

Wachholder and Altenburger 1927: Foundational Experiments for Current Hypotheses on Equilibrium-Point Control in Voluntary Movements

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Between 1923 and 1927 Kurt Wachholder and his assistant and collaborator Hans Altenburger published an impressive series of 11 papers on electrophysiological and kinematic studies on voluntary human movements in *Pflüger's Archive*, the leading journal for physiological studies in Germany at the time. Unfortunately, these excellent studies have remained largely unnoticed, partly because they are written in German and therefore inaccessible to many people in the post-World War II research community in motor control. Wachholder's name is sometimes only vaguely acknowledged as a pioneer in electromyography, as he was the first to report the tri-phasic pattern in discrete single-joint movements (Wachholder & Altenburger, 1926b). This study and one other paper on rhythmic movements have been recently translated, and their close reading provided astonishing insights, not only in an historical sense but also with respect to present-day research (Sternad, 2001; Sternad & Corcos, 2001; Wachholder & Altenburger, 1926a). The two studies gave a first impression of Wachholder's rigorous methodology, stringent logic, and far-reaching conclusions about the nature of movement generation that are more than just historical precursors but indeed of contemporary interest. At the end of this series of papers in *Pflüger's Archive* is the present study, unnumbered, but with an eye-catching title about the change of rest length in muscles. The topic of a changeable and controllable rest length in muscles has been a focus of attention in motor control since Feldman's seminal studies in the 1960s that gave rise to the equilibrium-point hypothesis (Feldman, 1966a, 1966b). To what degree is Wachholder and Altenburger's contribution a precursor to these thoughts?

A few remarks about Wachholder's perspective should provide a suitable backdrop to the present paper. After all, this paper is only one of the building blocks for Wachholder's comprehensive work on voluntary posture and movements, which culminated 1928 in a monograph (Wachholder, 1928). This book provides a well-rounded perspective on, effectively, motor control.

An outstanding characteristic of the physiologist Wachholder is that he combined his meticulous physiological experiments with a more encompassing psychological perspective, leading to broader-scale theorizing about the generation of human voluntary posture and movements. How does the nervous system control

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intentional movements? What are fundamental elements in more complex movements? What are characteristic features of natural movements? What pathologies can be discerned? His monograph begins with an attempt to provide a definition of his field of research on voluntary movements:

The objective of research should be to find out the lawful relations that determine the change in behavior. This is obtained by a systematic variation of the objective conditions, e.g., resistance to movements by external forces, and the subjective conditions, e.g., intentions and psychomotoric dispositions, which then reveal the corresponding variations in the execution of voluntary movements. (p. 23)

Explicitly, he contrasts his approach against the more prominent mechanistic physiology which, in his eyes, has delivered disappointingly little or nothing to the understanding of everyday activities, neurological issues, gymnastic movements, and movement pathologies. Indeed, he satisfies his own expectations when he concludes his detailed studies with applications and perspectives on ergonomic, gymnastic, and artistic movements and provides a classifications of movement pathologies.

For his methods, he used kinematic and electromyographic recordings of single-joint movements, typically of the upper extremities, such as wrist and elbow, but not limited to them. Specifically, the measurements of the so-called action currents in unperturbed movement execution were at the leading edge of the science of his time. He used platinum needles and a string galvanometer to perform intramuscular electromyographic recordings, a technique for which he is recognized as one of the pioneers. (For some technical information about the galvanometer method, see Sternad & Corcos, 2002.) His declared goal was to understand the interplay of active muscle forces (i.e., contractions) with passive muscle forces, such as elastic, viscous, and inertial forces, with and without the influence of external forces such as gravity. By a careful recording of both overt displacement and local muscle activity, he was able to arrive at an understanding of these forces. In this objective, he also showed his inclination towards biomechanical issues.

In his monograph, he summarizes a plethora of his own experiments, progressing from postural to movement tasks. The experiments examine the effects of voluntary stiffening and deliberately accentuating certain parts of the movement, the influence of external forces such as gravity or friction, and passive internal forces such as elasticity. He provides a detailed analysis of the complex frequencies in the action currents measured in agonists, antagonists, and synergists. Interestingly, typical for the approach of his time, he does not perform any statistic quantification of his spatial and temporal estimates. However, making up for this seeming deficiency is his unsurpassed integration and evaluation of referenced data.

An interesting conclusion of his studies is that he distinguishes three fundamental types of innervation and, hence, movements. Starting from the assumption that change in the muscle's rest position is the critical feature, he categorizes movements into those where the limb:

- remains in one position that is maintained by a continued postural innervation against external and internal perturbations (reflecting the disposition of *compensation*);
- starts from a rest position and ends in a new rest position—that is, a discrete

- point-to-point movement (reflecting the disposition of *adaptation*);
- starts and finishes in the same rest position—that is, back and forth movements around one rest position. Especially, when these movements are performed in a continuous periodic fashion, they are simpler than single target-directed movements and postural tasks, where change of rest length and postural control is a necessary part.

This three-fold distinction is supported by three distinct innervation patterns identified by their predominant frequency bands of the action currents, and their coordination patterns between agonist, antagonists, and synergists. These fundamental movement types can be merged by superposition, such as a slow discrete movement involving a change in rest length can be combined with a certain degree of stiffening, or co-contraction. Similar hypotheses have been proposed more recently (Sternad, Dean, & Schaal, 2000). It remains to be said that Wachholder also aimed to extricate the contribution of local reflexes, determined by inhibitory or excitatory connections between agonists, antagonists, and synergists, and impulses from a higher motor center in the cortex. He made his points by a diligent reading of action currents, their relative timing in different muscles in very carefully designed experiments. The present study gives a flavor of Wachholder and Altenburger's ingenious experimental approach, their stringent logic, and their rigorous interpretation of the data.

In the present paper, Wachholder and Altenburger address a seemingly simple question: Can humans relax muscles that cross a joint in any arbitrary joint position? In a way, the question seems nearly trivial: From everyday experience, we know that a person can relax within a wide range of body postures and joint configurations. However, the authors realized the importance of answering this question in a rigorous, scientific way. Now, more than 70 years later, we can appreciate the depth of their insight and the importance of this seemingly naive question for theories of motor control.

At the time the paper was written, elastic properties of muscles (and their tendons) had already been described (e.g., Hill, 1921, 1926, and other authors like Rieger that Wachholder cites). If a muscle is elastic, it is supposed to generate force when its length differs from its rest length. For simplicity, consider a joint spanned by two muscles, a flexor and an extensor. For the joint to be at equilibrium, the moments generated by the two muscles should be equal in magnitude. Apparently, the easiest way to solve this problem is to make sure that the rest lengths of both muscles match the actual joint position such that both moments are zero. Otherwise, accurate adjustments in muscle activation levels will be necessary, taking into account the actual joint position, the rest lengths of both muscles, the lever arms of their action at the joint, and so on. Hence, in order for the CNS to avoid complex computations, it needs to have the ability to modify the rest length of the muscles. This is the conclusion that Wachholder and Altenburger reached based on the results of their experiments. By doing so, they made a huge leap, some 40 years long, and moved very close to formulating the equilibrium-point hypothesis, arguably one of the most controversial hypotheses in motor control (e.g., Feldman et al., 1998a; Gottlieb, 1998).

The EP-hypothesis stands on three major assumptions, some of which can be considered proven facts. (1) The human motor system contains spring-like elements and tends to reach an equilibrium if no changes occur within the system as well as

in the external force field; (2) The central nervous system (CNS) has the ability to modify the rest length of muscles; and (3) The CNS controls movements by defining time patterns of the rest length of participating muscles to change equilibrium states for the moving effectors. The study of Wachholder and Altenburger presents strong arguments for the first two assumptions. They did not study movements, only postures, and therefore did not make the next logical step to formulate the third assumption.

The importance of their conclusions can be illustrated with an argument between the two versions of the EP-hypothesis, the so-called alpha-model (Abend, Bizzi, & Morasso, 1982; Bizzi, Accornero, Chapple, & Hogan, 1982) and the original lambda-model (Asatryan & Feldman, 1965; Feldman, 1986; Feldman & Levin, 1995; Latash, 1993). A main conclusion of Wachholder and Altenburger is that the CNS can control the rest length of the muscle (in accordance with the lambda-model). If stiffness of the muscle were controlled, as hypothesized by the alpha-model, non-zero levels of muscle activation would be expected at different joint positions. This paper should definitely be viewed as an intellectually very close predecessor of the seminal papers by Feldman in the 1960s that introduced the lambda-model.

Do Our Limbs Have Only One Rest Length?

A Contribution to the Measurement of Elastic Forces in Passive and Active Movements

(From the Institute for Physiology at the University of Breslau)

Kurt Wachholder and Hans Altenburger
Translated by Dagmar Sternad

It is widely known and accepted that the smooth muscles of our body, particularly the bladder, can adapt to the change in content, because smooth muscles have the ability to take on zero tension at different lengths (1). The form and size of the hollow organs at rest is therefore not fixed but can be changed.

The objective of the present paper is to address the question whether our skeletal muscles also have the ability to change their rest length, and whether our limbs can therefore take on not only one but different rest configurations. The rest

Wachholder, K., & H. Altenburger. (1927). Do our limbs have only one rest length? A contribution to the measurement of elastic forces in passive and active movements. *Pflüger's Archive für die gesamte Physiologie*, **215**, 627-640.

configuration of a limb is defined as the angular position at which the influence of all external forces, specifically gravity, is balanced by interior passive forces (elastic forces), without any active contraction of the muscle.¹

The question whether the rest length of our muscles is changeable was first addressed by Grützner in 1904 (2). The question became prominent in some of our studies on voluntary movements when we observed that our subjects could take on different limb configurations when no perturbing exterior forces were present, without showing any visible action currents.² This, however, was only observed in cases when the subjects had maintained a particular joint position for some time. Shortly following each movement there were pronounced action currents that gradually became weaker and, in many cases, disappeared entirely in the end.³ Hence, the execution of a voluntary movement perturbed this state of silence. Often, however, it was the instruction to the subjects to perform a movement alone, or sometimes it was even only the expectation of such an instruction that produced measurable action currents (3).

Therefore, we turned away from investigating voluntary movements and directed our attention to passive movements with the objective to examine this phenomenon further. These passive movements were executed after the subject received the instruction to yield to passive movements as best as he could, and to leave the limb relaxed in each of the positions that the experimenter placed it in.

We tested the behavior of forearm muscles during passive flexion and extension movements of the wrist joint in the horizontal plane, thereby excluding the action of gravity. The hand rested on a registration apparatus with ball bearings which allowed free joint movements.

In Figure 1 and the following graphs the action currents of the flexor carpi radialis are presented on the top of the graph. The thin line directly below it is the separation line between the two illumination fields of the two galvanometers. Further below are the action currents of the extensor carpi radialis. This signal is

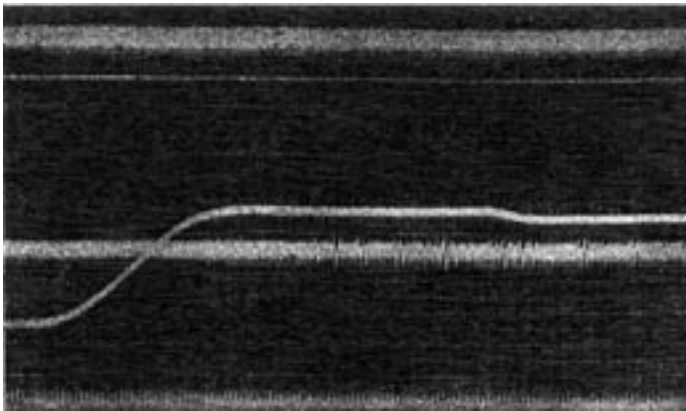


Figure 1 — In all figures the upper curve shows the flexor, the lower curve shows the extensor carp. rad. The latter is crossed by the displacement curve of the hand. Movement in the upward direction corresponds to dorsal flexion. The passive movement is between 20 deg volar to 5 dg volar. In Figure 1 the elastic rebound is compensated by an active tension of the ext. carp. rad. Time in 1/00 sec.

crossed by the movement trajectory of the hand. Upward direction means dorsal flexion and downward direction means volar flexion. The shown curves are all from one experiment and they all begin with a similarly performed passive dorsal flexion of the hand from 20 deg volar to 5 deg volar. At the bottom of the figure is the time in units of 1/100 seconds.

The measurements of the action currents were performed in the same manner as in our previous experiments, using needle electrodes and the string galvanometer by Edelman and Huth. The material of the needle electrodes was platinum that has enhanced polarization and excluded all slow displacements of the string, which were unimportant for the present purpose.⁴

If the subject truly follows the instruction and yields to the movements in a relaxed fashion, then the galvanometer strings remain completely motionless during a movement that otherwise involves both agonist and antagonist. If, however, the movement is arrested before the experimenter releases the limb, vivid currents are observed in both muscles. This indicates that the subject contracts his muscles in a cramp-like fashion, with the intention that this position has to be maintained by all means.

After several practice trials a number of subjects were successful in adapting to these passive movements in a relaxed fashion. The antagonist of the passive movements usually remained completely quiet.⁵ In the agonist, on the other hand, action currents are almost always observed, even after the new position is adopted (Figure 1). This means that the limb is fixated in the new position by a tetanic contraction of the agonist. A small number of subjects were capable to suppress even these currents and to leave the hand without any action currents in every position that the experimenter put it in (Figure 2).

Yet, to achieve this is rather difficult. Only a few subjects were able to leave their muscles completely relaxed and to avoid even the slightest activation. From subjective observations and experiments on ourselves, we found that it is absolutely essential for the success of the experiment that the subject fully concentrates on

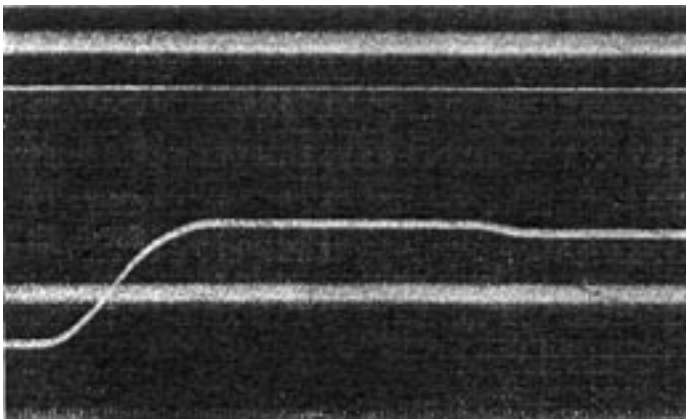


Figure 2 — The same passive movement as in Figure 1. The elastic rebound is almost completely compensated by adaptation to the new joint position without showing muscle activity.

the limb, excluding all distracting influences from the environment, and that he is determined to let everything happen and to adapt to it. The difficulty is to not only suppress any volitional movement of the limb, but also to avoid any thought of it, as this alone can already produce action currents. This characteristic state of full concentration is very difficult to maintain over a longer time.⁶ The smallest stimuli from outside can disturb this state and can destroy the entire experiment. This includes uncomfortable positions of the limb or the body, particularly any small painful sensations during the passive movements of the limb. It is also not possible to be successful every day, even for the best subjects, particularly not if the subject is agitated or otherwise indisposed.

Further, for the success of the experiment, it is absolutely necessary that the subject has a certain amount of time to get used to the change of position and adapt his muscles to it. The time necessary for this adaptation is, according to our experience, at least one second for a change of 15 deg in position, and even several seconds for differences of 30–40 deg. Only in very slow movements can the limb be released immediately after the repositioning because adaptation has occurred and been completed during the movement. In faster movements the experimenter has to hold the limb for a while in the new position to let the adaptation process take place. This was done in the experiment shown in Figure 2. Despite this, when the hand was released 0.9 seconds after the movement initiation, a small reverse movement shows that the adaptation to the new position had not been entirely completed.

But even if all these precautions were taken, the subjects could keep the passively obtained position only in the intermediate range between 30 deg volar to 5 deg dorsal flexion without showing action currents.⁷ If the passive movement went beyond that range, then action currents became immediately visible and grew to considerable strength the closer the new position was to these boundaries.⁸

At this point, the criticism can be raised that there may have been action currents even within this medium range of motion, only they occurred in other muscles than the ones measured. For instance, an agonist other than the extensor carpi radialis could have been contracted to fixate the limb in the new position. To examine this possibility we conducted a number of experiments in which simultaneous measurements were made in a number of different extensors. A first result was that the extensor carpi ulnaris could be neglected. In agreement with previous observations in voluntary movements, we repeatedly noticed that this muscle was far less active than the extensor carpi radialis in the passive dorsal flexion of the hand. It was also often completely inactive when the extensor carpi radialis was obviously active. The reverse was never observed. Following Braus (6), the extensor carpi ulnaris has only a very weak effect of dorsal flexion, due to its line of action, but a strong effect of ulnar abduction. On the other hand, the activity of the finger extensors has a strongly dorsal flexion effect on the wrist joint. Indeed, as one of us found earlier (7), the finger extensors are vividly active as agonists in purely voluntary dorsal flexions of the hand, yet only if the fingers are simultaneously extended and not when they are held in a flexed position. In agreement with this, we also saw action currents in the extensor digitalis during passive movements with extended fingers, while the extensor carpi radialis did not show any activity. But when subjects held their fingers in a relaxed flexed position, they could leave their hand in the new position without producing any activity in the extensor carpi radialis or in the extensor digitalis. This, for instance, was the case in the experi-

ment shown in Figure 2.

The criticism that activity could occur in another part of the muscle that is not measured by the needle electrode, can also not be sustained. As we and also Haas repeatedly showed in many studies with multiple simultaneous recordings of one muscle, the action currents rise slowly and simultaneously in all parts of the muscle when force is gradually increased from zero. The only exception is the biceps whose medial parts were found without currents even when other parts already showed activity.⁹

From these control experiments, we believe that the criticism can be rejected that in cases where no action currents are found, other parts of the muscle, or other muscles, are active. We believe that *within the range between 30 degrees volar to 5 degrees dorsal during passive movements of the wrist each position can be held without requiring activity or tension in the muscles.*

How can this result be explained? Two answers seem to be possible. There is either *one definite position*—approximately in the middle of this range of motion—that is the *rest length* of a limb. Every other position has to be maintained against the elastic forces of the stretched antagonist (9). The required muscle tensions for this are too small to be detectable by measuring action currents. Alternatively, the rest length of skeletal muscles is similarly adjustable as the one in smooth muscle. This rest length can be adjusted, at least within the above defined range of motion, and a stretching of the antagonists with resulting elastic forces that have to be compensated by muscle tension are thereby avoided. This means that the rest length of our limbs is not fixed but can be changed arbitrarily, at least within a medium range of motion.¹⁰

To decide between these two alternatives, we had to find a way to measure the elastic forces that arise when the limb is displaced from its rest length. Then it can be determined whether the compensation of this force requires muscle tension that produces action currents.

One way to measure the elastic forces is by looking at the so-called rebound of a movement. This is the phenomenon in which every moderately fast voluntary movement comes to rest only after a more or less significant involuntary movement in the reverse direction. Rieger (10) interpreted this finding as a sign of the muscle's elasticity. Conversely, Isserlin (11) and F.H. Levy (12) proposed that it reflects an active contraction of the antagonist. For fast voluntary movements we could confirm the conclusion by Levy with the finding that there are action currents in the antagonist shortly before the rebound (13). But we also found that they are missing if the movements are only moderately fast. In this case, the rebound is completely passive—and in very fast movements probably still partly passive. As the movements were performed under the exclusion of gravity, the underlying forces could only be due to the elastic forces generated by the stretched tissues, especially of the antagonist muscles, just as Rieger had assumed.

Such rebound can also be observed in all involuntary movements, no matter whether reflexory or passive (see Pfahl, 14). That it can be of a purely elastic nature can be seen in Figure 3. Here the hand was flexed dorsally, upon which it bounds back almost completely to the initial position. During this entire process both muscles remain without any currents. In the flexor carpi radialis, the antagonist of the passive movement, there is no activity that would indicate that a reflex was elicited. The rebound therefore happens purely due to passive forces and, as gravity

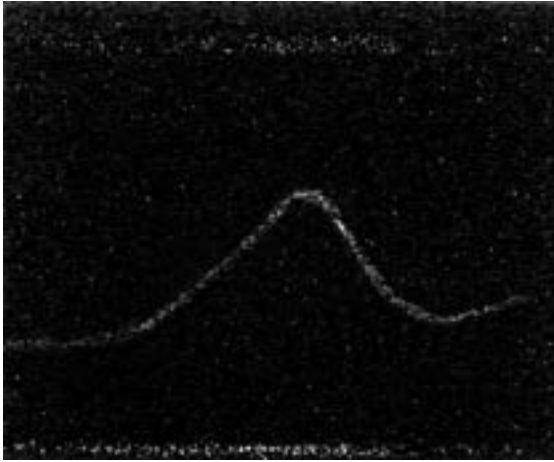


Figure 3 — Passive movement from 20 deg volar to 5 deg volar with elastic rebound.

was excluded, only elastic forces can be responsible.¹¹

For the generation of such a purely passive elastic rebound, it is required that subjects leave the hand completely relaxed without any cramp-like muscle tension. Not all subjects are able to do this. Most of them keep their limb constantly more or less stiff, as can be observed in the currents of the agonist and antagonist. In these cases the antagonist shows some larger biphasic fluctuations, as they are characteristic for reflexory contractions. These are more numerous and larger, the stiffer the limb is held (15).¹²

Such subjects cannot be used for the present purpose. We only used subjects who could keep their limb relaxed during longer sequences of experiments so that the rebound was not enhanced by a reflexory component. Further, subjects were distracted during experiments so that no voluntary movements could interfere. These were easily detectable by their action currents so that such trials could be excluded.

We attempted to measure and quantify the magnitude of the elastic forces that arose in such purely passive rebounds. To this end, we used a registration apparatus with a specially designed blocking mechanism, which left the passive movement in the first direction unaffected, but attached different counterweights in the reverse movement direction. By this method, we could measure for which counterweight the reverse movement or the elastic rebound disappeared.

The apparatus that we used was inspired by a construction by Pfahl, only that the imprecise arc-like movement notation was replaced by a linear one (Figure 4). The forearm rests on a support *St* which is tightly clamped onto the tabletop *T*. At its front side is a solid iron frame *R*. A freely rotating axis is inserted vertically into this frame and rests on two ball bearings *K*. The axis carries the support rail for the hand *Sch*. On top of this support rail is a flexible U-shaped metal bracket that tightly embraces the hand so that every movement is transferred onto the apparatus. The fingers protrude from the front part of the metal bracket and rest

on the support rail in a flexed fashion. If care is taken that all movements occur strictly in the horizontal direction, the limb does not experience any influence of gravity, which is an essential condition for the success of the experiment. At the bottom end of the vertical axis is a rubber wheel *ReSch*. Around its groove a string is wound that carries a lever across the slit of the optical recorder. The size of the wheel is so chosen that for a rotation of 1 deg the lever is moved by 1 mm. This is the case for a radius of 5.9 cm. Approximately in the middle of the axis is a second rubber disc of the same radius, or rather a sector of 90 deg of such a disc (*SpSch*) which freely turns around the axis. At this disc, the counterweights act via a string, in reverse direction of the passive movement with the purpose to compensate the rebound. Hence, the weights apply 5.9 cm in front of the center of the axis—that is, the axis of rotation of the joint. At the top and the bottom rim of this disc a small hook *SpH* can apply. The upper hook (*SpH₁*) is fixed to the frame *R*, and therefore is not turnable. The lower hook (*SpH₂*) is fixed to the axis and moves with every movement of the hand. Both hooks act in the same direction, so that a turn of the disc is prevented by the pull of the weights. If the hooks are folded back, the apparatus moves completely freely in both directions and can be used to register the trajectory of any passive or voluntary movement. If the objective is to measure the force of the elastic rebound, the hooks are applied and the counterweights are attached.

The process of such a measurement is as follows: The upper fixed hook fixates the weights in the initial position and prohibits the action of the weights during the first passive movement. During this movement, the lower hook drags across the lower disc in the direction of the pulley. If the movement stops, this hook locks into the rubber and, in the case of a rebound, moves the disc and the

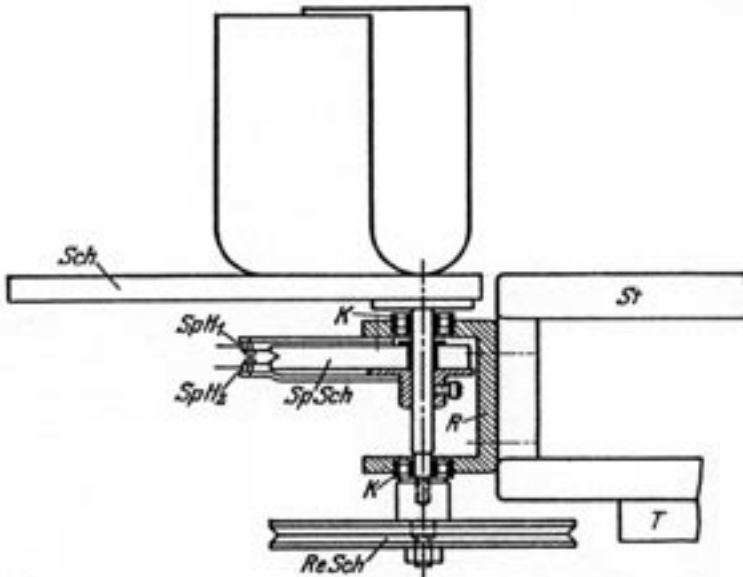


Figure 4 — Apparatus to register passive and active movements and measurement of the elastic forces. For a description, see text.

weights in this reverse direction. During this reverse movement the upper hook drags across the disc and only catches it when the backward movement terminates. Thus, this mechanism takes off the load for the subject in the new position. After releasing the hook, the disc has to be turned back to its initial position and another trial can be performed.

In this way, we achieve a situation in which the counterweights only act during the reverse movement and not during the passive forward movement, and especially not when the limb is at rest, no matter in which angular position. The subject does not have to interfere at any moment and resist the pull of the weights by a muscle contraction. The subject can and has to stay entirely passive. This is best achieved by constant distraction, but it has to be verified each time by the absence of action currents.

If the counterweights are increased in a step-wise manner for the same pas-

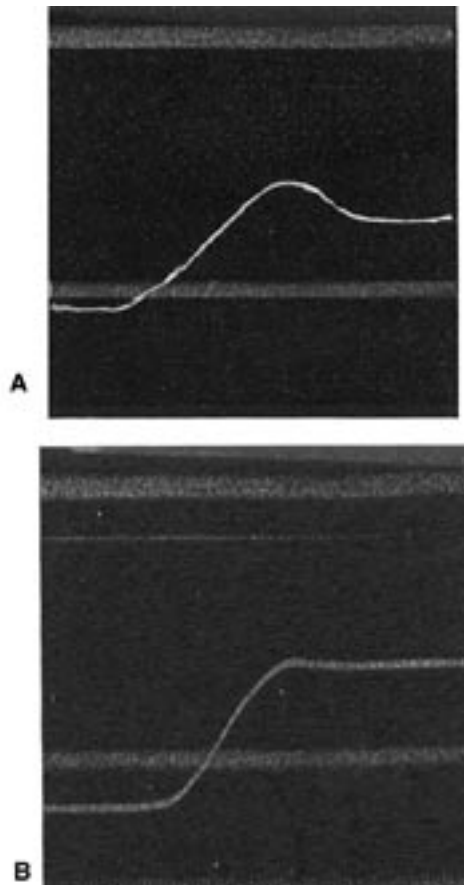


Figure 5 — A. The same passive movement as in Figure 3. Elastic rebound with a counterweight of 150 g which is partially compensated. **B.** The same passive movement. Elastic rebound with a counterweight of 250 g which is almost completely compensated

sive movements over a sequence of repetitions, the rebound becomes increasingly smaller and disappears completely from a certain weight onwards. Figure 5 shows an experiment with a passive movement between 20 deg volar and 5 deg dorsal. The rebound is compensated partially with a weight of 150 g (Figure 5A), but when using 250 g, the rebound disappears completely (Figure 5B). It should be mentioned that the very same result is obtained when the experiment is repeated several times, provided that the subject keeps still and does not tense his muscles.¹³

In this manner the elastic forces can be measured for various active and passive movements. More quantitative statements about the magnitude for different movement amplitudes, different initial positions, different subjects, and so on, shall be reserved for later publications.

At this moment we only want to state the following: If after a passive movement from 20 deg volar to 5 deg dorsal maintaining the new position was obtained by active muscle contraction, this contraction would have to be strong enough to balance a weight of at least 250 g. A contraction of this strength, however, always produces vivid action currents with our measurement method, even under identical conditions of limb position, distance of application of the force from the axis of rotation, and so on (Figure 6). The action currents were already visible for significantly smaller weights, at least from 100 g onwards, all other conditions being the same.

This result has answered our question. The possibility to maintain a new limb position without any action currents cannot be explained by the fact that the elastic rebound is prevented by some active tension of the agonist that is only too weak to be detected. Rather, the antagonists must have yielded and adjusted their rest length to the new position so that no tension of the agonists was necessary.

We considered corroborating this result in a different way using the method of measuring the resistance or rather hardness of the muscles in different limb positions. When looking through this literature, we found that Springer (15) already performed such measurements with the Gildemeister ballistic elastometer.

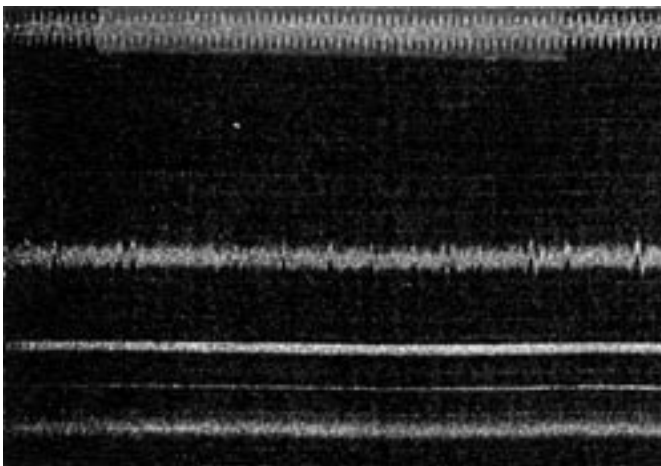


Figure 6 — Action currents when holding a weight of 250 g.

He found that the resistance of the biceps in all positions between 80 and 150 deg remained the same, and increased only from 70 deg or 170 deg onwards. Springer also recognized the importance of the time factor when he recommended that one should be careful to avoid after effects of the preceding movements and wait for a short while until a state of balance has been reestablished (16).

The results of Springer (17) provide a welcome complement to our findings. They also show that changing the rest length is not confined to the muscles of the wrist joint but that this finding probably has more general meaning for the muscles of all joints.

We therefore reach the conclusion that *our limbs do not have a single rest position and therefore our skeletal muscles do not have only one rest length, but that we can arbitrarily adapt this length such that—at least within a certain range—every possible limb position can become a rest position by changing the rest lengths of the muscles.*¹⁴

The magnitude of the change in rest length is not at all negligible. At the hand it should be 2 mm for each 10 deg of movement following some preliminary measurements. Over the range where we identified such an adaptation, this corresponds to 7 mm. We are planning to perform more anatomical investigations on this issue.

They should also bring clarity to why it is that only certain positions of the hand can be held without requiring muscular tension. Why is this only within the range of 30 deg volar to 5 deg dorsal and not across the entire range of motion? The best explanation appears to be that an adaptation of the muscle is still possible but that also other non-muscular tissues experience a stretch, and these elastic forces can only be countered by an active contraction of the muscles. This then obscures the rest length of the muscle. However, it is also possible that rest length adaptation is (phylogenetically?) only possible in the limited range.¹⁵

On the important question of how this change in rest length is brought about, we can only say very little at this moment. Considering the long time that is necessary for a change in rest length, it is feasible that it is a strong post-stretch effect that becomes a completely plastic change. However, that this cannot be the case becomes clear when subjects are actively prevented from adapting to the new position when we distract them. Under this condition, an elastic rebound can be obtained for a significantly longer time. In general, the necessity of a psychological disposition shows that it is not an entirely muscular phenomenon, but a change of state of the central nervous system.¹⁶ But the question as to which mechanism brings about such a change must be left unanswered for now. In the past years, the autonomous innervation of skeletal muscles has been frequently discussed as an explanation (18).

What meaning does the described phenomenon have for the control of normal movements? Our experiments have provided a characteristic example that we must not disregard: the psychomotoric disposition of the examinee. This holds for tests of the resistance against passive movements (e.g., clinical tests of tremor) or in diagnostic tests of voluntary movements. All results in this field can only be compared if the psychological attitude of the examinee to the respective movement is exactly known and considered. The entire problem of human movements can not only be understood as a physiological problem but a psychophysiological problem, as we already mentioned as a leitmotif in the beginning of this series of papers (19).

It is the achievement of von Weizsäcker to have said this in a clear statement for the case of passive movements, after O. Foerster had made similar statements about voluntary movements much earlier. Von Weizsäcker wrote a very readable critical essay, "On dynamical investigations on muscle tone in humans" (21), where he outlined two psychomotoric dispositions that are relevant for the present question: 1) compensation, which is the desire to maintain the original position against all exterior forces; 2) adaptation, understood as the desire to yield to exterior forces and to optimally adapt to them. He then also examined behavior with an adaptive disposition following Leibowitz (22). He deliberately restricted himself to investigating the subject's ability to adapt the muscle's active tetanic tension when instructed to passively yield. The great importance of this adaptation is unquestioned for the clinical testing of muscle tone. However, our experiments have shown that this does not yet exhaust the entire adaptive abilities of humans. There is another non-tetanic adaptation of muscle length that avoids the compensatory elastic counterforces, which actually has to take place if the adaptation is to be complete. Whether and to what degree an increase, or inability, of non-tetanic adaptation to play a role in pathological cases, as for instance in katatonia and decerebrate rigor (23), needs to be examined urgently. This, however, will not be easy, as there are superposed tetanic processes everywhere that are accompanied by action currents.¹⁷

If we now return to normal motor behavior, we have come to believe that the simultaneous adaptation or non-adaptation of the rest lengths of muscles plays a central role both in passive and active voluntary movements. Many differences between the execution of slow and fast movements can be explained when this fact is considered. In slow movements one can assume that complete adaptation takes place simultaneously with the movement. On the other hand, as these adaptations require time, they cannot keep pace with the change in the faster movements. This explains why there are such conspicuously small currents in the agonist during slow movements and a rapid increase once a certain movement speed is transgressed. It also explains the rebound that starts to occur only in medium fast and fast movements.¹⁸ Further, this can explain the results that it is only possible to adapt within the medium range of motion and that action currents or muscle activity increase, if the movements get closer to the limits of the range of motion. Therefore, such movements at range limits are regarded as uneconomical and coerced, and Trendelenburg (24) recommends to avoid them in artistic movements (e.g., playing the violin).¹⁹ Thus, our investigations of the adaptation of the muscle rest length during changes in joint angles probably revealed a hidden but not unimportant factor in the economical execution of coordinated voluntary movements.

Summary

In passive movements of the hand within the range of 30 deg volar to 5 deg dorsal, any arbitrary position can be maintained without requiring any action currents, assuming that the action of gravity is excluded.

By using an apparatus that measures elastic forces that arise in such movements, we could show that the rest length of the antagonists adapted to the different joint positions so that no tension of the agonists was necessary for maintaining these positions. However, a special psychomotoric disposition with a concentration on the adaptation to the passive movements of the subjects is necessary. Our limbs, therefore, do not only have one rest length, but— at least within a medium range of motion— any joint position can become a rest position by a change in the rest

length of the muscles.

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2. Grützner, Die glatten Muskeln. Ergebn. D. Physiol. 3, 2. Abt., p. 12, 1904, p. 80.
3. Compare with the corresponding observations by Allers and Scheminzky, *Pflüger's Archive*, 212, 169, 1926.
4. Figure 4, p. 634.
5. See footnote 1, p. 628.
6. Braus, Anatomie des Menschen, Bd I, Springer, Berlin 1921, p. 391, Figure 200.
7. Wachholder, *Pflüger's Archive*, 199, 625. 1923, p. 633.
8. Haas, *Pflüger's Archive*, 212, 651, 1926.
9. That such elastic forces are actually present is shown in the elastic rebound which is discussed next.
10. Rieger, Zeitschr. f. Psychol. u. Physiol. d. Sinnesorg., 31, 1, and 32, 377, 1903.
11. Isserlin, Kraepelins psychol. Arbeiten 6, 1, 1910.
12. F.H. Levy, Die Lehre vom Tonus und der Bewegung. Berlin 1923.
13. Wachholder and H. Atenburger, *Pflüger's Archive*, 214, 642, 1926.
14. Pfahl, Zeitschr. f. d. ges. Neurol. u. Psychiatrie 1, 503, 1910.
15. The results show that the stretch of a muscle—and that a stretch was present is seen in the existence of the rebound—is not sufficient to elicit a stretch reflex (“Eigenreflex” by Hoffmann), regardless of how fast it happened. The reflex also has to be primed by an existent contraction or innervation of the muscle. On the preparatory influence of muscle contraction, see Hoffman: Untersuchungen über die Eigenreflexe (Sehnenreflexe) in menschlichen Muskeln. Berlin 1922.
16. Similar results were obtained by R. Müller, using the Mangold’s sclerometer. *Pflüger's Archive*, 206, 106. 1924.
17. Springer, Zeitschr. f. Biol. 63, 201, 1914.
18. It needs especially mentioned here that the described shortening and lengthening reaction in the rigor following decerebration after cutting the rami communicantes should disappear (Royle). But this is disputed by others.
19. Wachholder, *Pflüger's Archive*, 209, 218. 1925.
20. O. Foerster, Die Physiologie und Pathologie der Koordination. Jena, 1902.
21. von Weizsäcker, Dtsch. Med. Wochenschr. 1923, No. 43.
22. Leibowitz, Dtsch. Zeitschr. f. Nervenheilk., 82, 314. 1924.
23. That the shortening and lengthening reaction in the rigor after decerebration probably goes along with a change of the rest length of the muscles can be concluded from the fact that Noyons and v. Uexküll found the muscle to be equally hard with and without load (Zeitschr. f. Biol. 56, 139, 1911).
24. W. Trendelenburg, *Pflüger's Archive*, 201, 198, 1923.

Postscript

Unfortunately, this publication of 1927 is the last article that Wachholder wrote on motor control. Following this, Wachholder published his monograph, which was his habilitation, required in the German academic system to be eligible for a professor position. After accepting a professor position in Breslau, he changed his field of research to nutrition. Hans Altenburger moved on to work in another institute working on EEG studies. But he died very prematurely a few years later.

In this monograph of 1928, however, Wachholder integrated his results of all previous studies into a comprehensive view of movement coordination. Not

only summarizing his previous work, he also extended his review by additional studies unpublished in his articles. Given the promise in the present paper for more quantitative analyses of the elastic properties of muscles and rest length, he indeed included further data in the monograph. As promised, he investigated several subjects over different ranges of motion. The following text is a translation of some paragraphs in this monograph (pp. 55-57) that smoothly extend from the summarized insights of the above article.

A not insignificant confirmation of the above summarized conclusions is provided when the elastic rebound is measured at different limb angles and when the different values are compared. In the results listed in the table below, one can see that the elastic rebound (within the measurement resolution of this method) has the same strength regardless whether the hand is moved from 30°–20° volar, or from 20°–10°, or from 10°–0°. This would not be possible if the limb had only a single fixed rest length, for instance at 20° volar. In this case, the rebound would have to be twice as strong from 10° to 0° compared to 20°–10°, as for the first movement the antagonists are stretched by twice the amount. Obtaining the same rebound is only possible if both antagonists in the two movements are stretched from a comparable rest length, that is, when the rest length is moved from 20° volar to 10° volar. These results of the elasticity measurements agree with the measurements of the action currents in one other sense. They show a considerable increase in force of the elastic rebound for a dorsal flexion of 10° onwards from the same position from which also action currents occur.

What determines this increase in the elastic rebound, or why is the change in rest length not possible over the entire range but only over a more or less confined range? One reason is surely that in the vicinity of the limits of the range of motion, other tissues, especially the ligaments, are stretched, and that these elastic forces can only be compensated by an active contraction of

Strength of the Elastic Rebound Measured in the Hand in Grams for Passive Movements of 10° From Different Initial Positions

Passive movements	Frau W.	Frau G.	Frl. Ki.	Ka.	A.	H.	Pr.	U.
30°–20° volar	250	300	350	—	270	350	370	350
20°–10° volar	270	270	320	250	270	350	350	350
10°–0° volar	270	270	400	250	350	420	370	370
0°–10° volar	300	400	400	270	420	520	470	370
10°–20° dorsal	400	550	450	400	450	620	500	470
20°–30° dorsal	550	—	450	500	500	800	600	500

Note. The values of women are lower than men. Only A. and especially Ka., who is very active in sports, have similarly low values. The subjects Frau W., Frau G. and Frl. Ki. are three female subjects, listed as Mrs. ('Frau') and Miss ('Fräulein').

the muscles. Unfortunately, as of yet there are no further studies that examine whether the onset of the ligament stretch is coincident with the joint angle at which action currents start to appear. Such studies are desirable because it is equally possible that the stretch of the ligaments occurs only much later and closer to the limits of the range of motion. Then, the identified boundary for adaptation is truly due to a limitation in the adaptability of the muscle's rest length. However, a preliminary conclusion can be gained from our measurements of the elastic rebound. If the latter hypothesis is true, it can be expected that the strength of the rebound follows Hooke's Law from the limit of adaptation onwards: Corresponding to the degree of passive stretch, there should be a linear increase in force. For a dorsal flexion of 20°, the rebound should be approximately twice as strong than for a flexion of 10°. As the values in the table show, the increase is significantly slower so that we can assume that also in this case a significant part of the elastic forces are compensated for. It therefore seems that an adaptation of the muscle's rest length is possible over the entire range. The limits for which an adaptation of rest length is possible are solely set by the stretch of the ligaments.

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Editor's Endnotes

¹This definition of rest configuration differs from the one accepted currently within the equilibrium-point hypothesis (Feldman & Levin, 1995; Feldman et al., 1998b). In the

latter, the rest configuration is defined as the state at which the external forces are balanced by the forces generated by active muscles.

²Wachholder and Altenburger use the somewhat obsolete term “action currents” to refer to electrical activity measured by intramuscular recordings.

³It is now well established that immediately following a voluntary movement, particularly a fast one, there is an increased level of co-contractions of the agonist-antagonist muscle pairs (for review, see Gottlieb et al., 1989). This co-contraction takes seconds or even tens of seconds to disappear, just as mentioned in the text.

⁴More information about the needle electrodes and a detailed explanation of the string galvanometer can be found in Sternad and Corcos (2001) and Sternad (2001).

⁵It is not exactly clear without further reading which muscle is referred to as the “antagonist” of the passive movement. For the discussed dorsal wrist flexion, Wachholder assumes that the wrist flexor muscle is the agonist and the wrist extensor is the antagonist. The fact that the agonist is active to fixate the limb in the new position indicates that the agonist needs to develop activity to counteract contraction induced by the antagonist’s stretch in the new position.

⁶These observations are similar to those reported later in experiments under the “do not intervene voluntarily” instruction (Asatryan & Feldman, 1965; Latash, 1994). In both cases, the subjects are expected to allow external forces to move their limb to a new position. However, in experiments by Wachholder and Altenburger, the subjects were always expected to keep their muscles relaxed while in the “do not intervene voluntarily” experiments, the subjects were to allow their limbs to move to a new equilibrium under the action of an external perturbation, while their muscles showed changes in their activation levels.

⁷In the 1928 monograph, Wachholder reports similar studies on forearm movements. The range where no active currents were found was between 70 and 160°. However, differences between individuals were reported to be relatively large.

⁸Within the equilibrium-point hypothesis, this observation would be interpreted as a limitation in the range of shifts of the threshold of the tonic stretch reflex for the involved muscles (Feldman & Levin, 1995; Latash, 1993). Recently, such limitations have been described and discussed in relation to spasticity (Jobin & Levin, 2000; Levin et al., 2000).

⁹This question whether different portions of a single muscle show the same activation patterns was the subject of extensive studies resulting in an entire chapter in the 1928 monograph. Wachholder compared signals from different locations with respect to their dominant frequency bands, specific periodicities, such as group-like bursts, and relative timing between parts of a single muscle and antagonistic muscles. These results led to the assurance that his method reports the one dominant activity. Also, the differences in the activity patterns have further led him to propose a classification into three innervation patterns: postural innervation, stiffening innervation, and movement innervation (see introduction on fundamental types of movements).

¹⁰This conclusion presents, in a very precise form, the basis of one of the major components of the equilibrium-point hypothesis, namely an ability of humans to modify the rest length of their skeletal muscles. Note that Wachholder’s study had been performed a quarter of a century before the pioneering animal studies by Matthews in the late 1950s (Matthews, 1959) and human studies of Feldman in the mid-1960s (Asatryan & Feldman, 1965; Feldman, 1966).

¹¹One cannot exclude effects of small changes in the muscle activation level in these experiments. On the other hand, since silent muscles are rather compliant, any elastic rebounds in these experiments were much more likely to be produced by the tendon’s elasticity (Zajac & Gordon, 1989).

¹²Phasic changes in the activation of the stretched muscles (the antagonist) were probably due to both the monosynaptic stretch reflex action and pre-programmed reactions (also known as triggered reactions, long-latency reflexes, and M2-3; Chan & Kearney, 1982; Nashner & Cordo, 1981; Phillips, 1969). The latter seem to be more likely, since pronounced monosynaptic reflexes are typically seen only during very fast changes in muscle length.

¹³Following this publication, the same experiment was performed on passive forearm

movements. The rebound is much stronger and is only compensated for by a counterweight of 700 g.

¹⁴This conclusion is only one step away from formulating the main principle of the equilibrium-point control: Movements from a certain body configuration to another body configuration result from changes in the centrally encoded equilibrium states of the muscles and limbs (cf. Feldman, 1966, 1986).

¹⁵These insights are well ahead of their time (cf. Bizzi et al., 1992; Feldman, Levin, 1995; Levin & Feldman, 1994; Levin et al., 2000). Can human muscles be relaxed over the whole range of anatomically possible joint motion? What is the role of the mechanical properties of passive tissues in defining equilibrium states of the muscles?

¹⁶This conjecture is close to suggesting that it can be neural signals that are centrally programmed rather than peripherally induced, similar to those associated with voluntary movements, that are responsible for changes in the rest length of muscles. This issue is further elaborated in the 1928 monograph. Here Wachholder explicitly addresses questions about the contribution of peripheral reflectory contributions as compared to central signals from higher motoric centers. He separates his discussion for the activation of agonists, antagonists, and synergists. Further, he questions to what degree the specific activation signals truly reflect properties of the central activation.

¹⁷The idea of non-tetanic contractions or Sperrung (blockage) has been discussed again in the monograph, as it was a vibrant idea in the 1920s. However, after stringent argumentation of various experimental results with metabolic and hardness measurements on human and animal muscles, *in vivo* and *in vitro*, Wachholder discarded this hypothesis as unsupported. Yet, the clinical relevance of these ideas remains and is exemplified by recent studies by Levin and her colleagues (Jobin & Levin, 2000; Levin & Feldman, 1994; Levin et al., 2000) who have interpreted uncontrolled muscular contractions in patients with spasticity as a consequence of an inability to shift the rest length of muscles beyond a certain range.

¹⁸This discussion of the role of an interaction between processes of muscle activation and elastic forces emerging during voluntary movements is still very fresh. Does an increase in movement speed require special control of the process of braking to avoid rebounds or terminal oscillations? Hypotheses based on control of muscle forces or muscle activation patterns (Atkeson, 1989; Gottlieb et al., 1989) assume that during a fast movement, the process of stopping the movement needs to be planned. Within the equilibrium-point hypothesis, two opinions have been expressed. One is that the feedback provided by velocity-sensitive components of proprioceptive reflexes is sufficient to stop a very fast movement (Feldman, 1986). The alternative is that non-monotonic (N-shaped) control signals are required to stop a fast movement (Latash, 1993; Latash & Gottlieb, 1991).

¹⁹Such connections between laboratory experiments and their possible implications for everyday movements, clinical testing, and here artistic movements such as playing the violin, reflect a deep concern of Wachholder. Critical of the mechanistic physiology prominent of his times, which limited its studies to frog preparations and microscopic recordings, he criticizes these insights as being too removed from any application to clinical and everyday work and gymnastic movements. In his 1928 monograph, he dedicates one long final chapter to deriving recommendations for gymnastics and ergonomic actions.

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