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The contribution of gravitational torques to limb position sense

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Summary. An experiment is reported which examined whether gravitational torque acting about a joint is used by the CNS in elbow joint angle matching. Subjects were required to match the joint angles of their two limbs while the external torques acting about each elbow were systematically varied. It was found that when the matching limb was differentially loaded, the error in the produced reference angle corresponded to the directional prediction of a proposed gravitational torque hypothesis. The data suggest that torque sensation is an accessory source of information in limb positioning.

Key words: Joint angle sense – Gravitational torque – Proprioception

Introduction

The ability of individuals to perform, without vision and with considerable accuracy, such tasks as the reproduction of a limb position or the matching of the position of one limb to that of the other, raises numerous questions about the characteristics of proprioceptively-guided movements (Stelmach and Diggles 1982). It is clear that the CNS needs to take into account external forces if these movements are to be accomplished accurately. The most important of these forces is the ubiquitous one of gravity, which continuously produces torques around each of the joints in the body. The role of gravitational torques in the regulation of movement is often alluded to, but has yet to be fully incorporated into theories of motor control. For example, Feldman and Latash (1982a, b) give muscles torque a central position in their equation governing the relationship between motor commands and joint position sense. Bizzi et al. (1976) explicitly state that external loads are a determinant of the equilibrium point governing final head (or limb) position. It is noteworthy that the experimental work exemplified by Bizzi's investigations of the mass-spring model of limb and head positioning have employed only horizontal supported movements precisely because of the varying external torque produced by gravity in movements in other planes. Gravitational torques complicate this otherwise parsimonious account of how limbs are positioned. Kelso and Saltzman (1982) also emphasize the inseparability of gravitational torques and limb orientation, pointing out that the relative contributions of gravity and muscle stiffnesses for a stable equilibrium angle vary with the arm's orientation in the gravity field, and that nervous system control must complement the force field of the environment. In spite of this speculation, the ways in which gravitational torques are sensed, compensated for or utilized in control have not been addressed.

Watson et al. (1984) have shown that force signals and position signals are both used in the judgment of limb positions. In their experiment subjects first attained a criterion position while the movement of the arm was opposed by a spring. The blindfolded subjects then attempted to reproduce the position against springs of different stiffness. A weaker spring produced an overshoot relative to the error when the same spring remained in place for the reproduction movement. A stronger spring, conversely, led to a relative undershooting. The results suggest that subjects associated specific arm flexor forces with positions, and were unable to ignore force

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Offprint requests to: C. J. Worringham (address see above) information in position judgments even when they were told to do so. A similar explanation is given by Fitger (1976) to account for the error in the setting of a bar to the subjective horizontal in different gravitational conditions. She concluded that tactile-kinesthetic judgments are influenced by gravity independently its effect on the visual system, that this direct gravitational effect is probably mediated by muscle receptors, and that the arms represent a system for the perception of the direction of gravity independent of each other and of information from the vestibular apparatus.

The association of limb positions and the muscular forces necessary to oppose gravitational torques is the most plausible explanation for the types of errors which have been found in aiming movements in zero-gravity. During testing while in the zero-g phase of parabolic aircraft flights Gerathewohl et al. (1957) found that subjects systematically hit above the center of the target in aiming movements even though these were visually guided. A more dramatic overshooting was demonstrated by Von Beckh (1954) in similar tests when vision was not permitted. Investigations for the Soviet space program have shown similar systematic hitting above the target in zero-g (Yegorov and Pavlov 1966).

Soechting (1982) found that subjects can match arm orientations in the gravity field more accurately than they can match elbow angles *per se*, and also tested some subjects with a 2.5 kg load on one arm and none on the other. Since no deterioration in performance was seen, he concluded that torques are not used in limb positioning. We question this conclusion for three reasons: first, the subjects were aware that only one arm was loaded and could have largely over-ridden torque information; second, subjects could still have used torque information independently for each limb (i.e. relative, rather than absolute torque-matching); and third, its conclusions were based on variable error data which gives no information about directional bias.

Since the nature of torque involvement in limb positioning seemed unclear, an experiment was performed to determine whether the accuracy of elbow angle matching is susceptible to influence by manipulation of the elbow joint torques. Specifically, it was hypothesized that if the CNS is sensitive to and uses gravitationally produced joint torques in the estimation of limb positions, differential loading of both forearms would lead to systematic errors in direction and magnitude. For example, if the matching limb is loaded with a slightly smaller torque than the reference limb, a correspondingly greater angle should be produced at the matching limb elbow if the subject is matching torques. If torques were in no way involved in position sense, torque differences should have no systematic effect on matching errors.

It was felt that the best way to test our hypothesis was to examine torque differences which are below those which can be consciously discriminated, since discriminable differences may be deliberately compensated for.

Methods

Twenty subjects participated in the experiment (16 male, 4 female; mean age: 25.3 years, range: 20–34). The blindfolded subjects sat at a table with their upper arms resting on a surface inclined at 45° to the horizontal, with hands supinated. Foam-rubber backed splints were attached to each arm with a crepe bandage. The splints projected beyond the finger-tips to a point 80 cm from the elbow (the trochlear notch was assumed to be the axis of rotation). 1003.8 gm masses could be attached to each splint and moved closer to or further from the joint. When placed 65 cm from the joint, the external torque was 6.4 N.m with the forearm and splint horizontal. This served as the 'reference' torque. A fine wire cable was attached to the splint and ran through pulleys across a calibrated scale. The cable was kept in tension by a 5 gm mass. The scale allowed each forearm's inclination to the vertical to be measured. Subjects were told that the task was one of elbow angle matching, but it was pointed out that since their upper arms were parallel, producing equal elbow angles would be the same as making the forearms parallel. The task was thus an elbow angle matching and forearm inclination matching task simultaneously.

Subjects were told that the torques would be identical for each arm, but that they would both be changed every four trials. In fact, the torques were identical for only one-third of the trials. For another one-third, the torque on the matching limb was 5% greater than that on the reference limb. The torque was 5% less for the remaining one-third of the trials. These differences proved to be too small for subjects to reliably notice and were chosen because in earlier psycho-physical testing a mean value of 6.67 (±3.8) % torque difference was found to be necessary for subjects to be better than chance in reporting which of the two limbs was loaded more heavily. On average, subjects made errors in torque judgment at torque differences as high as 12.9%. We attribute the relatively poor ability of subjects to discriminate consciously between different torques to the fact that they were prevented from using vision to align the arms, and, in an agreement with our hypothesis, they could not successfully differentiate the force signals attributable to different torques from those attributable to different arm positions. In addition, they could not independently estimate the inertial properties of the load by rapid oscillating movements, the mechanism which allows mass discriminations to be made (albeit less accurately) in space flight (Ross 1984). On questioning, only three subjects mentioned any suspicion that the torques were not the same, and these subjects thought that the torques may have been different on only one or two of the 96 trials.

Subjects were instructed to slowly flex either the right or the left elbow until instructed to stop by the experimenter. They were then required to hold that position and match it with the other arm. The experimenter recorded both angles and told the subject to return each forearm to the surface of the table, one at a time. Both left and right arms served as the reference arm an equal number of times for each subject, in a quasi-random order. Four different target angles were used: 45, 55, 65 and 75° of forearm inclination to the horizontal.

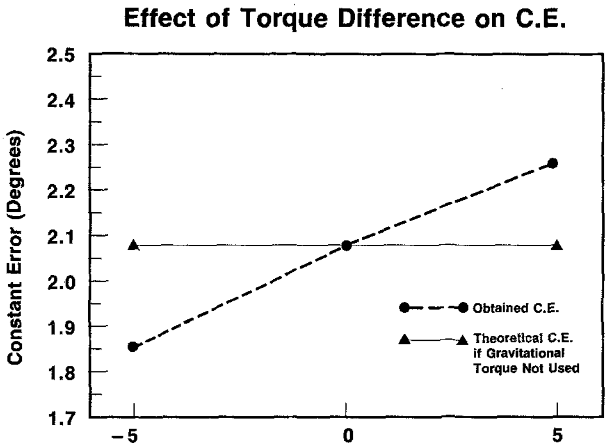

Fig. 1. Mean obtained and theoretical constant errors plotted as a function of the torque difference (in percent) for the matching arm

Table 1. Mean constant errors (CE) for torque differences in degrees

Torque differences	Target angles 45°	55°	65°	75°
+5%	1.8	2.2	1.8	1.6
0	2.1	2.4	2.0	1.8
−5%	2.0	2.6	2.4	2.0

Results

Constant Error (CE) data from the experiment were analyzed with a 3-way factorial ANOVA with repeated measures. Factors were TORQUE (5% less, equal, 5% more); ANGLE (45, 55, 65, 75° of inclination); and ARM (left or right arm serving as the reference arm). There was a consistent tendency for subjects to overshoot the reference limb's position when moving the matching limb. This is shown by the grand mean of +2.06° of CE, with CE calculated by subtracting the matching limb's inclination from that of the reference limb.

Neither ARM nor ANGLE showed significant effects ($p > 0.05$) but on average the CE was larger when the right arm was the matching limb. The effect of different target angles was equivocal. No specific predictions about the effect of angle or CE were made prior to the experiment. Although the absolute torque values increase at the larger angles by virtue of the increased horizontal distance between the joint and center of mass, the matching and reference arms had the same *relative* loading independent of angle. It is thus not at all clear whether errors should be larger at one angle than at another. In addition, movements form the table surface to each angle were shortest to the larger angles, and since errors normally increase with displacement, this effect may complicate the interpretation of angle effects. The effect of the torque manipulation on constant error was significant ($p < 0.05$). Errors were in the direction predicted by the hypothesis: compared to the mean CE when the torques were identical, the mean CE was smaller when the torque on the matching limb was 5% less than that on the reference limb, and larger when the torque was 5% larger. This corresponds to a tendency of subjects to produce matching arm positions which are biased in the direction necessary to match the torques acting about each elbow (see Fig. 1). Difference between the 5% less and the equal conditions, and between the 5% more and equal conditions were not significant ($p > 0.05$), although a majority of subjects showed the predicted directional error (13 and 12 out of 20, respectively). Seventeen of the 20 subjects' data conformed to the predicted directional error when 5% less and 5% more conditions are compared. None of the interactions between these three factors approached significance. The effect of the torque manipulation was uninfluenced by which arm performed the matching, and the effect of arm was simply additive. The same is true of the interaction between target angle and torque: Table 1 shows approximately additive effects for all but one of the 12 means represented. With 45° as the target angle, an increased torque failed to lead to larger CE.

The effect of the torque manipulation was small, but significant. In order to produce some standard against which the size of the effect could be sensibly measured, anthropometric data from each subject was used to estimate the size of the errors which would be expected if torque alone was being used in the matching task. (Of course, this would never be the case as other sources of feedback are always available). The masses of each subject's forearms and hands and the location of their centers of gravity were estimated using equations from cadaver studies of segment masses (Dempster 1955). These data, together with the masses and center of gravity locations of the splints and loads, were used to calculate by means of a trigonometric function the expected CE for each subject for a notional 60° inclination (the median of the angles actually used in the experiment). The relative contribution of the torque-sensing mechanism may be approximated by the magnitude of the actual matching error as a proportion of the theoretical error calculated on the basis of torque information only being used by the subject.

In both the −5% and +5% torque conditions, the actual CE expressed as a percentage of the theoreti-

Table 2. Observed and theoretical CE differences

	Observed CE	Theoretical CE if torques alone are used[a]	Observed CE difference as proportion of theoretical CE difference
+5%	1.85 ± 2.0	−1.35	6.43%
0	2.07 ± 1.8	2.07	0
−5%	2.26 ± 1.7	4.99	6.51%

[a] adjusted for overall positive CE

cal CE was very similar: 6.43% and 6.51%, respectively. The sources of information concerning limb position available to the subject may be considered as comprising 'torque information' and 'non-torque information'. The experimental results could be accounted for if the former is accorded a 'weighting' of about 6.5% and the latter one of about 93.5%. When the two sources of information are in conflict, and the subject is aware of this, torque information may be partially over-ridden. The averages of these expected errors are larger than the errors actually found and are shown in Table 2. Although the observed errors were not large, it should be recalled that the theoretical values against which they are compared in Table 2 represent matching of torques alone. It is highly improbable that all non-torque information would be ignored in this manner, particularly as the subjects were instructed to match elbow angles.

Discussion

As early as 1922 Weber had speculated that the sense of position and gravitationally induced force are intimately connected: "To begin with, our muscles always perceive space *as affected by gravity,* their own weight invariably ensures this result." Our results lead us to support this conclusion. We propose that the sensation of gravitational torques is an accessory source of information in slow limb positioning.

We believe that our findings substantially underestimate the true contribution of gravitational torques for the following reasons: first, the experimental manipulation of torques is not simple. If larger torque differences had been used, subjects would have been conscious of the conflict between torque and angle information and would have distrusted the former, as in Soechting's (1982) experiment. In real movements, torque information is completely reliable and may therefore be utilized to a greater extent. Second, real movements about multiple joints provide far richer torque information. For example, even during movements of the elbow in the horizontal plane where the gravitational torque at the elbow does not change with elbow flexion or extension, there is a specific relationship between degree of elbow extension and shoulder torque. Thus, torques at neighboring joints can contribute to limb position sense. In non-horizontal movements, both individual joint torques and neighboring joint torque patterns provide a reliable source of information about limb position which was available to our subjects in only an impoverished form.

Muscle afferents (both spindles and GTOs) are the likely peripheral receptors for sensing torque information, although we cannot rule out the possibility that joint afferents also mediate torques to some degree, because of the relationship which exists between gravitational torques and the reaction forces acting on a joint. This is in agreement with the conclusions of others who have shown force sensation to be inextricably linked with position judgements (Roland 1975; Rymer and D'Almeida 1980; Watson et al. 1984). Where our data complement these studies is in showing that the *negative* constant errors produced when an artificial external load is increased (e.g. elbow flexion against a stiffer spring, Watson et al. (1984)) contrast with the *positive* constant errors seen when the gravitational torque is increased (also for elbow flexion). In both cases the same mechanism, i.e. tension sensation (presumably through muscle receptors), appears to be interpreted by the CNS as giving information about position. The geometry of the gravitational load predicts an overshoot to bias the position towards the associated with the 'reference' torque, while that of the 'spring load' yields an undershoot. Since the use of the direction of gravity as a reference frame would lead to the overshooting found both in our study and in zero-g (Von Beckh 1954; Gerathewohl et al. 1957; Yegorov and Pavlov 1966), the previous findings of muscle afferent contribution to joint position sense may be given a more specific interpretation: tension in a muscle or group of muscles during slow limb movements or in static equilibrium is seen by the CNS as one reliable indication of the orientation of the relevant segment(s).

How can gravitational torques provide reliable limb position information since changing the load on a limb also changes the absolute value of the torque at any given position? We suggest that the 'rules' by which positions are inferred from torques need not use absolute values since the relationship between relative torque and absolute inclination is independent of any external load. A joint torque is always minimal of the center of mass of the segment and load is aligned vertically with the joint, and always maximal when it is at its maximum horizontal distance from the joint, whatever the load.

It is our position that the torque information is sensed at a relatively low level, analogous to the concept of unconscious proprioception; such that only large differences impinge on consciousness. That would explain why subjects in this experiment were unaware of the torque differences but nevertheless partially compensated for them. This phenomenon has been noted before: Henry (1953) found that subjects were capable of making very precise force adjustments to keep a lever in a constant position while it was perturbed by an irregular cam and that pressure changes 20 times larger were necessary for a subject to be conscious of them. The CNS appears to delegate much of the detailed processing of afferent signals to lower levels just as it does with efferent signals.

We suggest that the role of torque information is greatest at slow movement speeds, and is most useful during slow exploratory movements without visual guidance (e.g. locating an object with the hand in the dark) because a premium is put on accurate peripheral inputs in these cases. Hollerbach and Flash (1982) have shown that the gravitational component of total joint torques becomes smaller in relation to inertial and velocity torques as movement speed increases, but that "during sufficiently slow movement . . . the effect of gravity will completely dominate all other dynamic terms".

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