RESEARCH ARTICLE

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Loads applied tangential to a fingertip during an object restraint task can trigger short-latency as well as long-latency EMG responses in hand muscles

Received: 9 August 2002 / Accepted: 19 December 2002 / Published online: 26 July 2003 Springer-Verlag 2003

Abstract Electrical stimulation of the digital nerves can cause short- and long-latency increases in electromyographic activity (EMG) of the hand muscles, but mechanical stimulation of primarily tactile afferents in the digits generally evokes only a long-latency increase in EMG. To examine whether such stimuli can elicit shortlatency reflex responses, we recorded EMG over the first dorsal interosseous muscle when subjects $(n=13)$ used the tip of the right index finger to restrain a horizontally oriented plate from moving when very brisk tangential forces were applied in the distal direction. The plate was subjected to ramp-and-hold pulling loads at two intensities (a 1-N load applied at 32 N/s or a 2-N load applied at 64 N/s) at times unpredictable to the subjects (mean interval 2 s; trial duration 500 ms). The contact surface of the manipulandum was covered with rayon—a slippery material. For each load, EMG was averaged for 128 consecutive trials with reference to the ramp onset. In all subjects, an automatic increase in grip force was triggered by the loads applied at 32 N/s; the mean onset latency of the EMG response was 59.8 ± 0.9 (mean \pm SE) ms. In seven subjects (54%) this long-latency response was preceded by a weak short-latency excitation at 34.6 ± 2.9 ms. With the loads applied at 64 N/s, the long-latency response occurred slightly earlier $(58.9±1.7 \text{ ms})$ and, with one exception, all subjects generated a short-latency EMG response $(34.9\pm1.3 \text{ ms})$. Despite the higher background grip force that subjects adopted during the stronger loads $(4.9\pm0.3 \text{ N} \text{ vs }$ 2.5 ± 0.2 N), the incidence of slips was higher—the manipulandum escaped from the grasp in $37±5\%$ of trials with the 64 N/s ramps, but in only $18±4\%$ with the 32-N/s ramps. The deformation of the fingertip caused by the

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tangential load, rather than incipient or overt slips, triggered the short-latency responses because such responses occurred even when the finger pad was fixed to the manipulandum with double-sided adhesive tape so that no slips occurred.

Keywords Loads · Fingertip · Object restraint task · Short-latency EMG responses · Long-latency EMG responses · Hand muscles

Introduction

Unpredictable pulling forces applied to an object held between the index finger and thumb evoke reactive increases in grip force normal to the contact surface that serve to prevent escape of the object from the grasp (Cole and Abbs 1988; Johansson et al. 1992a, 1992b, 1992c; Macefield et al. 1996a; Macefield and Johansson 1996). Anaesthetic block of the digital nerves has demonstrated that these grip-force responses to loads applied tangential to the skin of the fingerpad depend on cutaneous afferents (Johansson et al. 1992c; also see Häger-Ross and Johansson 1996). Moreover, microneurographic recordings have shown that tactile afferents in the glabrous skin of the digits are the only receptors capable of triggering these increases in grip force (Macefield et al. 1996a); muscle and joint afferents respond only during the resultant increases in grip force, not before (Macefield and Johansson 1996).

The latency of the grip force response is inversely related to the rate of the imposed loading ramps; the faster the ramp the shorter the latency (Johansson et al. 1992b). With brisk pulling loads (1 N, 32 N/s) applied tangential to the skin of the digits, the EMG response in the first dorsal interosseous muscle (FDI) occurs at a mean onset latency of 61 ± 2 ms (mean \pm SEM) (Macefield and Johansson 1994). This is comparable to that of the longlatency response to stretch of this muscle $(59\pm 1 \text{ ms})$; Macefield et al. 1996b). Interestingly, while muscle stretch can also elicit a short-latency increase in FDI

EMG at 37 ± 2 ms (Macefield et al. 1996b), such an early response has never been observed during restraint of a manipulandum held between finger and thumb (Cole and Abbs 1988; Johansson et al. 1992a, 1992b, 1992c; Macefield et al. 1996a; Macefield and Johansson 1996). Yet, given that electrical stimulation of the digital nerves of the index finger is known to cause (in most subjects) short-latency $(35\pm1 \text{ ms})$ as well as (in all subjects) longlatency responses $(58\pm1 \text{ ms})$ in FDI (Evans et al. 1989), one might expect that short-latency responses could also be generated by mechanical stimulation of cutaneous receptors. Indeed, in one study, in which a manipulandum was restrained by the index finger alone, short-latency $(34±1 \text{ ms})$ as well as long-latency responses $(60±1 \text{ ms})$ were seen in FDI (Macefield et al. 1996b). The purpose of the present study was to examine whether very brisk tangential loads to the pad of the index finger can consistently evoke short-latency responses in FDI EMG. To this end we compared EMG responses to loads applied at two rates and amplitudes: a rate of 32 N/s (which is the highest employed in this laboratory) and a rate twice as fast as this (64 N/s). We also tested the hypothesis that overt slips of the manipulandum are required to trigger short-latency responses.

Materials and methods

Experiments were performed on eight male and five female subjects (aged 18–55 years), each of whom provided informed consent. The procedures were carried out in accordance with the Ethics Committee of Umeå University.

Experimental apparatus

Subjects were seated with the forearm and hand supported prone on a table in front of them, with all fingers other than the index finger curled around the edge of the table (Fig. 1). Supported below the table was a torque motor, on the shaft of which was a 10-cm-long perpendicular arm and a manipulandum that was equipped with strain gauge elements for measuring the tangential (load) and normal forces exerted at the fingertip and an accelerometer for recording the onset of movement. The manipulandum consisted of a flat aluminium disc (diameter 3 cm), oriented horizontal to the table. Unless otherwise indicated, the surface of the disc was covered with rayon (synthetic silk), a smooth woven material. The motor was controlled by a laboratory microcomputer that pseudorandomly generated ramp-and-hold command signals every 1.5– 4.0 s (mean interstimulus interval 2.0 s). Two loading profiles were used: a 1-N load delivered at 32 N/s and a 2-N load delivered at 64 N/s, and the hold phase was maintained for 500 ms after the load ramp. Angular position was monitored by a potentiometer on the shaft of the motor and provided servo-regulated resetting of the zero position before a series of trials was delivered. The motor provided no audible cues to the subject.

Data collection

Electromyographic activity (EMG) was recorded with 2-mmdiameter surface electrodes (interelectrode separation 12 mm) embedded in a small $(15\times15\times3-mm)$ preamplifier. The electrodes were coated with electrode jelly and then firmly attached to the skin overlying the FDI with double-sided adhesive tape. Such an arrangement effectively eliminated movement artefacts. The EMG

Fig. 1 Schematic representation of experimental apparatus. The subject was instructed to restrain a manipulandum with the pad of the index finger which, at unexpected times, was pulled away from the finger

signal was amplified (gain 2×10^3 , bandwidth 10 Hz-1 kHz), root mean square (r.m.s.) processed with a rise time constant of 1.0 ms and a decay time constant of 3.0 ms and sampled at 800 Hz. Load and normal force, position and acceleration signals (DC-120 Hz) were digitized at 400 Hz. All signals were recorded by a laboratory computer, using SC/ZOOM software (Physiology Section, IMB, Umeå University), and stored on magnetic and optical media. During each trial data were collected over a time window extending from 200 ms before the onset of the motor stimulus to 500 ms afterwards.

Experimental protocol

The index finger was flexed $\sim 15^\circ$ at the metacarpophalangeal joint so that the finger pad contacted the centre of the manipulandum. Subjects were asked to keep the finger straight so as to limit the contribution of the long finger-flexor muscles. The subject contacted the manipulandum with sufficient force (2.0 N) to trigger the computer to commence delivering a block of 128 trials with identical loading profiles, and was instructed simply to prevent the manipulandum from escaping from the grip. The subject was not penalized if the manipulandum did slip; the computer directed the motor to drive the manipulandum back to its starting position and the missed trial was repeated. Subjects were blindfolded and received no instruction as to the amount of force they should apply to the manipulandum. In some experiments the subject's finger pad made contact with double-sided adhesive tape (Tesa Tape, Beirsdorf AG, Hamburg, Germany) placed in the centre of the manipulandum. This prevented slips from occurring.

Analysis

All analyses were performed offline. Short- and long-latency EMG responses were identified based on averaged responses in individual subjects. EMG was averaged together with the mechanical signals and averaging was synchronized to the computer-generated stimulus signal. All measurements were made with cursors at high temporal resolution. Absolute latencies were determined from the positive initial peak of the acceleration signal, which represented an early measure associated with the onset of the movement of the manipulandum and hence the time when the cutaneous receptors would have been excited. Force rates were obtained as a function of time by symmetrical numerical time differentiation within a time window corresponding to ± 5 data samples. Statistical evaluation of the data was performed with the Statistica analysis package (v6, Tulsa, OK, USA). Normally distributed data were compared using the t-test and non-normally distributed data were compared using the Wilcoxon matched pairs test or the Mann-Whitney U-test. Values are expressed as means and standard error and differences were considered statistically significant at $P<0.05$.

Results

EMG responses to tangential pulling loads applied to the finger

In all subjects brisk ramp-and-hold pulling loads applied tangential to the skin of the index finger pad generated automatic increases in ongoing EMG of the first dorsal interosseous (FDI) muscle. Averaged records from one subject are shown in Fig. 2. Pulling loads (1 N) applied at 32 N/s (thin lines in Fig. 2) elicited a long-latency increase in EMG at 61.3 ms in this subject, followed by a smaller increase at twice this latency (126.9 ms) that possibly reflects a fast voluntary response to the stimulus. Interestingly, the faster and larger ramps (64 N/s, 2 N) also triggered a short-latency increase at 36.9 ms, which is compatible with a spinal reflex. The initial fall in normal force during the load ramp is a direct mechanical consequence of the direction of the tangential force with reference to the posture of the hand. That is, in the present experiments the contact surface was in a horizontal plane located below both the interphalangeal and the metacarpophalangeal joints, such that the tangential force caused an instantaneous extension of the digit and hence a decrease in the normal force. The subsequent increase in the normal force, however, reflects the muscle contraction associated with the long-latency response and the subsequent response; the short-latency component generated no discernible increase in normal force.

With one exception, short-latency increases in EMG were observed in all 13 subjects following the 64-N/s ramps, but in only seven following the 32-N/s ramps. Mean peak amplitudes of the short-latency EMG responses were $37\pm8\%$ of the long-latency responses for the 64-N/s ramps $(n=12)$ and $23\pm5\%$ for the 32-N/s ramps $(n=7)$. In four subjects, the peak amplitude of the third, possibly volitional, component was smaller than that of the long-latency component (e.g. the subject illustrated in Fig. 2), whereas in six it was larger. On average, though, there was no significant difference in mean peak amplitudes of these response components. Mean onset and peak latencies for each component are presented in Table 1. Compared with the slower ramps, peak latencies of the long-latency and 'volitional' responses were significantly shorter during the faster ramps.

Fig. 2 Averaged records from one subject during application of pulling loads to the pad of the index finger. The contact surface of the manipulandum was rayon. Traces shown with *thin lines* were obtained with 1-N loads applied at 32 N/s (128 trials with no overt slips); traces shown with *thick lines* were obtained with 2-N loads applied at 64 N/s (128 trials with no overt slips). The vertical lines refer to the 64-N/s data: the first line indicates the onset of the stimulus (peak acceleration); subsequent lines indicate the onset and peak latencies of the short-latency, long-latency and 'volitional' responses. Normal and tangential force rate are the first timederivatives of the grip force (GF) and load (LF) forces, respectively

Table 1 Mean onset latencies $(±$ SE) for the three excitatory responses in ongoing EMG of the first dorsal interosseous muscle. Peak latencies are indicated in *brackets*, *n* refers to the number of subjects in which the component was identified, * indicates a significant difference between mean values obtained during the 32 N/s and 64 N/s ramps

Ramp rate	Short-latency	Long-latency	'Volitional'
32 N/s (1 N)	34.6 ± 2.9 ms $[46.7 \pm 2.7$ ms]	59.8 ± 0.9 ms	139.8 ± 10.3 ms $[102.1 \pm 6.9 \text{ ms}]$ $[180.1 \pm 11.8 \text{ ms}]$
	$(n=7)$	$(n=13)$	$(n=13)$

Background force and the occurrence of slips

Except for the requirement to apply a 2-N normal force to the manipulandum during the trials, subjects received no instruction as to the amount of force they should apply to the manipulandum with their index finger. For the 32-N/s ramps, in which short-latency EMG responses were evoked in seven subjects but absent in five, there was no significant difference in background grip force adopted by the subjects $(2.3\pm0.1 \text{ N vs } 2.7\pm0.3 \text{ N}$, respectively). As a consequence of slip events in which the manipulandum escaped the grasp early in the test series, subjects adopted a background normal force during the fast ramps that was twice as high as that generated during the slower ramps $(4.9\pm0.3 \text{ N vs } 2.5\pm0.2 \text{ N})$. This strategy was necessary to prevent slips because, with the brisk load ramps used, all of the load increase took place well before the onset of any possible reactive increase in normal force. Thus, the function of the triggered normal force responses in this task is not primarily to prevent slips but to restore a reasonable safety margin during the hold phase of the load. This is also reflected in the fact that the peak normal forces triggered by the present loads were rather modest: 9.5 \pm 1.0 N for the 64-N/s ramps and 5.4 \pm 0.8 N for the 32-N/s ramps. That is, in terms of the reactive normal force increase, the subjects appeared largely to habituate to the brisk loads when presented for many trials in which mainly the background force was the critical factor for preventing slips. It is indeed well established that one mode of control of grasp stability in reactive grip tasks is to regulate the pre-trial normal force in anticipation of tangential loads that rapidly increase some time in the future (Johansson and Westling 1988; Johansson et al. 1992b; Cole and Johansson 1993; Serrien et al. 1999; Winstein et al. 1999). While the background grip force during the 64-N/s ramps was double that of the 32-N/s ramps, the mean ratio between the evoked grip force and the background force was around two for both conditions (9.5/4.9=1.9; 5.4/2.5=2.2). Clearly, the increase in background normal force was not strong enough to prevent the manipulandum from escaping: during the load ramp it slipped away from the finger twice as often with the 64- N/s ramps $(37\pm5\% \text{ of trials})$ as with the 32-N/s ramps $(18\pm4\%)$. Slips were observed throughout a block of trials, not just at the beginning. As expected, the background normal force was significantly lower in those trials in which slips did occur than in those in which they did not: 3.7 ± 0.3 N vs 4.9 ± 0.3 N for the 64-N/s ramps, 1.9 \pm 0.4 N vs 2.5 \pm 0.2 N for the 32-N/s ramps. The ratio of the background force when slips were absent to that when slips were present was identical for the two ramp rates (1.32). However, the background grip-force to load-force ratio was lower when slips occurred than when they did not (1.85 vs 2.45 for the 64-N/s, 2-N ramps; 1.90 vs 2.50 for the 32-N/s, 1-N ramps).

The patterns of EMG activity were similar for trials with and without slips. This is illustrated in Fig. 3, in which averaged records from a single subject are compared for trials with the 64-N/s ramps in which slips occurred (thin lines) with trials without slippage (thick lines). In this subject, the contact surface of the manipulandum was covered with sandpaper, because too many slips occurred when the surface was rayon (74% of trials with 64 N/s resulted in escape of the manipulandum from the finger pad in this case). Note that the short-latency response, occurring around 33 ms, was very pronounced in this subject, comparable in amplitude to the later response but smaller than the intermediate long-latency response. It is apparent that all three phases of the triggered EMG responses were present in the slip trials,

Fig. 3 Averaged records from one subject during application of 2- N pulling loads (64 N/s) to the pad of the index finger. The contact surface of the manipulandum was sandpaper. Traces shown with *thick lines* were obtained for trials $(n=128)$ in which overt slips did not occur, and trials with slips $(n=30)$ are represented by the traces with *thin lines*. For the latter the display gains of the acceleration and position records have been reduced to 50 m/s² and 20 mm, respectively, for clarity. Vertical lines refer to the non-slip condition and indicate temporal events as in Fig. 2

although the long-latency component seems to have been terminated prematurely—perhaps because of the sudden unloading of the muscle when the manipulandum escaped from the finger.

EMG responses generated in the absence of slips

Finally, we analysed whether incipient or local slips in the area of contact between the digit and the manipulandum were important for the evolvement of the various components observed in the EMG signal of the FDI. In six subjects, the manipulandum was prevented from slipping because the finger pad contacted thick doublesided tape. In all subjects, a clear impression of the finger prints was embedded in the tape after the finger was removed from the tape at the conclusion of the trials, indicating that no slippage occurred between the skin and the manipulandum. Nevertheless, despite the knowledge that they did not have to respond to the stimuli, subjects still responded to the tangential shear forces. Averaged

Fig. 4 Averaged records from one subject during application of 2- N pulling loads (64 N/s) to the pad of the index finger. Traces shown with thin lines were obtained in which the contact surface of the manipulandum was rayon (128 trials); traces shown with thick lines were obtained when the finger pad was stuck to the manipulandum with double-sided tape (128 trials), which prevented slips from occurring. Vertical lines refer to the rayon condition and indicate temporal events as in Fig. 2

records are shown for one representative subject in Fig. 4. All three phases of the triggered EMG responses were present, although the amplitude of the responses was weaker when the fingertip was glued to the manipulandum. Measured from the 64-N/s trials, the background normal force was significantly lower when double-sided tape was used $(2.9\pm0.4 \text{ N})$ than when the contact surface was rayon $(5.1\pm0.4 \text{ N})$. This makes sense: because no slips occurred with double-sided tape (compared to slips in $20±4\%$ of trials when rayon was used), subjects would need to exert less background normal force in the intervals between stimuli (i.e. just a 2-N force to trigger the trials). Although the peak grip force response was significantly lower when double-sided tape was used $(4.3\pm0.6 \text{ N vs } 8.5\pm1.2 \text{ N})$, the fact that triggered increases still occurred indicates that neither localized nor overt slips are required for the generation of the spinal, the long-latency and the subsequent responses to shear load forces applied tangential to the finger pad.

Discussion

This study has shown that short-latency, as well as longlatency and later, possibly volitional, responses can be generated in muscles acting on the digits when an object in contact with the finger pad is unexpectedly pulled

away. Until now, only long-latency increases in grip force have been observed in this laboratory (Johansson et al. 1992a, 1992b, 1992c; Macefield and Johansson 1994; Häger-Ross and Johansson 1996; Häger-Ross et al. 1996); yet short-latency EMG responses to similar stimuli have been observed in another laboratory by one of us (Macefield et al. 1996b). The fast load ramps used in the present study $(2 \text{ N at } 64 \text{ N/s})$, combined with extensive data averaging, may have contributed to our detection of short-latency responses; in previous studies from this laboratory the fastest load applied was 0.5– 1.0 N delivered at 32 N/s.

Triphasic EMG response to pulling loads applied to the index finger

Unpredictable pulling loads applied tangentially to the pad of the index finger at either 32 N/s or 64 N/s consistently generated long-latency increases in EMG of the first dorsal interosseous (FDI) muscle, a muscle involved in force generation in the precision grip between the index finger and thumb. Distinct short-latency responses were generated in 12 of the 13 subjects during the 64-N/s ramps, and weaker short-latency responses were discerned in 7 of the 13 subjects during the 32-N/s ramps. Measured from the faster ramps, onset latencies of the short- and long-latency responses were 34.9 ± 1.3 ms and 58.9 ± 1.7 ms, similar to those reported in another laboratory by Macefield et al. (1996b) when using the index finger alone $(34.0\pm1.4 \text{ ms and } 60.2\pm1.3 \text{ ms})$, as in the present study. They are also comparable to the short- $(34.8\pm1.3 \text{ ms})$ and long- $(57.8\pm1.3 \text{ ms})$ latency increases in FDI EMG evoked by electrical stimulation of the digital nerves of the index finger (Evans et al. 1989). Moreover, the long-latency response to the 32-N/s ramps $(59.8\pm0.9 \text{ ms})$ occurred at the same time as when 32-N/s ramps were delivered to the index finger *and* the thumb $(60.6±2.4 \text{ ms})$ in an earlier study from this laboratory (Macefield and Johansson 1994). Why short-latency responses were absent in the latter condition may reflect the greater security in restraining an object with two digits (thumb and index finger) than with the finger alone as in the present study.

In contrast to the much smaller and briefer shortlatency responses, the long-latency increase in EMG was associated with a subsequent increase in normal force that would have served to restore a reasonable safety margin during the load force plateau and thereby support grasp stability. Thus, although short-latency reflexes may be triggered under certain circumstances, as demonstrated in the present study, we believe that the robust long-latency responses are most important in reactive control of grip force, supported by the later increases in EMG at latencies that may have represented a fast volitional component. Like the short-latency component the latter component may have occurred because the restrain task was limited to one digit rather than two and the contact surface was rayon, both of which would increase the likelihood of slips. EMG responses at longer, possibly volitional, latencies were also observed in the study by Macefield et al. (1996b), in which pulling loads were applied only to the index finger. However, during the load conditions of the present study none of these response components appeared fast enough to prevent escape of the manipulandum during the loading phase. Accordingly, an inadequate background force was the fundamental reason why slips occurred (Johansson and Westling 1988; Johansson et al. 1992b; Cole and Johansson 1993; Serrien et al. 1999; Winstein et al. 1999).

Adequate stimulus for generating EMG responses

Given that triggered increases in EMG still occurred when slips were prevented from occurring (by having the finger pad stuck to the manipulandum via double-sided tape), this strongly supports the idea that overt or incipient slips are not required to elicit normal force responses to changes in tangential load (Edin et al. 1993). Nevertheless, in this experimental condition shear forces would still have been produced between the skin and the object, and it is these that must be responsible for generation of the spinal and long-latency responses to the pulling stimuli. In microneurographic studies from this laboratory we have shown that three of the four classes of tactile afferent present in the finger pad—the fast-adapting type I (FAI) and slowly adapting types I and II (SAI and SAII)—could encode tangential components of fingertip forces (Macefield et al. 1996a; Birznieks et al. 2001). Moreover, afferents of each of these classes of lowthreshold cutaneous mechanoreceptors could respond to the loading ramp before the subsequent increase in normal force in a restraint task engaging the precision grip, supporting their roles in triggering the motor response (Macefield et al. 1996a). It is likely that afferents of each class would respond to the tangential load stimuli also when the fingerpad is stuck to the manipulandum. That is, we know that nearly all afferents of these three types that innervate the fingertip respond to tangential forces around 1 N, including afferents supplying the sides and the ends of the fingertip outside the area of contact with a flat surface (Birznieks et al. 2001). Yet given that nearly half of the FAI afferents in the finger pad responded to the loading ramps at latencies early enough to trigger an increase in grip force, compared to only a fifth of the SAI and SAII afferents, it is likely that FAI afferents in the finger pad are primarily responsible for triggering the automatic increases in grip force (Macefield et al. 1996a). This interpretation would also apply to the short-latency and long-latency increases in FDI EMG observed in the present study, whereas other afferent classes—including muscle spindles (Macefield and Johansson 1996)—might contribute to the later responses to the imposed pulling loads.

Conclusions

Electrical stimulation of the digital nerves has demonstrated that the neural substrate exists for eliciting shortlatency increases in FDI EMG during mechanical stimulation of cutaneous afferents. The present study has shown that such responses can occur during brisk pulling loads applied tangential to the pad of a finger, though they are unlikely to be important during reactive control of grip force in manipulation. Nevertheless, while there is evidence that tactile afferents can facilitate spinal motoneurones at short latencies during static contractions (McNulty et al. 1999; McNulty and Macefield 2001), we maintain that the long-latency EMG response, which is larger and more robust than the short-latency response, is more important for the automatic control of grip force.

Acknowledgements The authors gratefully acknowledge the technical expertise provided by Anders Bäckström. This work was supported by the Swedish Medical Research Council (project 08667). V.G. Macefield was a recipient of the Sunderland Award from the Ian Potter Foundation, Australia.

References

- Birznieks I, Jenmalm P, Goodwin AW, Johansson RS (2001) Encoding of direction of fingertip forces by human tactile afferents. J Neurosci 21:8222–8237
- Chambers MR, Andres KH, Duering MV, Iggo A (1972) The structure and function of the slowly adapting type II mechanoreceptor in hairy skin. Q J Exp Physiol 57:417–445
- Cole KJ, Abbs JH (1988) Grip force adjustments evoked by load force perturbations of a grasped object. J Neurophysiol 60:1513–1522
- Edin BB, Howe R, Westling G, Cutkosky M (1993) A physiological method for relaying frictional information to a human teleoperator. IEEE Trans Syst Man Cybern 23:427–432
- Evans AL, Harrison LM, Stephens JA (1989) Task-dependent changes in cutaneous reflexes recorded from various muscles controlling finger movement in man. J Physiol (Lond) 418:1– 12
- Häger-Ross C, Johansson RS (1996) Non-digital afferent input in reactive control of fingertip forces during precision grip. Exp Brain Res 110:131–141
- Häger-Ross C, Cole K, Johansson RS (1996) Grip force responses to unanticipated object loading: load direction reveals bodyand gravity-referenced intrinsic task variables. Exp Brain Res 110:142–150
- Johansson RS (1978) Tactile sensibility in the human hand: receptive field characteristics of mechanoreceptive units in the glabrous skin area. J Physiol (Lond) 281:101–123
- Johansson RS, Westling G (1984) Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects. Exp Brain Res 56:550–564
- Johansson RS, Westling G (1987) Signals in tactile afferents from the fingers eliciting adaptive motor responses during precision grip. Exp Brain Res 66:141–154
- Johansson RS, Westling G (1988) Programmed and triggered actions to rapid load changes during precision grip. Exp Brain Res 71:72–86
- Johansson RS, Riso R, Häger C, Bäckström L (1992a) Somatosensory control of precision grip during unpredictable pulling loads. I. Changes in load force amplitude. Exp Brain Res 89:181–191
- Johansson RS, Häger C, Riso R (1992b) Somatosensory control of precision grip during unpredictable pulling loads. II. Changes in load force rate. Exp Brain Res 89:192–203
- Johansson RS, Häger C, Bäckström L (1992c) Somatosensory control of precision grip during unpredictable pulling loads. III. Impairments during digital anesthesia. Exp Brain Res 89:204– 213
- Macefield VG, Johansson RS (1994) Electrical signs of cortical involvement in the automatic control of grip force. Neuroreport 5:2229–2232
- Macefield VG, Johansson RS (1996) Control of grip force during restraint of an object held between finger and thumb: responses of muscle and joint afferents from the digits. Exp Brain Res 108:172–184
- Macefield VG, Häger-Ross C, Johansson RS (1996a) Control of grip force during restraint of an object held between finger and thumb: responses of cutaneous afferents from the digits. Exp Brain Res 108:155–171
- Macefield VG, Rothwell JC, Day BL (1996b) The contribution of transcortical pathways to long-latency stretch and tactile reflexes in human hand muscles. Exp Brain Res 108:172–184
- McNulty PA, Macefield VG (2001) Modulation of ongoing EMG by different classes of low threshold mechanoreceptors in the human hand. J Physiol 537:1021–1032
- McNulty PA, Turker KS, Macefield VG (1999) Evidence for strong synaptic coupling between single tactile afferents and motoneurones supplying the human hand. J Physiol 518:883–893
- Phillips JR, Johnson KO (1981a) Tactile spatial resolution. II. Neural representation of bars, edges and gratings in monkey primary afferents. J Neurophysiol 46:1192–1203
- Phillips JR, Johnson KO (1981b) Tactile spatial resolution. III. A continuum mechanics model of skin predicting mechanoreceptor responses to bars, edges and gratings. J Neurophysiol 46:1204–1225
- Serrien DJ, Kaluzny P, Wicki U, Wiesendanger M (1999) Grip force adjustments induced by predictable load perturbations during a manipulative task. Exp Brain Res 124:100–106
- Winstein CJ, Horak FB, Fisher BE (2000) Influence of central set on anticipatory and triggered grip-force adjustments. Exp Brain Res 130:298–308