low	mod	none
1/2	mrk		low	max	max	mrk			low		mod	none	low	low			
2/1		mrk					NA <sup>2</sup>	max		mrk	mod	mrk		max	max	mrk	mrk
2/2	max		mrk	max	max	max			mod		mrk	max	max	max			
3/1		max					mrk	max		max	mod	mod		mrk	mod	mrk	mrk

<sup>1</sup> Session 1: 1995; session 2: 1996, small hammer.

<sup>2</sup> Missing data.

TABLE 4. Modal strike levels of all muscles monitored: dominant hand

Subject/ session <sup>1</sup>	Muscle														
	FPB	OP	D1	P1	APT	FDM	ADM	ODM	P3	FCU	FPL	EPL	EPB	FDP2	FDP5
1/1	mod	mod	mrk				mrk	mrk		max	mod		low	mod	mod
1/2	mod		mod	mrk	low	mod			none		low	low	low	mod	
1/3	mod		mrh	mrk	low	mod			low		low	low	low	low	
2/1	mrk	mod	low				mrk	low		mod	mod		low	mod	mrk
2/2	mod		mrk	low	max	mrk			mrk		mrk	max	low	mod	
2/3	mrk		mrk	low	max	mrk			mrk		mrk	max	mrk	mod	
3/1	mod	low	mod				low	mrk		low	low		low	mod	low

<sup>1</sup> Session 1: 1995; session 2: 1996, small hammer; session 3: 1996, large hammer.

in Subject 2 (with the exception of moderate for P3, nondominant hand) and moderate in Subject 3 for the EPL and EPB sessions in which he participated. In the nondominant hand, EDC2 peaked at a low level and EDC5 was not recruited at all in Subject 1. These muscles peaked at moderate-to-maximum levels in Subjects 2 and 3.

Finally, it should be noted that the ODM muscle does not fall into any of the three categories. It peaked at the maximum level in the dominant hand of Subject 1, but since the second subject exhibiting a high level was #3, rather than #2, the muscle does not meet the criterion of high level recruitment in the two experienced subjects.

#### Patterns of muscle recruitment

There is a consistent tendency in all three subjects for the peak levels of muscle activity during the strike cycle to exceed the levels recorded exactly at strike (compare Table 4 with Table 2 and Table 5 with Table 3). There is also a consistent tendency in the dominant hand for intrinsic thumb/index finger muscles (FPB, OP, D1, P1), FDP2 and FDP5 to peak before strike, and for the fifth finger intrinsic muscles (FDM, ODM, ADM) to peak shortly after strike, although in several cases the latter muscles peak at

strike (Table 6; Fig. 3). The EPB also regularly peaks after strike.

In the nondominant hand the FDM, ADM, FPB, APT, and EDC2 consistently peak before strike and FPL, D1, EPB, and FCU after strike (Table 7).

In all subjects the OP, ODM, and to some extent ADM of both hands continue activity at lower levels throughout the cycle. The FCU is always active at the same time as ADM in the nondominant hand.

It can be seen from Tables 6 and 7 that the remaining muscles in the two hands are less consistent in recruitment sequence across subjects and across sessions for single individuals.

#### DISCUSSION

We anticipated that in this EMG study of complex manipulative activities there would be variability in degrees and patterns of muscle recruitment among individuals for a given activity and even for single individuals repeating an activity over several trials and several sessions. It has been shown, for example, that there is no strictly coherent interindividual pattern of muscle synergies in humans for clearly specified manipulative tasks, even when kinematic invariances are observed in these tasks. Instead, the central

TABLE 5. Modal strike levels of all muscles monitored: nondominant hand

Subject/ session <sup>1</sup>	Muscle																
	FPB	OP	D1	P1	APT	FDM	ADM	ODM	P3	FCU	FPL	EPL	EPB	FDP2	EDC2	FDP5	EDC5
1/1		mod					mrk	low		mod	mod	mod		low	low	low	none
1/2	mrk		none	mrk	mod	mrk			low	low	low	none	none	none	mod	low	mod
2/1		mod					NA <sup>2</sup>	mod		low	low	mrk		low	mod	low	mod
2/2	max		mod	mod	mrk	max			low	low	max		mod	mrk			
3/1		mod					low	mrk		mod	low	mod		mod	mod	mod	mrk

<sup>1</sup> Session 1: 1995; session 2: 1996, small hammer.

<sup>2</sup> Missing data.

TABLE 6. Percentage of trials for which peak activity was pre, post, or on strike: dominant hand<sup>1</sup>

Muscle	Subject 1			Subject 2			Subject 3		
	Pre	Post	On	Pre	Post	On	Pre	Post	On
FPB	71	27	2	94	4	2	94	6	0
OP	94	6	0	88	12	0	81	19	0
D1	63	31	6	100	0	0	88	6	6
P1	63	31	6 <sup>2</sup>	100	0	0			
FDP2	77	19	4	56	44	0	63	37	0
FDP5	75	13	12	94	6	0	63	37	0
FDM	16	84	0	31	56	13			
ODM	38	50	12	38	56	6	6	81	13
ADM	19	63	18	56	38	6	44	50	6
EPB	40	60	0	17	79	4	19	81	0
EPL	9	84	7	56	38	6			
FPL	46	48	6	81	19	0	0	100	0
APT	38	56	6	78	22	0			
P3	3	97	0	47	53	0			
FCU	88	12	0	81	19	0	19	81	0

<sup>1</sup> Percentage calculated for total number of strikes across sessions. The number of sessions varied from 1-3.

<sup>2</sup> Although the percentages for D1 and P1 are the same across sessions 1 and 2 for both subjects, they are different within sessions, indicating that there was not an identity of signals caused by close proximity of the muscles.

nervous system appears to use flexible short-term combinations of muscles for the tasks (Maier and Hepp-Reymond, 1995; Hepp-Reymond et al., 1996). However, it was

predicted that some muscles would be recruited consistently at high levels during hard hammer percussion manufacture of Oldowan tools, indicating that these muscles

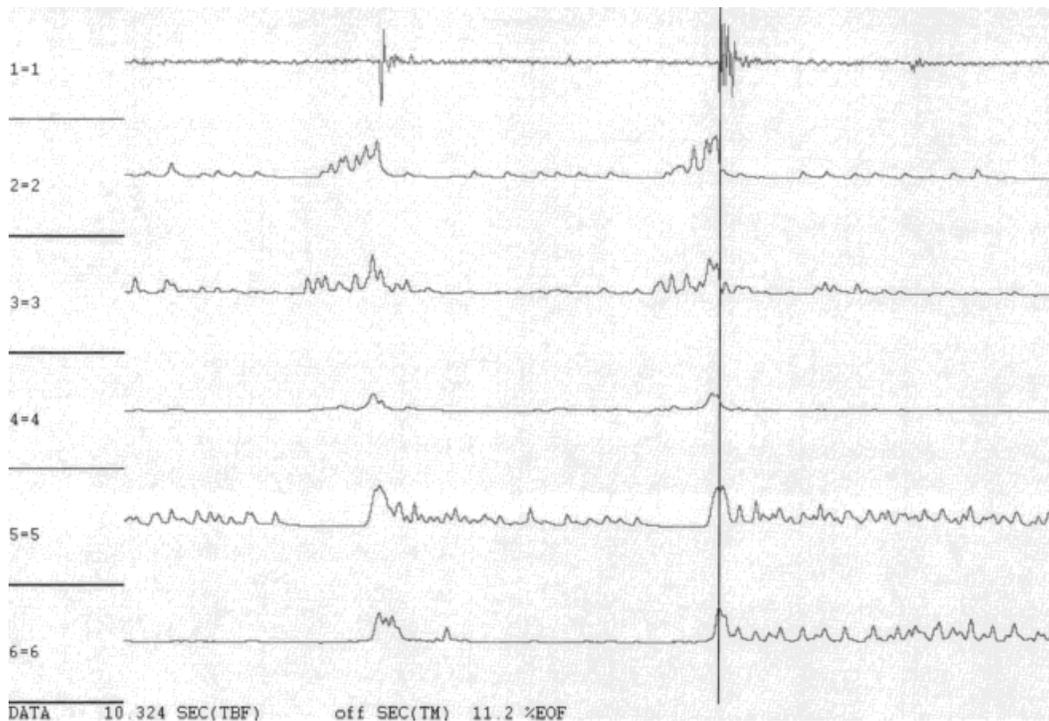


Fig. 3. WINDAQ screen display. Hammerstone strike signals are on the top line, followed below by signals for D1 (line 2), OP (3), FPB (4), ODM (5), and ADM (6). The vertical line runs through the beginning of a strike signal. Note that the peaks of the three intrinsic thumb muscles (D1, OP, FPB) precede the strike line and the peaks of the intrinsic fifth finger muscles are after strike (ODM) and at strike (ADM).

TABLE 7. Percentage of trials for which peak activity was pre, post, or on strike: nondominant hand<sup>1</sup>

Muscle	Subject 1			Subject 2			Subject 3		
	Pre	Post	On	Pre	Post	On	Pre	Post	On
FDM	94	6	0	75	25	0			
ADM	63	31	6	100	0	0	50	50	0
FPB	56	31	13	56	44	0			
APT	56	44	0	75	25	0			
EDC2	69	25	6	100	0	0	88	6	6
FPL	31	69	0	38	62	0	25	75	0
D1	0	94	6	25	75	0			
EPB	6	94	0	31	69	0			
FCU	25	75	0	0	100	0	19	81	0
EPL	38	62	0	59	41	0	50	50	0
FDP2	6	94	0	47	53	0	50	50	0
FDP5	63	37	0	12	88	0	44	56	0
EDC5	6	88	6	88	12	0	38	62	0
OP	94	6	0	19	81	0	19	81	0
P1	75	25	0	0	100	0			
P3	19	81	0	75	25	0			
ODM	31	69	0	0	100	0	50	44	6

<sup>1</sup> Percentages calculated for total number of strikes across sessions. The number of sessions varied from 1–2.

are likely to have become important components of flexible muscle synergies as early hominids became increasingly dependent on hard hammer percussion manufacture of Oldowan tools. It was also hoped that patterns might emerge in the recruitment of muscles associated with distinctive patterns of skeletal morphology in humans, which might lead to hypotheses explaining the origins of the distinctive features.

It turned out that, indeed, five muscles were consistently strongly recruited (at levels of marked to maximum) in at least one hand of all three subjects (FPB and FCU in both hands; D1, FDP2, FDP5 in the dominant hand). These form our top category of importance as evidence for likely high-level muscle recruitment in fossil hominid tool-making species.

Two additional muscles (OP and ADM of the dominant hand) were at marked/maximum levels in the two experienced subjects, compared with a moderate level in the third subject. Although by our criteria this result places the two muscles in Category 2, it is noteworthy that these are the only two trial series in which Subject 3 differed when Subjects 1 and 2 exhibited marked/maximum levels, and the difference was by only one level.

Three additional muscles peaked at high levels for the two experienced subjects in the sessions that did not include Subject 3 (also Category 2): FDM in both hands and APT

and P1 at maximum level in the nondominant hand. The FPB muscle, which peaked at marked/maximum levels in the dominant hand of all subjects, also peaked at these high levels in the nondominant hand of the two subjects for whom it was monitored.

Of this total group of ten muscles (one in both categories, four in Category 1, and five in Category 2), four are in the region of the fifth finger and six are in the thumb/index finger region. Only three (FCU, FDP2, and FDP5) are extrinsic muscles.

Interesting patterns in the recruitment of these muscles were discerned, in addition to consistencies in the levels of activity. The possible relevance of these findings to the functional interpretation of hand structure in fossil hominids is discussed below.

#### Distribution and sequence patterns of strongly recruited muscles

In the nondominant hand holding the core, the fifth finger plays critical roles in 1) maneuvering the core into position for removing each flake, and then 2) stabilizing the core against impact by the hammerstone. Frequently, the hammerstone strikes downward right over the fifth finger pad, which is directed upward and cradles the base of the core, whose edge lies either directly above the finger pad or slightly overhanging it. The fifth finger is flexed and stabilized at the metacarpophalangeal and carpometacarpal joints by the FDM and

ADM and is held extended at the more distal joints, providing maximum contact of the volar skin with the core. (Note that proximal and distal interphalangeal extension is a natural accompaniment to contraction of the ADM because this muscle sends a tendon to the extensor expansion.) As the core is reduced in size, flake removal moves toward the levels of the fourth and third fingers and the fifth finger curls out of the way.

In the dominant hand, the fifth finger buttresses the fourth finger, which in turn supports the lateral side of the hammerstone. Flexion of the distal phalanx of the fifth finger by the FDP5 keeps it clear of the striking surface, while contraction of the intrinsic muscles draws the fifth finger against the fourth finger and stabilizes the fifth carpometacarpal and metacarpophalangeal joints.

The FCU appears to play an important role in functions of the ADM muscle. It is always contracting in the nondominant hand when the ADM is in action. Since both muscles attach to the pisiform bone, whose joint with the triquetrum allows approximately 1 cm of movement, contraction of the FCU is necessary to stabilize the pisiform for effective ADM action (Brand and Hollister, 1993). The ADM abducts and stabilizes the fifth finger carpometacarpal and metacarpophalangeal joints of the nondominant hand when the finger positions and then stabilizes the core against displacement by hammerstone strike. The FCU usually peaks after strike, flexing and adducting against downward displacement of the core by the hammerstone.

The FCU function of wrist flexion/adduction was also important in the dominant hand of Subjects 1 and 2. The muscle peaked when the wrist flicked, accelerating the stone immediately prior to strike. However the wrist was maintained more in line with the forearm in Subject 3 and FCU peaked after strike when the subject flexed and adducted the wrist and rotated the hammerstone 90 degrees before beginning the upward swing.

All but one of the thumb/index finger muscles with marked to maximum peaks (FPB, D1, OP, P1, APT, and FDP2) are intrinsic muscles, acting on the trapeziometacarpal and both metacarpophalangeal

joints. Since nearly half of D1 originates along the proximal ulnar shaft of the first metacarpal (Linscheid et al., 1991), it is probably functioning not only to flex and abduct the index finger but also (when it contracts with FPB) to stabilize the thumb metacarpal against the pull of FPB, as predicted by Brand and Hollister (1993). These two muscles, together with OP, tend to peak prior to strike in the dominant hand, which is wielding the hammerstone with a three-jaw chuck precision pinch grip. The FDP2 muscle functions at the same time relative to strike, securing the index finger component of the grip. In the nondominant hand, the APT tends to peak at the same time as FPB relative to strike, in keeping with the functional pattern predicted by Brand and Hollister (1993). Although P1 is strongly recruited in the nondominant hand, the relative timing of its strongest contraction is not clearly predictable.

The data on muscle peak sequence indicate that the muscles at the radial side of the dominant hand prepare the hammerstone for a forceful strike and then relax the grip right at strike, minimizing the upward reaction force of the core on this part of the hammerstone hand. Following strike (or at strike), muscles on the ulnar side of the dominant hand help to resist displacement of the hammerstone by the core reaction force and maintain the grip as the arm is raised for the next cycle.

In the nondominant hand, the FDM and ADM consistently peak before strike, when the finger is flexed at the metacarpophalangeal joint with the phalanges extended under the core, performing a crucial function of stabilizing the core against the force of the hammerstone blow. Peak contraction by the FPB and APT muscles at the same time relative to strike apparently maintains pressure of the thenar region against pressure by the hypothenar region.

The distribution and sequence patterns of the strongly recruited muscles lead to the conclusion that an important source of the distinctively human ability to control cores and hammerstones *by one hand* lies in the intrinsic muscles at the margins of the hand. Paleoanthropologists therefore need to extend their focus beyond the extrinsic flexor

pollicis longus muscle to skeletal features that reflect the size and moment arms of these intrinsic muscles. In particular, features enhancing torque of the fifth finger muscles and tolerance of load associated with their strong contraction were probably as important to early tool-making hominids as features relating to the high recruitment of intrinsic muscles in the thumb/index region. The probable importance of the fifth finger in the power ("squeeze") grip has been discussed previously (Marzke et al., 1992), but our findings here suggest that use of the precision grips associated with forceful manipulation of stone tools in hard hammer flake removal may also have been a significant factor early in the evolution of the hominid hand.

#### Flexor pollicis longus / extensor pollicis brevis functions

It is interesting that the FPL muscle was not consistently strongly recruited at high levels in any subject for the nondominant hand, or in our most experienced subject (#1) for either hand during strong precision pinch grips in the tool-making experiments. Maier and Hepp-Reymond (1995) also found in their EMG analysis that the FPL muscle is not a primary contributor to pinch grips. There are two possible, related explanations for this finding, suggested by Subject 1, who actually exhibited the lowest overall EMG activity for the FPL muscle in our sample (Fig. 4). First, he has found that maintenance of an *extended* distal interphalangeal joint of the thumb enhances his grip by providing contact between the full surface of the free thumb and the stone. (Note that distal interphalangeal extension of the thumb is a natural accompaniment to metacarpophalangeal flexion when the thumb moves into opposition to the fingers, because both the abductor pollicis brevis and adductor pollicis muscles send tendons to the extensor expansion.) Second, he has also found that his thumb muscles soon become fatigued when he uses a firm pinch grip involving only the distal thumb pad. Fatigue may be attributed in part to the small moment arm of the FPL, compared with the larger intrinsic muscle moment arms at the more proximal thumb joints reported by

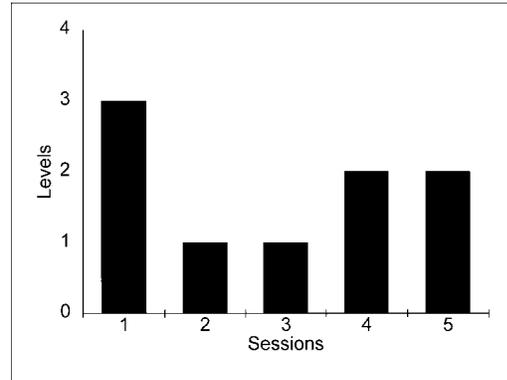


Fig. 4. Peak level modes for FPL activity in each of five experimental sessions for Subject 1. The dominant hand is shown in sessions 1–3 and the nondominant hand in sessions 4–5. Level 1: low; level 2: moderate; level 3: marked; level 4: maximum.

Smutz et al. (submitted). It has been noted by Brand and Hollister (1993) that use of the FPL muscle for pinch requires much larger moments at the proximal joints than at the distal because of the need to maintain thumb stability. Thus, it seems likely that Oldowan tool-makers would have avoided pinch grips that required repeated high-level contraction of the FPL because these grips would have elicited greater thumb muscle contraction overall, leading to earlier onset of fatigue.

However, in tool-using activities monitored immediately after tool-making in our first experiment, we found that FPL was recruited by the dominant hand at consistently high levels in two of the three subjects (#1 and #2). The muscle peaked at the marked level when a power squeeze grip was used to wield a cylindrical digging stick, and at the maximum level when they clubbed with a cylindrical tool. This finding is consistent with the observation by Ohman et al. (1995) about the probable role of power gripping in the evolution of human thumb morphology.

It is also possible that manipulative activities other than tool-making and tool use may have been factors in the evolution of the hominid FPL apparatus. In this connection, we are examining thumb use among nonhuman primates, looking for possible correlates among their varied patterns of FPL musculoskeletal morphology and demands

of their manipulative and locomotor behaviors.

Like the FPL, the EPB muscle is more frequently present in humans than in great apes. It extends the metacarpophalangeal joint independently of the interphalangeal joint, and is thus able to maintain the metacarpophalangeal joint in extension while the distal phalanx is flexed by the FPL muscle (Ou, 1979, p. 17, indicates co-contraction of the FPL and EPB muscles during thumb interphalangeal joint flexion). This pattern raises the question of whether the two muscles might have increased in frequency together, with the evolution of early hominid manipulative behaviors requiring this combination of thumb joint positions. Three activities requiring the combination can be cited in support of an affirmative answer. First, the control of large cores by the non-dominant hand requires metacarpophalangeal extension by EPB while the distal interphalangeal joint flexes and extends independently in precision maneuvering of the core. Second, activities eliciting strong contraction of the FPL require stabilization by strong contraction of muscles at all positions around the metacarpophalangeal joint, including the EPB. Since hard hammer percussion manufacture of Oldowan tools does not seem to require this latter combination at high levels, other possible tool-making, tool-using, and foraging activities are being examined. (It is interesting to note that FPL and EPB both consistently peaked before strike during use of the cylindrical tool in digging, using the power squeeze grip.) Third, if the earliest stone tool-makers lacked modern human relative thumb proportions and/or large intrinsic thumb muscle torque potential, an FPL with relatively high torque potential, together with an EPB to help stabilize the metacarpophalangeal joint, might have contributed the torques needed to control stones by one hand against external forces, albeit with fatigue.

#### **Opponens pollicis/opponens digiti minimi functions**

The OP and ODM muscles were distinctive during the experiments in their tendency to contract in both hands throughout the strike cycle. These muscles both origi-

nate from the flexor retinaculum over the wrist, and contraction of one tends to draw the other into contraction (Forrest and Basmajian, 1965). They are important positioning muscles which cup the palm, accommodating the palm and fingers to varying shapes of the stones. They peak in activity when strong pinch grips require not only positioning but also stabilization of the carpometacarpal joints of the thumb and fifth finger during flexion of the metacarpophalangeal joints.

#### **Possible skeletal correlates of muscle function**

The results of the EMG experiments direct our attention to the fifth finger and thumb/index finger metacarpal regions as primary sources of evidence for habitual hard hammer percussion capabilities in early tool-makers. The intrinsic muscles, in particular, position the thenar and hypothenar regions of the palm, together with their phalangeal links, in accommodation to the shapes and sizes of the hammerstones and cores and they generate the force needed to maintain the grips as the hammerstone is accelerated and strikes the core. These are the regions that appear to sustain the greatest stress associated with repeated, strong intrinsic muscle contraction. Following are four types of skeletal morphology that might reveal evidence for strong recruitment of these muscles.

#### ***Large tendon and muscle moment arms.***

Data have recently been obtained on kinematic moment arms of thumb tendons in chimpanzees and humans (Marzke, 1997; Marzke et al., 1997a, submitted; Smutz et al., submitted), using methods developed at Mayo Clinic (Chao et al., 1989; An et al., 1991). The results show larger moment arms of all thumb muscles in humans except the transverse adductor pollicis muscle for at least one axis of rotation at one thumb joint. The differences are significant at the  $P = 0.02$  level and below. These findings justify 3-D quantitative comparison of contemporary and fossil hominid and great ape skeletal configurations that determine the relative sizes of these moment arms. This comparison is now in progress. Since the

experimental study showed in many cases a greater contribution of moment arms than muscle physiological cross-sectional areas to differences between the species in potential torque, reliable skeletal moment arm measurements will strongly improve our ability to recognize human-like intrinsic muscle torque capabilities (and, therefore, stone tool-making capabilities) in fossil hominids.

The larger moment arms in humans provide greater mechanical advantage to these muscles. Facility for economical, constant use of thumb and fifth finger intrinsic muscles in forceful pinch grips by each hand separately is essential for the one-handed control of stones required by habitual hard hammer percussion tool manufacture. Intrinsic muscle size is limited to some extent by the small surface areas available for muscle attachment in the hand bones. Extension of origins to adjacent muscle fascia is not a significant option, since it compromises the independent actions of muscles required for dexterous manipulative behavior.<sup>1</sup> Intrinsic muscle size is also restricted by limits to the size of the joint surfaces that must accommodate the high loads by the contracting muscles. It is therefore advantageous to have skeletal features that maximize the moment arms of these strongly recruited hand muscles, thus enhancing muscle torque without requiring further increase of muscle size.

Tool use involving the power squeeze grip may explain an interesting feature of thumb skeletal morphology in early hominids that enhances the FPL moment arm. The large volar fossa on the distal phalanx of fossil hominid species, which is reported to have been the insertion area of tendon fibers for an FPL muscle (Napier, 1962; Trinkaus, 1983; Susman, 1988b, 1989; Ricklan, 1990; Marzke, 1997), actually has been found to accommodate a sesamoid bone, which is

regularly present in the distal interphalangeal joint capsule of humans (Joseph, 1951) and raises the tendon above the center of joint rotation, providing leverage for FPL flexion of the distal phalanx (Marzke et al., 1997b).<sup>2</sup> Our recent dissections of the joint have shown that the sesamoid articulates with the proximal end of the distal phalanx at its anterior midpoint in humans and in other, nonhuman species. When the distal phalanx flexes, the sesamoid runs into the shaft of the proximal phalanx and the fossa of the distal phalanx abuts against the distal end of the sesamoid. The fossa is filled with areolar tissue, and in some cases with a fat pad. The FPL tendon inserts primarily into a ridge of bone that forms a horseshoe around the sides and distal end of the fossa. Thus, the size of the fossa may not necessarily reflect the size of the muscle in fossils; it probably does reflect the presence of a sesamoid, which would have aided in giving the muscle its reasonably large-sized moment arm.

***Relatively high first and fifth metacarpal robusticity.*** A comparison of the Hadar and Sterkfontein australopithecines with chimpanzees and humans shows that the Hadar australopithecines resemble chimpanzees in having a relatively gracile fifth metacarpal, whereas the Sterkfontein australopithecines resemble modern humans, in which the fifth metacarpal is the most robust of metacarpals 2–5 (Marzke et al., 1992). A systematic comparison of large samples of great apes and humans is needed to further explore these differences and to determine whether all apes have relatively gracile fifth metacarpals. An additional comparative cadaver study is needed to determine whether variations in fifth finger robusticity correlates with variations in fifth finger muscle size. The same complementary skeletal and

<sup>1</sup>In fact, dexterity in humans is enhanced by extensive differentiation of the thumb muscles. For example, a separate slip of the oblique adductor muscle, the first palmar interosseus, inserts into the extensor expansion of the thumb rather than into bone and capsule, and another probable offshoot of the oblique adductor muscle, the deep head of the FPB muscle, usually inserts exclusively into the radial sesamoid and the metacarpophalangeal joint capsule, rather than into the extensor expansion like the superficial FPB head (Linscheid et al., 1991). These muscle offshoots are seen in some monkey species, as well as in humans (Lewis, 1989).

<sup>2</sup>We have found a large sesamoid bone in the distal pollical interphalangeal joint capsule of *Papio cynocephalus*, together with a human-like attachment of the FPL tendon on the distal phalanx. A similar, proportionately smaller sesamoid bone was found in a specimen of *Pan troglodytes*, which has an FPL tendon with only tenosynovial attachment to radial fibers of the flexor pollicis longus muscle. In both a gibbon and a siamang thumb, the FPL tendon was observed to be raised slightly away from the joint by a thickening of the fibrous capsule. We suspect that additional nonhuman primate specimens, with and without a functioning flexor pollicis longus muscle, will exhibit a similar pattern.

cadaver studies are needed with regard to first metacarpal robusticity. If correlations are found among relative intrinsic muscle size and relative metacarpal robusticity, this skeletal feature could be an important indicator of tool-making capability in fossil hominids.

**Relatively large muscle stress markings on hand bones.** It has long been assumed that variations in the size of muscle markings on hand bones correlate with variations in hand muscle size in living species (see, for example, Susman's 1988b discussion of the opponens pollicis muscle, pp. 152 and 169). This assumption is currently being tested in our laboratory. Among the markings that are most interesting in connection with tool-making capabilities, and which should be possible to measure, are the D1 origin area on the thumb metacarpal and the OP and ODM insertion areas along the first and fifth metacarpal shafts.

The D1 origin area is important because of the apparent role these first metacarpal fibers play in stabilizing the metacarpal of the dominant hand during strong contraction of the FPB. Presence in a fossil hominid thumb metacarpal of both a large moment arm for the FPB muscle and a large origin area for D1 on the first metacarpal would imply habitual use of the hand in activities like hard hammer percussion manufacture of stone tools, since this activity elicits contraction of these muscles at high levels.

#### Evidence for asymmetries in muscle recruitment

There is evidence in the data for substantial differences between the dominant and nondominant hands in muscle recruitment. Differences of three levels were recorded in Subject 1 for D1, ODM, and APT (Fig. 5), and a difference of three levels (ODM) was found in Subject 2. Note that the higher levels were not restricted to the dominant hand. This finding indicates that clues to right- or left-hand dominance in samples of fossil hominid hands will need to be sought in skeletal features associated with specific muscle groups. The finding is consistent with our observations that 1) both hands are subjected to considerable stress when a stone

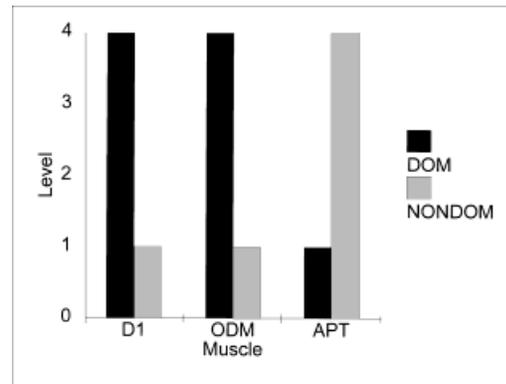


Fig. 5. Asymmetries in muscle recruitment. Peak level modes for three muscles are compared for the dominant and nondominant hands of Subject 1. Level 1: low; level 2: moderate; level 3: marked; level 4: maximum.

in one hand is struck by a stone in the other hand, and 2) both hands tire during hard hammer percussion manufacture of stone tools.<sup>3</sup> It is also interesting to note that there was a greater range of variability of peak levels and timing in the nondominant hand. Muscles of the nondominant hand account for five of the six trial series that exhibited a range of variation across four levels, and only half the muscles in the nondominant hand exhibited consistent peak timing relative to strike, compared with two-thirds in the dominant hand.

#### Evidence in muscle recruitment for economy in tool-making

We are impressed by the difference between Subject 1 and the other subjects in muscle recruitment levels. His activity signals were consistently lower relative to his maximum possible signals, often by two or three levels. His data account for the two cases in which muscle levels did not exceed the level of "none," 13 of the 14 occurrences of the low modal level, and 11 of the 21 moderate level occurrences, whereas Sub-

<sup>3</sup>It is interesting to note that the radiologist who read a CT scan of the hands of Subject 1 (our most experienced tool-maker), without any information about the background and occupation of the subject, inferred from the relative muscle development apparent in the scan that the subject was left-handed. In fact, the subject is right-handed, but apparently the many years of prehistoric tool replication have generated relatively greater development of at least some muscles in the nondominant hand that holds the core.

ject 2 exhibits the two highest levels for all muscles except P1 and ODM (dominant hand), and P3 and FPL (nondominant hand). Subject 1 also exhibited substantially less discernable muscle activity between strikes, except for the OP and ODM muscles. In Subject 3, almost all the muscles were continually active. Subject 2 was intermediate, with several muscles continually active. The difference probably reflects the many years of practice for Subject 1 (compared with less practice in Subject 2 and no practice in Subject 3), involving adjustments in the sensorimotor control of grip patterns and hand movements which minimize prolonged stress on the musculoskeletal system and exploit the larger moment arms of intrinsic muscles. We suspect that the grips and muscle recruitment patterns he has arrived at are quite likely to approach those of Oldowan tool makers, to the extent that these would have been facilitated by early hominid hand morphology.

The higher level of overall muscle recruitment by Subject 2 also may be explained in part by the smaller size of her hand, compared with that of the two male subjects.

### CONCLUSIONS

Based on the results of the experiments reported here, our conclusions are:

1. The primary muscles involved in hard hammer percussion manufacture of Oldowan tools are likely to have been the FPB, FDM, and FCU of both hands, the OP, D1, ADM, FDP2, and FDP5 of the dominant hand, and the APT and P1 of the nondominant hand. Five of these muscles (FPB, D1, FDP2, FDP5 of the dominant hand and FCU of both hands) had marked/maximum peak levels in all three subjects, constituting the first, most compelling category of evidence for their importance in Oldowan tool-making. The other five muscles had marked/maximum peak levels in the two experienced subjects, constituting our second category of strong implications for importance in tool-making. (This second group of five muscles includes OP, ADM, and FDM of the dominant hand and APT and P1 in the nondominant hand.) These ten muscles are probably the ones that would have secured the one-handed precision pinch grips of ham-

merstones and cores against the large external forces in stone tool-making, and would have stressed the joints with their strong contraction.

2. Skeletal features associated with the human FPL muscle are not likely to have evolved exclusively in association with use of precision pinch grips in tool-making activities. The muscle in the dominant hand of our most experienced tool-maker peaked at a high level during only one of three sessions, and its recruitment for all subjects was at relatively low levels in the nondominant hand. However, in the two experienced subjects it did peak at the two highest levels during use of the power squeeze grip of cylindrical objects for two tool-using activities, digging and clubbing.

Distal interphalangeal thumb joint morphology reflects the relative size of the FPL tendon moment arm, perhaps more clearly than the size (and relative force potential) of the FPL muscle. This morphology, together with thumb use in non-tool-making activities, should be reexamined comparatively in catarrhines before further inferences about tool-making and tool-using capabilities are drawn from the specific morphology of this region in early hominid thumb bones.

3. The high level of intrinsic muscle recruitment in Oldowan core reduction is likely to have been accommodated by adjustments in robusticity and in bone and joint configurations of the first, second, and fifth metacarpals relating to muscle force production and tendon moment arms (some during lifetime and others in the course of hominid evolution). A productive search for skeletal evidence of habitual Oldowan tool-making behavior would therefore be in the first, second, and fifth metacarpal regions.

4. Comparative data from subjects with different levels of experience in Oldowan tool-making clearly demonstrate the advantage of flexible muscle synergies, which were inferred by Hepp-Reymond et al. (1996) from the results of their controlled studies of human precision gripping. The ability to achieve economy through flexible, selective muscle recruitment in repetitive and stressful manipulative behaviors such as tool-making, illustrated by Subject 1, would have been advantageous to early hominids, just

as increased cerebral control of the forelimb postulated by Vilensky and Larson (1989) for early primates would have enhanced their increased forelimb use in feeding and other manipulative behaviors.

5. Finally, it is possible that clues to hand preference in fossil hominids may be sought in the future through skeletal features associated with specific and different sets of muscle groups in the right and left hands of fossil hominid samples. Both hands were submitted to large external and internal forces in hard hammer percussion manufacture of stone tools, but the stresses were different for each hand.

It should be kept in mind that the Oldowan tool-making activity analyzed in this report is only one in a wide range of manipulative activities that are likely to have been facilitated and enhanced by the distinctive patterns of hand morphology that emerged in the course of early hominid evolution. In fact, as noted in our discussion of FPL, we included in the experiments several tool-using activities (e.g., digging and clubbing), whose associated grips and muscle recruitment will be reported on more fully in future communications. It is also possible that other food-gathering and food-processing activities without tools, for example, breaking nuts or breaking bones for marrow, may have been important components of early hominid foraging behavior and may have depended on strong, repeated contraction of some of the same muscles heavily recruited for tool behaviors. This hypothesis remains to be tested by tooth-wear analysis and by EMG analysis of hand muscle activities in these behaviors.

We would also like to stress that the results of our experiments illuminate morphological features that we think needed to be in place in early hominids for habitual, effective Oldowan tool-making. But tool-making did not necessarily lead to the *evolution* of all these features. If fossil hominid hands lack these features, they probably were not used habitually for making stone tools. If they have these features, we can reasonably predict that they *could* have been the hands of tool-makers.

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