Corticospinal-evoked responses in lower limb muscles during voluntary contractions at varying strengths

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Oya T, Hoffman BW, Cresswell AG. Corticospinal-evoked responses in lower limb muscles during voluntary contractions at varying strengths. J Appl Physiol 105: 1527–1532, 2008. First published September 11, 2008; doi:10.1152/japplphysiol.90586.2008.—This study investigated corticospinal-evoked responses in lower limb muscles during voluntary contractions at varying strengths. Similar investigations have been made on upper limb muscles, where evoked responses have been shown to increase up to ∼50% of maximal force and then decline. We elicited motor-evoked potentials (MEPs) and cervicomedullary motor-evoked potentials (CMEPs) in the soleus (Sol) and medial gastrocnemius (MG) muscles using magnetic stimulation over the motor cortex and cervicomedullary junction during voluntary plantar flexions with the torque ranging from 0 to 100% of maximal force. MEPs and CMEPs were also investigated to assess whether any changes were occurring at the cortical or spinal levels. Differences between the MEP and CMEP amplitudes [normalized to maximal M wave (Mmax)] showed an increase, followed by a plateau, over the greater part of the contraction range with responses increasing from ∼0.2 to ∼6% of Mmax for Sol and from ∼0.3 to ∼10% of Mmax for MG. Because both MEPs and CMEPs changed in a similar manner, the observed increase and lack of decrease at high force levels are likely related to underlying changes occurring at the spinal level. The evoked responses in the Sol and MG increase over a greater range of contraction strengths than for upper limb muscles, probably due to differences in the pattern of motor unit recruitment and rate coding for these muscles and the strength of the corticospinal input.

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MEPs and CMEPs may well reach their peak around the upper limit of the contraction range with responses increasing from ∼0.2 to ∼6% of Mmax for Sol and from ∼0.3 to ∼10% of Mmax for MG. Because both MEPs and CMEPs changed in a similar manner, the observed increase and lack of decrease at high force levels are likely related to underlying changes occurring at the spinal level. The evoked responses in the Sol and MG increase over a greater range of contraction strengths than for upper limb muscles, probably due to differences in the pattern of motor unit recruitment and rate coding for these muscles and the strength of the corticospinal input.

MEPs and CMEPs from the medius and vastus lateralis muscles were recorded using magnetic stimulation of the motor cortex or electrical stimulation of the corticospinal tract (corticospinal-evoked potentials) demonstrated MEPs and CMEPs from the brachioradialis and biceps brachii using a high-stimulus intensity peak in amplitude around 50–75% of MVC followed by a progressive decline up to MVC. Interestingly, MEPs and CMEPs elicited in biceps brachii using a lower stimulus intensity peaked at slightly higher contraction strengths (21). In both cases, the similar shaped stimulus response curves for the MEP and CMEP suggest that the decline in both evoked responses beyond 75–90% of MVC may stem from a change in responsiveness of the motoneuron pool, because CMEPs do not reflect changes occurring within the motor cortex.

MEPs and CMEPs for biceps brachii and brachioradialis peaked at higher levels of MVC compared with those from the first dorsal interosseous muscle. Similarly, for abductor digiti minimi, the level of force where evoked responses reached a peak (10) and where complete motor unit recruitment is thought to take place occurred at ∼30% of MVC (28).

IT IS A COMMON PRACTICE TO evaluate central nervous system mechanisms related to human movement using electrical and magnetic stimulation protocols. The basic premise is that the characteristics of an unknown system can be assessed by determining the input-output relationship of the system by systematically varying parameters such as stimulus intensity and system gain. Because the level of voluntary activation, measured by underlying force output or electromyographic (EMG) activity can be thought to correspond to the combined gains of the motor cortex and motoneuron pool, it is expected that an increase in the level of system gain will increase the responsiveness of an evoked response.

From studies that have examined individual motor unit responses to stimuli (1, 4, 16, 17), all agree that as a motor unit increases its firing rate as a contraction progresses, the probability of obtaining a response to a stimuli decreases, irrespective of the recruitment threshold of the motor unit or the source of the input (e.g., Ia-afferent or descending input). The recruitment of motor units progresses to a limit as the force of a contraction increases. This limit is known to be muscle specific, with small muscles, such as adductor pollicis, having all of its units recruited by ∼50% of maximal voluntary contraction (MVC), whereas muscles that produce large force, like biceps brachii, may continuously recruit new motor units up to ∼90% of MVC (18). Additional force output after all motor units are recruited can only be achieved by increasing firing rates.

For low-force contractions of the upper limbs, a linear increase between increasing voluntary effort and the size of motor-evoked potentials (MEPs) elicited by transcranial magnetic stimulation (TMS) has been observed (29). At these low force levels, MEPs elicited via TMS are thought to represent corticospinal excitability (29). However, mounting evidence suggests that evoked responses to cortical and subcortical stimulation do not necessarily show a continuous increase with increasing voluntary effort, particularly at higher force levels. Studies by Todd et al. (31) and Martin et al. (21) using magnetic stimulation of the motor cortex or electrical stimulation of the corticospinal tract (corticospinal-evoked potentials) demonstrated MEPs and CMEPs from the brachioradialis and biceps brachii using a high-stimulus intensity peak in amplitude around 50–75% of MVC followed by a progressive decline up to MVC. Interestingly, MEPs and CMEPs elicited in biceps brachii using a lower stimulus intensity peaked at slightly higher contraction strengths (21). In both cases, the similar shaped stimulus response curves for the MEP and CMEP suggest that the decline in both evoked responses beyond 75–90% of MVC may stem from a change in responsiveness of the motoneuron pool, because CMEPs do not reflect changes occurring within the motor cortex.

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To date, there appears to be only one study that has evaluated the motor-evoked responses to cortical stimulation over a large range of force production in one of the lower limb muscles, soleus (Sol) (19). In that study, a continuous increase in MEP amplitude from low to high contraction strengths was observed. Unfortunately, evoked motor responses from stimulation to the descending pathway at the cervicomedullary junction (CMEPs) were not recorded, nor were responses from the synergist, medial gastrocnemius (MG). Unlike the upper limbs muscles, where the number of motor units recruited with respect to contraction strength has been investigated (18), little information is available for the human Sol muscle. Therefore, based on animal studies (12), Lavoie et al. (18) suggested that Sol may well use sequential recruitment of motor units as the predominant mechanism for force development to high levels, and as such, evoked potentials such as MEPs and Hoffman reflexes ought to be graded over a large part of the contraction range.

The present study therefore aimed to determine the relationship between contraction strength and motor response size evoked in the descending neural pathway onto muscles of the triceps surae. To determine whether any change in excitability is due to cortical or motoneuronal modulation, the change in amplitude of the MEPs and CMEPs over contraction strengths will be compared. To achieve these aims, Sol and MG MEPs and CMEPs will be investigated using magnetic stimulation during the performance of a number of voluntary isometric plantar flexion contractions over the entire range of contraction strengths. Despite difficulty in envisaging the possible relationship between contraction strength and motor response size, the examination of the motor-evoked responses to cortical stimulation over a large range of contraction strengths is due to cortical or motoneuronal modulation, the change in amplitude of the MEPs and CMEPs over contraction strengths will be compared. To achieve these aims, Sol and MG MEPs and CMEPs will be investigated using magnetic stimulation during the performance of a number of voluntary isometric plantar flexion contractions over the entire range of contraction strengths. Despite difficulty in envisaging the possible response behavior of these muscles, on the basis that Sol H reflexes and MEPs have in some cases been reported to increase in amplitude (19, 20), we anticipate that both MEPs and CMEPs may also increase to MVC or that they at least not show a decline like upper limb muscles at high forces.

**METHODS**

**Subjects**

Sixteen healthy subjects, consisting of nine men and seven women, (mean ± SD for age, height, and weight were 26.4 ± 5.0 yr, 1.70 ± 0.07 m, and 68.7 ± 1.5 kg, respectively) participated in the experiment. All subjects gave their written informed consent after explanation of the experiment and the risks involved. The procedures were approved by the university ethics committee and performed according to the Declaration of Helsinki.

**Plantar Flexion Torque and EMG Recordings**

Subjects were instructed to lie prone on an experimental bench with their right foot firmly strapped to a footplate that was connected to a torque transducer (Maywood Instruments, Hampshire, UK). The ankle angle was positioned to 90° and the knee close to full extension to allow for the MG to fully participate in producing plantar flexion torque (6). The plantar flexion torque signal was amplified (BK 1-5, Nobel Elektronik, Karlskoga, Sweden) and displayed on a monitor as visual feedback of the torque they produced (see Fig. 1).

EMG activity was recorded from the Sol and MG muscles using Ag-AgCl electrodes (diameter 10 mm, Tyco Healthcare Group, Neustadt, Germany). For Sol, a pair of electrodes was placed longitudinally ~2 cm distal to the bifurcation of the heads of the gastrocnemius muscles with an interelectrode distance of ~1.5 cm. For MG, a pair of electrodes was placed longitudinally over the belly of the medial head with an interelectrode distance of ~1.5 cm. A reference electrode of the same type was placed on the head of fibula or ankle of the left foot. EMG signals were amplified either 100 or 400 times (NL844 preamplifier, Welwyn Garden City, Hertfordshire, Digitimer, UK, or MA300 DTU, Motion Lab Systems, respectively) and band-pass filtered between 10 and 1,000 Hz (NL 900L, Digitimer). All signals were analog-digitally converted at a sampling rate of 10 kHz using a 16-bit Micro 1401 mk-II and Spike2 (Cambridge Electronic Design, Cambridge, UK).

To establish the maximal amount of plantar flexor torque each subject could produce, the subjects performed three MVCs of the plantar flexors with strong verbal encouragement by the experimenters. The highest torque produced out of the three contractions was used as the MVC torque for subsequent testing.

**Stimulation Conditions**

Motor responses from the Sol and MG were elicited by means of electrical peripheral nerve stimulation to the posterior tibial nerve, magnetic stimulation over the motor cortex (motor cortical stimulation), and magnetic stimulation of the cervicomedullary junction (cervicomedullary stimulation).

**Peripheral nerve stimulation.** To evoke a maximal M wave (\(M_{\text{max}}\)) in Sol and MG muscles, peripheral electrical stimulation was applied to the posterior tibial nerve with an anode (coal rubber pad, 10.2 cm × 4.6 cm; Empi, St. Paul, MN) placed over the lower thigh proximal to the patella and a cathode (Ag–AgCl electrode, diameter 10 mm) placed over the optimal stimulating site in the popliteal fossa. Current pulses, with a 1-ms duration, were delivered via a constant current stimulator (DS7A, Digitimer). \(M_{\text{max}}\) was determined by increasing the stimulus intensity until M waves from both muscles failed to continue in increase in amplitude. To ensure the maximal response, the test intensity used throughout the remaining experiment was set at 1.2 times the intensity that evoked \(M_{\text{max}}\).

**Motor cortical stimulation.** In 10 subjects, MEPS from the Sol and MG were elicited via TMS over the motor cortex in the left hemisphere using a magnetic stimulator (MagStim 200\(^\circ\), MagStim, Sheffield, UK) and double-cone coil (diameter 12 cm for 2 circular coils making an angle of 90°) placed with the center of the root of the coil slightly lateral to the vertex (Fig. 1) with current flowing counterclockwise sagitally. The test stimulus intensity was determined with respect to the active motor threshold (AMT) for MEPs from Sol. AMT was determined as the intensity that elicited an average of five MEPs with an amplitude of ~0.1–0.2 mV with the subject producing an isometric plantar flexion torque of ~20% of MVC. The subsequent test intensity was set at 1.2 × AMT and expressed as a percentage of maximal stimulator output. This intensity allows for MEPs in either Sol or MG to be either facilitated or depressed.
Strong motor cortical stimulation. In an additional set of experiments, which were designed to examine whether stimulus strength would affect MEP response behavior, six subjects were stimulated with TMS intensities that were as strong as possible over the motor cortex. The procedure was the same as described above, except that contractions were held at 25% of MVC and the test intensity was determined by increasing the stimulus strength of the magnetic stimulator until MEPs reached a maximum and showed no further increase with increasing intensity. The average output of the stimulator for these experiments was 95 ± 4.7% of its maximal output.

Cervicomedullary stimulation. CMEPs were elicited via magnetic stimulation, which causes less pain than electrical stimulation (32). The same coil as used for the motor cortical stimulation was positioned over the back of the head with the center of the coil over the inion (Fig. 1) and the direction of current flowing clockwise in the sagittal plane. The stimulus intensity was determined as for motor cortical stimulation, i.e., with respect to AMT. For some subjects it was difficult to obtain CMEPs comparable in amplitude to MEPs at 20% of MVC, even with the stimulator output set at 100%. In such cases the maximal stimulator output was used if it could provide a CMEP that could be discriminated from the background EMG activity. Otherwise, cervicomedullary stimulation was abandoned for that subject.

Protocol

Subjects performed five 3-s contractions at each of five torque levels (20, 40, 60, 80, and 100% of MVC) for each of the three stimulation conditions. For strong motor cortical stimulation, torque levels were set at 25, 50, 75, 90, and 100% of MVC. A stimulus was delivered at a time in the contraction when the subject had matched and held their developed torque to the prescribed level aided by visual feedback. Each torque level was pseudorandomized, and the timing of the stimulation was unpredictable. Three stimuli of each type were also applied to the subject at rest. To minimize the effect of fatigue, at least 10 s of rest was given between trials and for contractions at torque levels of 80% and above, a minimum of 1 min of rest was given.

Data Analysis

For analysis of Mmax, MEP, and CMEP, peak-to-peak amplitudes were measured on the average of the five recordings at each contraction intensity. As Mmax is assumed to represent the maximal response, CMEPs and MEPs were normalized to Mmax and grouped with respect to the various underlying levels of MVC.

Statistics

Group data are presented in the text as means ± SD. For graphical presentation, data are presented as means ± SE. To test for main effects and/or interactions between the level of contraction and the types of stimulation (MEP vs. CMEP) a two-way ANOVA was conducted for each muscle. When any interaction was detected for types of stimulation, differences between CMEPs and MEPs at each level were investigated. When a main effect was found for the contraction strength, a pairwise multiple comparison for the MEP and CMEP means between contractions levels was examined using Ryan’s method for each muscle. The level of significance was set at \( P \leq 0.05 \).

RESULTS

Evoked responses were recorded from Sol and MG after stimulation of the peripheral nerve (Mmax), the motor cortex (MEPs) and the corticospinal tract (CMEPs) while the subjects were performing plantar flexion efforts at contraction strengths ranging from 0 to 100% of MVC.

Effect Due to Site of Stimulation

Differences between the amplitudes of CMEPs and MEPs were examined with increasing contraction strength for each muscle. A two-way ANOVA showed that there was no significant main effect or interaction due to the site of stimulation (i.e., corticospinal or motor cortex) in each muscle. As such, any changes in MEPs or CMEPs with increasing contraction strength are likely due to underlying changes at the spinal level.

Evoked Responses From Voluntary Contractions of Increasing Strength

Only two of the eight subjects exhibited a detectable CMEP at rest. In Fig. 2, individual and averaged responses for Mmax, MEPs, and CMEPs from Sol are shown from one of the eight subjects who completed both protocols. For this subject, Mmax remained unchanged and the amplitudes of the normalized Sol MEPs increased continuously up to 100% of MVC. A similar increase to MVC was seen in five other subjects, while two subjects showed a plateau and two a decrease after 80% of MVC. For Sol CMEPs, seven of the eight subjects showed a continuous increase in amplitude to 100% MVC. The overall amplitude of the MEPs and CMEPs in the subjects that showed an increase was \(-6.7 \pm 4.1\) and \(4.7 \pm 4.1\%\) of Mmax at MVC, respectively. Figure 3 shows data from MG for the same subject as in Fig. 2. For this subject, normalized MEP amplitudes for MG increased up to 100% of MVC. This was seen in one other subject, while five subjects showed a decrease and two plateaued after 80% of MVC. For MG CMEPs, three subjects showed an increase in amplitude while five showed a decrease after 80% of MVC.

Grouped data are presented in Fig. 4 for both Sol and MG. Significant main effects were observed for MEP and CMEP amplitudes with levels of contraction strength for each muscle. For Sol, mean MEP and CMEP amplitudes showed an increase...
MEPs Evoked With Strong Stimulus Intensities

MEPs elicited with strong stimulus intensities are shown in Fig. 5. High stimulus strengths resulted in only a small increase in MEP amplitude at rest (4.8 ± 3.6 vs. 0.2 ± 0.4% and 3.1 ± 1.6% vs. 0.3 ± 0.2% of M_max for Sol and MG, respectively, for strong vs. weak stimulus strengths). The higher stimulus strength resulted in a larger response during an MVC in Sol (14.2 ± 4.6 vs. 5.8 ± 3.4% of M_max), whereas the MG response was practically unchanged (14.6 ± 9.0% vs. 13.7 ± 10.0% of M_max). The change in MEP amplitude with increasing contraction strength was similar to that described for the experiments using a lower stimulus intensity, with a plateau in MEP amplitude occurring at high contraction strengths. Ryan’s test showed a statistical difference in amplitude for both muscles between rest and contraction strengths above 50% MVC, whereas no significant differences were found between contraction strengths of 50, 75, and 100% of MVC.

DISCUSSION

The main finding of the present study was an increase in cortically (MEP) and corticospinally (CMEP) evoked responses in the muscles of the triceps surae over a large part of their contraction range. The evoked responses from Sol and MG exhibited similar changes over the entire range of force production.

MEPs and CMEPs With Increasing Voluntary Contraction

Past research (8, 9) has shown that TMS of the motor cortex elicits multiple descending volleys. The number and amplitude of these volleys (I waves) has also been shown to increase as voluntary effort is intensified. In contrast, cervicomedullary stimulation initiates a single volley in the corticospinal tract, whose resulting amplitude is not affected by the strength of contraction.
voluntary activation (8). This difference in the input characteristics to the motoneuron pool is thought to affect the evoked responses observed from a muscle. Thus TMS-induced MEPs constitute a composite effect of excitability stemming from both spinal and cortical regions, whereas CMEPs are predominantly affected by the excitability of the motoneuron pool within the spinal cord. Moreover, unlike the spinally mediated H reflex, the corticospinal tract is not susceptible to presynaptic inhibition (14, 25); therefore, any difference between a cortically initiated MEP and a cervicomedullary evoked CMEP can be attributed to changes in the neural circuitry within the motor cortex.

In the present study, no difference in the behavior of the MEP and CMEP response curves was observed for either the Sol or MG muscles. Given the similarity in the curves, it is likely that the changes in the motor responses resulted predominantly from a change in excitability occurring at the motoneuron level. This finding is consistent with similar motor-evoked responses obtained from upper limb muscles over their entire force range (21). It remains somewhat unclear as to why MEPs and CMEPs are so similar, despite the fact that TMS should have induced multiple intensified volleys reaching the motoneuron pool as contractions were strengthened. Further detailed investigations are required to determine why MEPs fail to show larger response in size compared with CMEPs when the strength of the contraction level becomes quite strong.

**Excitability of the Motoneuron Pool**

At the motoneuron level, any change in the size of an evoked potential is largely determined by changes in the firing rate and the number of active motor units within the motoneuron pool. As the muscle is increasingly activated, both firing rate and the number of recruited motor units have been shown to increase (2, 18, 23, 24). Although there is a limit at which all motor units are recruited, further force output can be achieved by increasing the firing frequency of the already firing motor units (11, 18, 28).

It has been shown that the discharge probability of a single motor unit in response to excitatory stimuli (either by descending or peripheral Ia input) decreases monotonically as its firing rate is increased voluntarily (4, 15, 17). The reason for the decreased discharge probability is presumably due to the fact that the motor unit becomes less responsive as the asymptotic region of its afterhyperpolarization becomes deeper and steeper as its firing rate increases (16). As a muscle is voluntarily activated, progressive recruitment and decreasing probability of individual motor unit responses will likely result in the aggregate evoked motor output increasing up to the point where all motor units are recruited, thereafter declining as the effect of decreasing probability becomes relatively stronger. Because the point where progressive recruitment becomes limited is muscle dependent (11, 18, 28), the point at which MEPs and CMEPs either plateau or decrease with increasing contraction intensity is likely to be muscle dependent. This assumption was recently put forward by Martin et al. (21) and supported by Gelli et al. (10). These authors showed that for biceps brachii, where motor unit recruitment takes place up to ~90% of MVC, decreases in MEPs and CMEPs occurred slightly earlier, around 75% of MVC. For an intrinsic hand muscle, whose recruitment ceases around 50% of MVC, peak evoked responses occurred at ~30% of MVC for MEPs in adductor digiti minimi and 50% of MVC for MEPs in the first dorsal interosseous muscle.

The results of the present study on lower limb muscles appear to deviate from the observations made on upper limbs muscles (10, 21) because no significant decrease occurred in either of the evoked responses as the level of contraction increased. The lack of decrease in this study are in accordance with the finding of Lavoie et al. (19), who showed that cortically evoked potentials in Sol continued to increase up to large levels of force production. Although data on human subjects are lacking, cat studies suggest that Sol predominantly uses progressive recruitment of motoneurons with wide ranges of recruitment thresholds for incremental force control (12). If this is the same in humans, then the observed differences between the evoked responses between upper limb and lower limb muscles may be reconciled by the different range of active motor unit recruitment in these muscles. To our knowledge, unlike the biceps brachii and intrinsic hand muscles, there is no information as to the level of contraction whereby all motor units in Sol and MG are fully recruited. To unequivocally maintain that a monotonic increase in the evoked responses results from the difference in the balance of progressive recruitment and discharge rate of motor units, further investigations and data are required on the recruitment and firing properties of the Sol and MG motoneuron pools.

**Relationship With Input Size and Its Potential Variation**

Alternative possibilities may also lie behind the behavior of the evoked responses found in the present study. According to a simulated model (5, 22), the probability of discharge of individual motor units is also dependent on the stimulus strength as well as the background motor unit firing rate. The higher the stimulus intensity, the greater the extent that the probability decreases with increasing firing rate, and vice versa. This relationship may well affect the aggregate motor output. Indeed, it has been shown that a lower stimulus intensity shifts the peak of motor output to higher levels with respect to MVC (21). In the present study, CMEPs were elicited using magnetic stimulation instead of electrical stimulation to minimize subject discomfort. Unfortunately such stimulation somewhat compromises the size of the possible evoked response. However, when performing additional experiments with higher stimulus intensities, we still observed no significant decrease in MEP amplitude at high contraction strengths. Interestingly, the size of the evoked response in both Sol and MG with high stimulation intensity was still relatively small compared with those reported in the upper limb muscles by Martin et al. (21). This may be due to the inability of the stimulating device to completely reach the motor area innervating the lower limb muscles and/or a possible scarcity of corticospinal tract projections onto lower limb motoneurons. The later can be supported by the fact that evoked responses in the tibialis anterior are generally larger and easier to elicit than those in Sol or MG and that the TA motoneuron pool receives inputs of comparable strength as those of the upper limbs [de Noordhout et al. (7) and Brouwer and Ashby (3)]. Thus the observed small responses in Sol and MG at low and high stimulus strength may well be due to the scarcity or low strength of the corticospinal projections to those particular motoneuron pools.
However, another alternative that must be considered is that the net input, resulting from mixed excitation and inhibition, could vary among different motoneuron pools. Unlike the demonstrated monosynaptic corticospinal pathway in the upper limbs (27), there has not been clear evidence regarding the existence of monosynaptic corticospinal pathway onto lower leg motoneuron pools. Considering that indirect polysynaptic pathways originating from the motor cortex may project onto motoneuron pools for leg muscles (13) and that cortical stimulation activates inhibitory pathways with lower threshold than excitatory pathway for the leg (26), we cannot exclude the possibility that inhibitory input activated by cortical stimulation may have shaped the observed response.

**Implications**

Although there are still issues to be addressed, such as whether weak corticospinal input is intrinsic to planar flexor muscles, a monotonic increase in motor-evoked response from the triceps surae, either by means of cortical or corticospinal tract stimulation, suggests that the increase is likely to stem from alterations at the motoneuron level and is likely due to relatively smaller input size of cortical origin and a large range of motor unit recruitment thresholds within the Sol and MG motoneuron pools. This finding provides a good basis for assessing the effect of exercise-related alterations in evoked responses, such as during fatigue or the performance of dynamic contractions. For example, any departure from similarity between the MEP and CMEP response curves due to fatigue could be attributed to changes in cortical mechanisms as when fatigue progresses, cortical mechanisms not only increase descending drive, but also modulate some excitatory/inhibitory circuitry within the cortex (30).

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**REFERENCES**


