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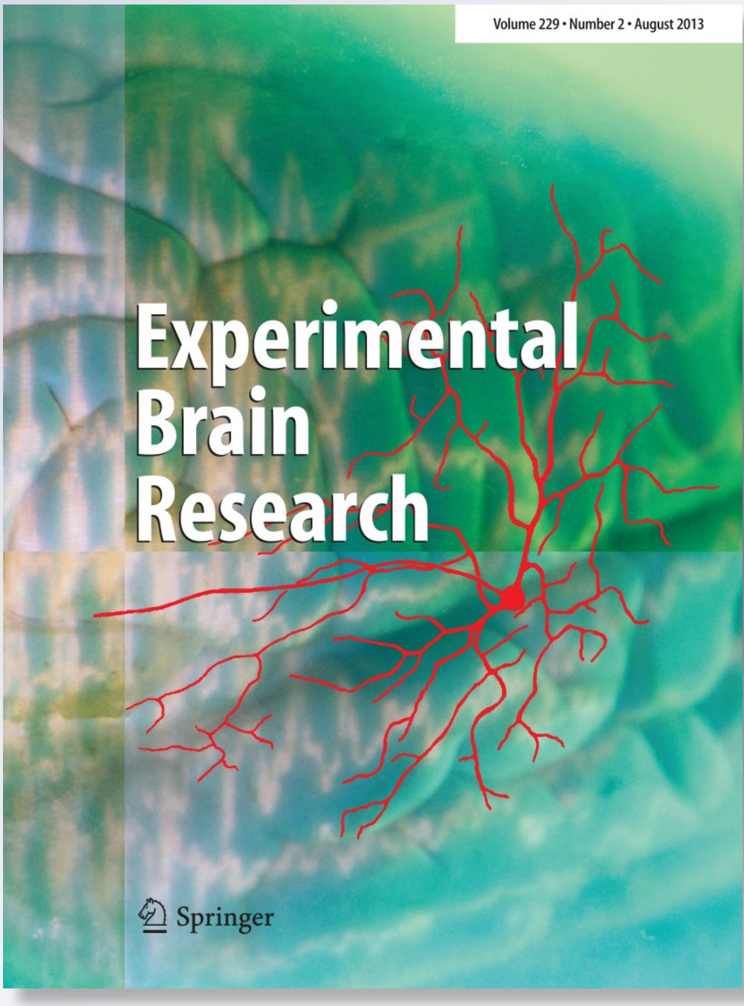

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RESEARCH ARTICLE

Pointing to oneself: active versus passive proprioception revisited and implications for internal models of motor system function

Charles Capaday · Warren G. Darling · Konrad Stanek · Carl Van Vreeswijk

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Abstract We re-examined the issue of active versus passive proprioception to more fully characterize the accuracy afforded by proprioceptive information in natural, unconstrained, movements in 3-dimensions. Subjects made pointing movements with their non-dominant arm to various locations with eyes closed. They then proprioceptively localized the tip of its index finger with a prompt pointing movement of their dominant arm, thereby bringing the two indices in apposition. Subjects performed this task with remarkable accuracy. More remarkably, the same subjects were equally accurate at localizing the index finger when the arm was passively moved and maintained in its final position by an experimenter. Two subjects were also tested with eyes open, and they were no more accurate than with eyes closed. We also found that the magnitude of the error did not depend on movement duration, which is contrary to a key observation in support of the existence of an internal forward model-based state-reconstruction scheme. Three principal conclusions derive from this study. First, in unconstrained movements, proprioceptive information provides highly accurate estimates of limb position. Second, so-called active proprioception does not provide better estimates of limb position than passive proprioception. Lastly, in the active movement condition, an internal model-based estimation of limb position should, according to that hypothesis, have occurred throughout the movement. If so, it did not lead to a better estimate of final limb position, or lower variance of the estimate, casting doubt on the necessity to invoke this hypothetical construct.

Keywords Proprioception · Active proprioception · Internal models of motor control · Corollary discharge

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Introduction

Proprioception is the sense of movement, posture, and spatial localization of the articulated body parts. It was termed the "*muscular sense*" by Sherrington (see Matthews 1982) and is rightly referred to as the sixth sense. A long-accepted principle of sensorimotor physiology is that a self-generated movement of a body part provides for greater accuracy in localizing it proprioceptively compared to its displacement by an external agent (Paillard and Brouchon 1968). They further emphasized that it was the active movement itself and not the self-maintained posture at movement termination which provided for the greater acuity of localization. Subsequent studies have in the main supported the idea that proprioceptive localization accuracy is better in active than in passive movement conditions (e.g., Adamovich et al. 1998; Gritsenko et al. 2007; Fuentes and Bastian, 2010; Monaco et al. 2010). However, recent work (Jones et al. 2010) found similar accuracy under active and passive conditions in a highly constrained setup using a verbal judgment of index position relative to visual or proprioceptive references instead of a reaching movement as in most previous work. Paillard and Brouchon (1968) proposed two non-mutually exclusive mechanisms to explain their results. First, Ia-spindle afferents may be more sensitive during active movements due to activation of γ-dynamic motoneurones. Second, a central estimate of limb position based on a corollary discharge may also contribute during active movements. The idea was prescient, as by the 1990s the closely related concepts of internal models, derived from engineering control theory, began to emerge (e.g., Wolpert et al. 1995; Wolpert and Kawato 1998).

Here, we deal specifically with internal forward models. The basic idea as it relates to the control of movements is that limb position can be derived, in principle, from the motor command, and a neuromuscular model of the limb contained within the CNS. Moreover, the predictions of the internal model can be combined with movement-related feedback to obtain an estimate of limb position, which ought to be more accurate and less variable than from either source alone. This signal processing scheme is known as state estimation, of which the Kalman filter is an example. Wolpert et al. (1995) reported that subjects tend to overestimate the final position attained by the arm when guided only by proprioception. They suggested that this could be fully accounted for by assuming that the motor command (corollary discharge) and the sensory feedback (re-afference) were used by CNS circuits operating as a state estimator. However, to obtain a qualitative fit between their simulation of a state estimator and the experimental data, the gain coupling force input to the arm model was set to a value greater than one and the sensory feedback had a lower variance than the arm model's estimates. This ensures that the state-estimate will be biased toward the arm model's prediction.

We sought to re-examine the issue of active versus passive proprioception in natural, unconstrained, movements in 3-dimensions. And, in the process, also subject the state-reconstruction scheme proposed by Wolpert et al. (1995) to an independent test. We asked subjects to make proprioceptively guided movements of their dominant arm to touch, with the index fingertip, that of their non-dominant arm. The latter was positioned actively by the subject or passively by the experimenter. In the active condition, proprioceptive feedback and putatively an internal model-based estimate would be available for determining the absolute spatial location of the index finger, whereas only proprioceptive information would be available in the passive condition. We found no difference in localization accuracy, or variability, between active and passive conditions. This is an important physiological finding that stands on its own and has strong implications for the state-estimation hypothesis proposed by Wolpert et al. (1995).

Methods

Experiments were done on eleven subjects, ten males, aged between 24 and 52 years of age. One subject was left-handed. The study was approved by the local ethics committee. Subjects agreed to participate in the study, after being informed of its nature and purpose.

Experimental rationale

If a state-estimator scheme is used by the CNS, then the estimate of limb position ought to be better, or less variable, for active than for passive movements. This is because, for active movements, motor commands and sensory feedback would be used conjointly to determine limb position. By contrast, only sensory inputs, which according to the hypothesis are noisy, would contribute during passive movements. Thus, the notion that the sense of position is allegedly better following an active versus a passive movement appears consistent with the state-estimation hypothesis. Nevertheless, all studies showing better proprioceptive localization during active movements involved unnatural motor tasks requiring memory, or that constrained movements in one, or two, dimensions and were carried out in special laboratory apparatuses that provided cutaneous inputs not usually present during natural limb movements (e.g., Adamovich et al. 1998; Gritsenko et al. 2007; Fuentes and Bastian 2010; Monaco et al. 2010). For the present study, we used a very simple task with no constraints on motion of the shoulder, elbow, wrist, or digit joints. Importantly, our tasks were purely proprioceptive in nature, requiring no memory of target locations.

Behavioral task

Subjects sat on a round stool adjusted so that their feet rested firmly on the floor. Their arms rested on the thighs with the hands just proximal to the knees (start position) and their eyes were closed throughout the experiment. In the active movement task, the subjects were asked to move their non-dominant arm (target arm), with index finger outstretched, from the rest position on the ipsilateral thigh to a self-determined location in extra-personal space and maintain it there until they brought the index finger of the contralateral (dominant arm) in apposition to that of the actively moved target arm (non-dominant arm). Put simply, they were asked to bring the tip of their index fingers together by first moving one arm and then promptly moving the other. They were instructed to make target arm movements deliberately, without hesitation, and to a wide range of locations throughout extra-personal space. The typical range of target positions relative to the starting position of the dominant fingertip were within 70 cm forward/backward, 50–60 cm left/right (greater amplitudes toward the non-dominant side), and up to 80 cm upward. Movements of the dominant arm to the target arm typically began in <200 ms following stop of the target arm.

Only two constraints were imposed. First, that they not make movements terminating in a fully outstretched target arm and second, not to grope to touch the target finger. That is, the movement to touch the target fingertip had to be made in one "fell swoop" and the final position of the fingertips held for a short time before returning the arms to their start position. Before beginning the experiment, all subjects, in order to familiaze themselves with the task, practiced the active movement task with about a dozen trials, eyes closed. Importantly, this was the only occasion they had throughout the experiment to practice the finger apposition task, and they were given no feedback concerning accuracy during these practice trials. The passive movement task was identical in all respects, except that the target arm was moved and maintained in its final position by one of the experimenters. The experimenter moved the subject's arm supporting the forearm at the hand and elbow, keeping the index finger slightly outstretched. The subjects were instructed to remain relaxed when manipulated by the experimenter. In all cases, no muscle tone (resistance) was detected by the experimenter. In both tasks, subjects had some 10–15 s between trials. Typically, subjects made 20–30 active movements in one block of trials (condition) and about an equal number of passive movements were imposed by an experimenter in another block of trials. The order of the trial blocks was random from one subject to another. We also determined accuracy of dominant arm movements to touch the actively positioned non-dominant arm fingertip with eyes open in two of the eleven subjects.

Kinematic measurements and analysis

Movement kinematics and final position attained were measured by small (1 × 2 cm) 6° of freedom electromagnetic sensors (Polhemus, Colchester, VT) attached to the fingernail of each index finger. The sensor signals were digitized at 60 Hz/channel. Only the position coordinates in three orthogonal (x, y, and z) directions were used in the present analysis. End of motion was assessed visually on a display of 3D movement speed and position as the time when the fingertip stopped and maintained a consistent position. The point at which movement speed first dropped below 2 cm/s was also measured to remove effects of any groping for the target finger on localization errors. This resulted in only slightly larger errors than those measured visually (see results). The difference in position between the two fingertips at movement termination, the positioning error, was simply the Cartesian distance between the coordinates signaled by each sensor. It should be noted that the positioning error measured from the sensors cannot be zero, since it is impossible for the two sensors to be in the same spatial location. Indeed, even when the fingertips are touching, the two sensors averaged about 3 cm (range: 1.8–3.5 cm) apart. Notably, a similar distance "error" could be measured if the subject touched a more proximal part of the target fingertip or was besides (not touching) the end of the fingertip because the distance between the sensors was similar to that when the fingertips were touching. Thus, we not only measured the 3-dimensional Euclidean distance errors on individual trials, but also examined errors in the X (anterior), Y (medial–lateral), and Z (vertical) dimensions to fully characterize the errors.

Statistical analysis

We computed mean Cartesian distance errors and variability (standard deviation or SD) of those errors for each subject as well as constant (mean) and variable (SD) of errors in each of the X, Y, and Z dimensions for each subject. Paired t-tests were used to test for differences between mean and SD of Cartesian distance errors in the active and passive conditions to test our primary hypothesis and that errors in the passive condition are similar to those in the active condition. We also performed two-factor (condition—passive, active; dimension—X, Y, and Z) repeated-measures analyses of variance on constant and variable errors in the X, Y, and Z dimensions to test for differences in bias (constant error) and variability of these errors in passive and active conditions. Huynh–Feldt adjustments were used to adjust p-values for the dimension factor.

Results

We will first show that a wide range of target positions was studied and that passive and active movements to those target positions were smooth, as were the movements made by the reaching hand. We then report three main sets of observations. First, that proprioceptive localization of absolute position is very accurate. Second, that it is no better following an active movement than it is following a passive movement. And third, that there is no amplitude or directional bias error as a function of movement duration.

Movement characteristics and explored workspace

The target positions we studied encompassed most of the workspace that could be reached by subjects without fully extending the left or right arm. An example of the range of target positions attained by one subject is shown in Fig. 1. Most of the target (left index fingertip) positions were in front of, to the left, and above the starting position of the right index fingertip (Fig. 1a, b). There were a few target positions behind the reaching fingertip (i.e., close to the body). For all subjects, the target positions in both conditions

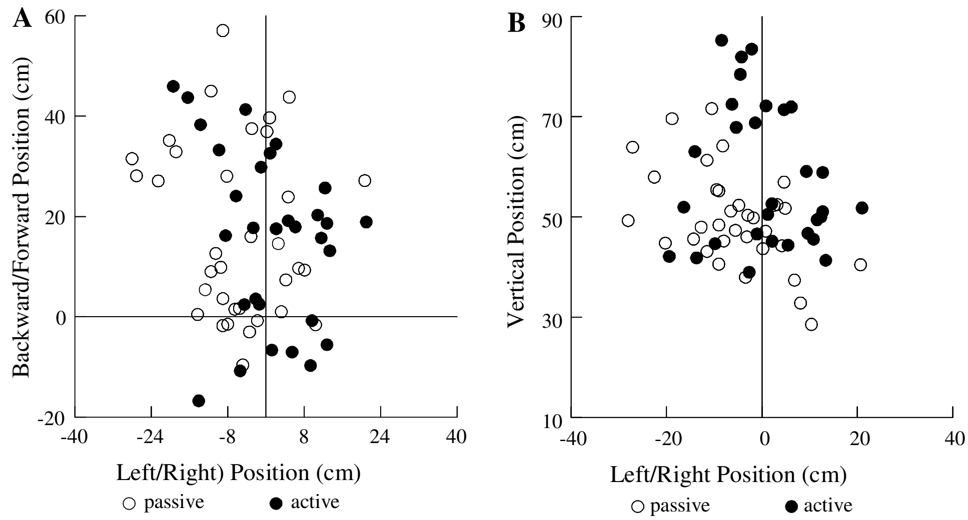

Fig. 1 Target positions for the active and passive conditions in subject AL. Each plotted point is *left index fingertip* position for a single trial in the *horizontal plane* (**a**) and frontal plane (**b**) relative to the starting position of the *right index fingertip* on the *right thigh* (0,0 origin of each graph). The subject's right shoulder would be located about 40 cm above and about 20 cm behind the origin

encompassed large and comparable regions of the natural arm workspace, as can be appreciated from Fig. 1.

Movements of the target hand by the subject (active condition) and experimenter (passive condition) were smooth with bell-shaped velocity profiles, as were movements of the subject's reaching finger to the target (Fig. 2). Note also that movements of the reaching finger began either shortly after (200 ms or less) the target finger stopped moving (e.g., Fig. 2 a, b, d), or nearly simultaneous with end of the target finger motion (e.g., Fig. 2c). Importantly, the displacement of the moving finger was not terminated by it accidentally colliding with the target finger. This is clear from the smooth, discontinuity free, tangential velocity profile of the moving finger. This shows that subjects moved in one fell swoop, voluntarily stopping the motion at the endpoint, as instructed. There were also some cases when the reaching finger began motion shortly before target finger motion stopped. Moreover, in some cases, the target hand made a second small movement during reaching finger motion in the active condition when the subject actively moved the target finger (e.g., Fig. 2a, b). These very small secondary movements of the target hand did not always occur and were assumed to be involuntary, resulting from the active motion of the body and pointing arm. Importantly, these secondary movements, when they occurred, were directed vertically away from the pointing arm, rather that toward it. Moreover, they did not affect the subject's performance as can be seen in Fig 2a, b. Movements made in the eyes open active condition were quite similar to those in the eyes closed active and passive conditions with smooth single-peaked velocity profiles of the target and reaching fingertips (Fig. 2e, f). As can be seen in those figures, there are very small movements of the target hand. Here too, however, they are directed vertically away from the moving hand. In simple terms, it is difficult for subjects to maintain the target arm perfectly fixed in space while moving the pointing arm, because movement of the trunk, shoulder, and arm segments required to move the pointing arm can produce motion of the target arm. Indeed, as can be seen in Fig 2,the secondary movements follow shortly after the start of the pointing arm's motion. What is clear is that the target arm finger motion was directed away form the pointing arm finger in all cases. That is, the subjects did not move the target finger toward the pointing finger. More importantly, if subjects actively reached the pointing finger with a motion of the target finger, which they were instructed not to do, they ought to have done better in the active than in the passive task, but this was not the case.

Proprioceptive versus visual localization of the Index finger

For the two subjects tested for a variety of target fingertip positions with eyes open, the mean distance errors were nearly identical to those in the eyes closed conditions (Fig. 3; Table 1). Note also that the small biases in *X*, *Y*, and *Z* direction errors were similar to eyes open (active) and eyes closed (active and passive). Thus, biases under visual and proprioceptive conditions were similar. However, *X*, *Y*, and *Z* variable errors were very slightly lower with eyes open (indicating more consistent relative positioning of the two fingertips in this condition), which is expected from the known function of vision in determining the terminal portion of a visually guided movement. Similar results were obtained when movement endpoint was measured using the 2 cm/s speed criterion. This demonstrates that subjects did not grope/search for the target fingertip in the active or passive condition, which is also clear in the examples shown in Fig. 2. Mean distance errors increased by 1–3 mm and variable (SD) distance errors increased by 0.3–5 mm when using the speed criterion. Overall, the results presented in Fig. 3 show how remarkably

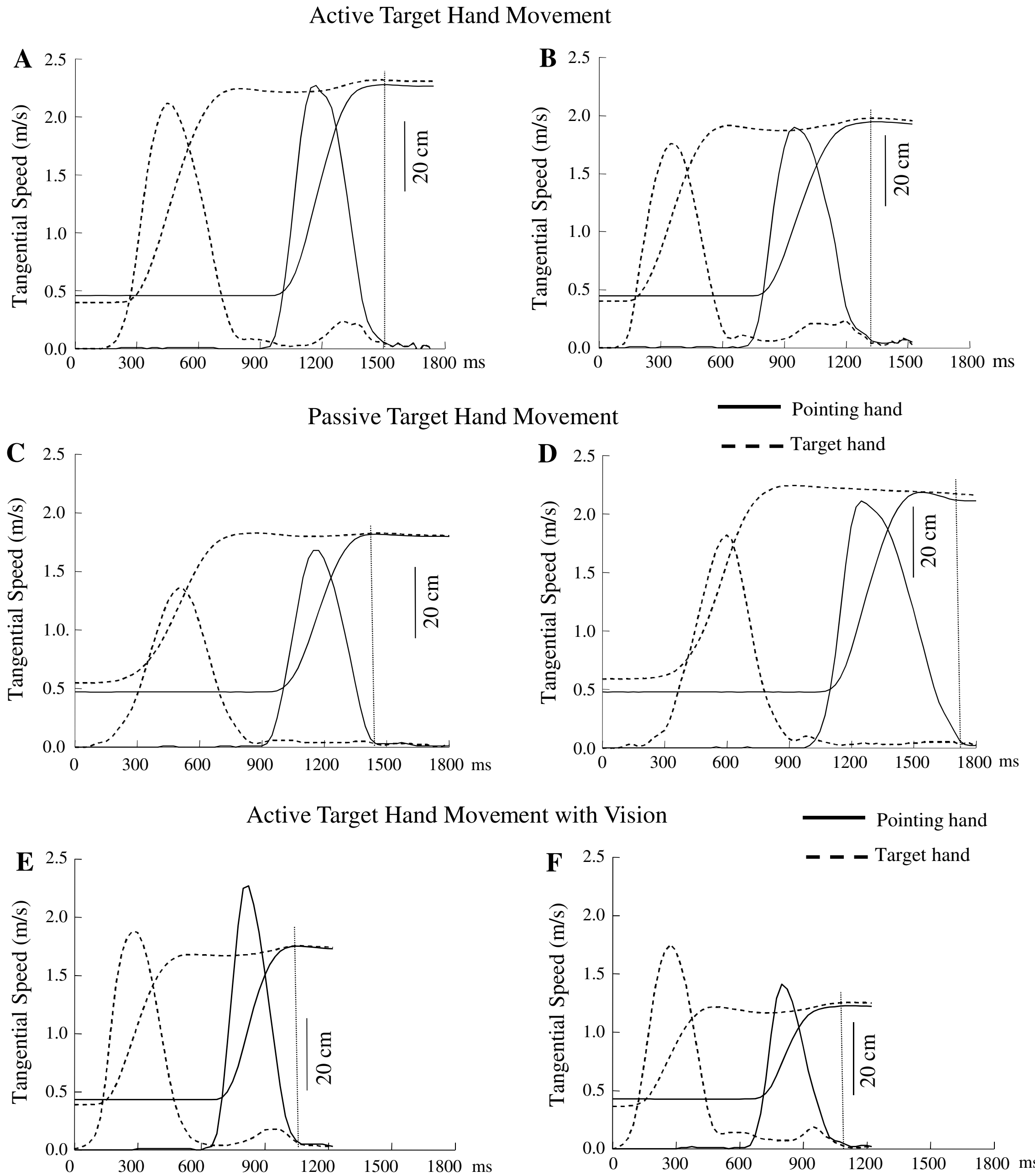

Fig. 2 Examples of tangential speed and vertical displacement temporal profiles of the target index tip (*dashed lines*) and pointing index tip (*solid lines*) for subject OH. The vertical calibration bar is for vertical displacement. The *vertical dotted line* indicates the 2 cm/s tangential speed criterion for time of movement endpoint (i.e., the time at which measurements were made). **a**, **b** Movements in the active condition and **c**, **d** movements in the passive condition (target hand displaced by the experimenter). **e**, **f** Movements in the eyes open active condition. Note that the pointing hand decelerated smoothly to stop at nearly the same height as the target hand in all conditions

accurate subjects were in pure proprioceptive localization under active and passive conditions. And, that they were no more accurate when vision was allowed, as there was only a 1-mm difference in mean distance errors with similar variable errors. The eyes open condition also makes the point that our measurements accurately reflect the close apposition of the two finger tips in the purely proprioceptive tasks.

Proprioceptive accuracy in active versus passive movement conditions

Pointing errors were small, and there were no differences in errors between active and passive positioning of the target arm. Position constant errors on individual trials were usually small (<4 cm) in each of the *X*, *Y*, and *Z* directions

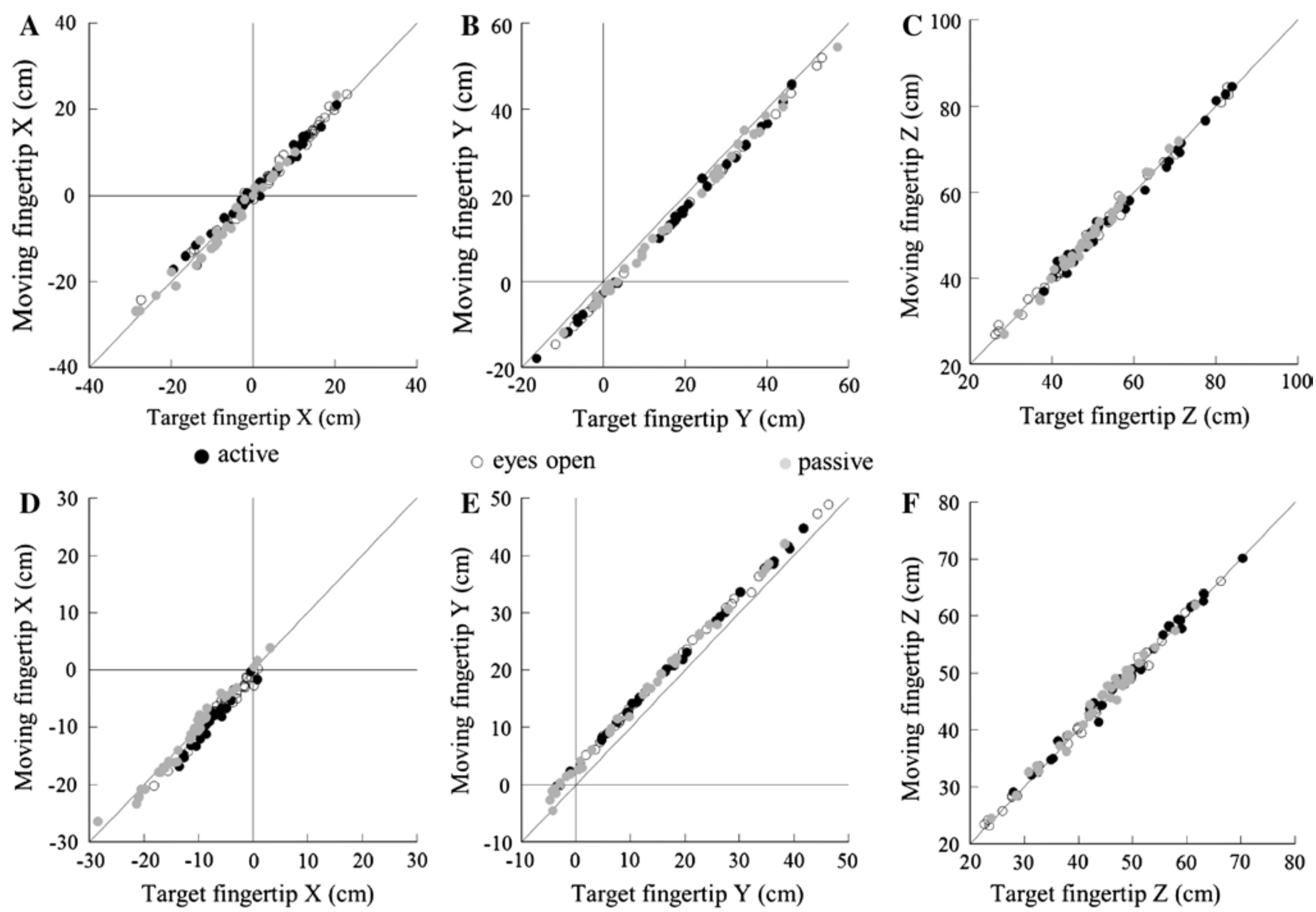

Fig. 3 Right index tip position at the end of the movement versus target (*left index tip*) in Cartesian coordinates with origin at *right index tip* starting position for two subjects (AL—*top*, OH—*bottom*) in three conditions (active and passive proprioception conditions with eyes closed and eyes open). Each *plotted point* is data from a single trial. The *solid line* is the line of identity

Table 1 Endpoint errors in eyes open and eyes closed conditions in two subjects

Sub	Eyes open				Eyes closed							
					Active				Passive			
	X	*Y*	*Z*	Dist	*X*	*Y*	*Z*	Dist	*X*	*Y*	*Z*	Dist
					Mean error (SD)							
OH	0.9 (0.9)	−3.1 (0.4)	0.3 (0.8)	3.5 (0.2)	1.1 (1.1)	3.0 (0.5)	0.6 (1.0)	3.6 (0.2)	0.0 (1.1)	−3.0 (0.8)	0.5 (1.0)	3.5 (0.4)
AL	−0.6 (1.2)	3.1 (0.8)	−0.1 (1.3)	3.7 (0.4)	−0.5 (1.3)	−2.9 (1.1)	−0.4 (1.6)	3.7 (0.5)	0.5 (1.7)	2.8 (1.4)	0.2 (1.3)	3.7 (1.1)

in both active and passive conditions, although there were a few larger errors. There were no consistent large biases (constant errors) across subjects in any direction (Fig. 4a). Furthermore, the distance errors showed no dependence on workspace location (e.g., see Fig. 3). Importantly, constant errors in each of the *X*, *Y,* and *Z* directions did not differ between active and passive conditions (Fig. 4a, $F_{1,10} = 1.88$, $p = 0.2$), nor was there an interaction of condition and direction ($F_{2,20} = 1.38$, $p = 0.273$) showing that the pattern of biases was similar in the two conditions (Fig. 4a). Constant errors also did not differ among X, Y, and Z directions ($F_{2,20} = 1.08$, $p = 0.342$). Variable errors averaged <2 cm in each direction and also did not differ between conditions (Fig. 4b, $F_{1,10} = 1.57$, $p = 0.239$. Cartesian distance errors averaged about 3.5 cm in the two conditions (Fig. 4c, $t_{10} = 0.78$, $p = 0.453$). These errors were comparable to the average distance between the sensors on the two fingertips when the fingers were voluntarily

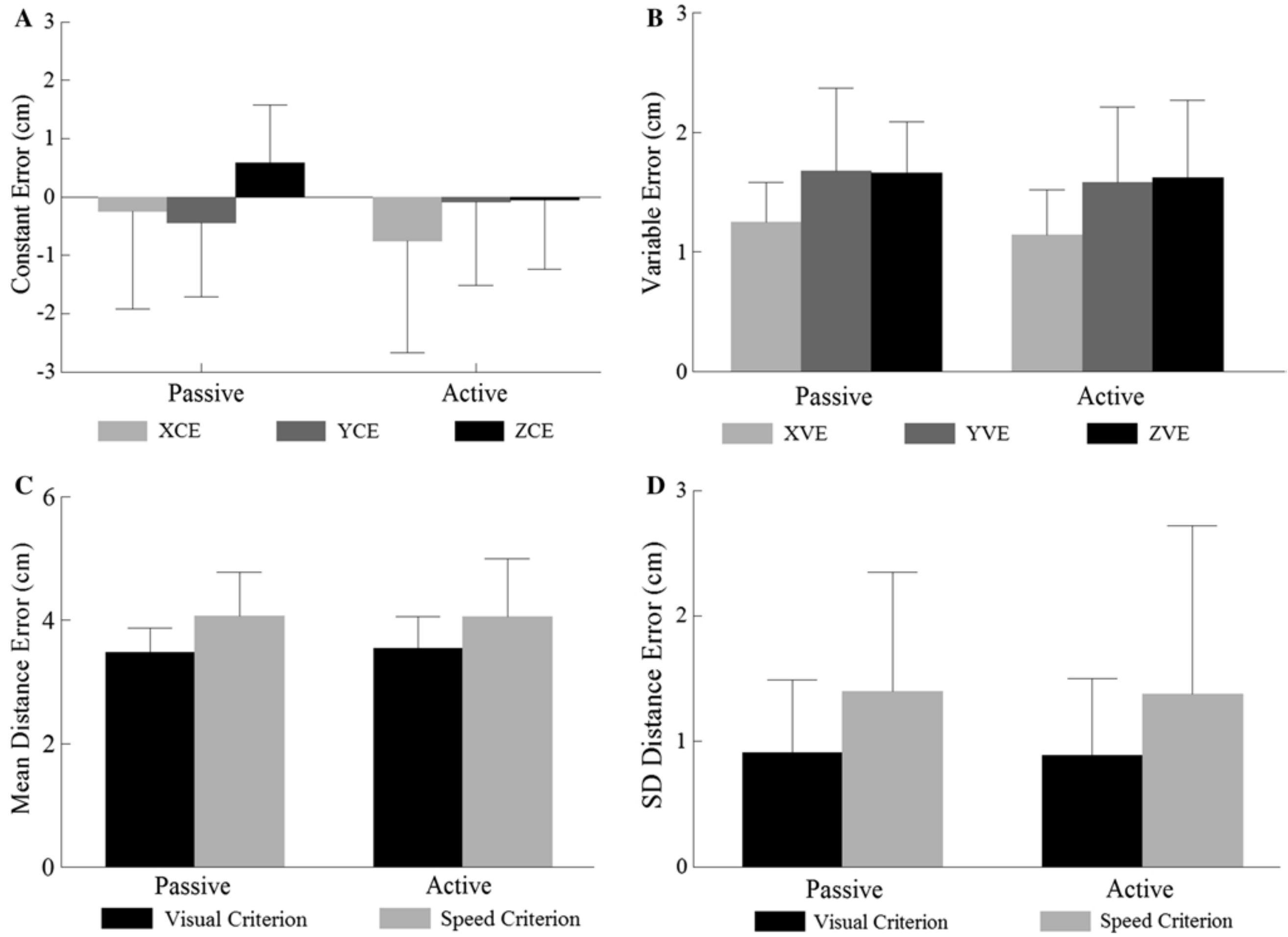

Fig. 4 Constant (**a**) and variable (**b**) errors in *X*, *Y*, and *Z* directions and distance errors (**c** mean distance errors, **d** standard deviation of distance errors) in the active and passive conditions. Distance errors using a visual criterion and 2 cm/s speed criterion for movement endpoint are shown. *Each bar* is the mean error for 11 subjects. *Error bars* are 1 SD

brought tip-to-tip by the subject with eyes open. Variability of the distance errors averaged less than 1 cm and did not differ between active and passive conditions (Fig. 4d, $t_{10} = 0.17$, $p = 0.868$). Distance errors measured using the speed criterion were slightly larger than those measured visually ($p < 0.05$), but did not differ between passive and active conditions ($p > 0.4$ for mean and standard deviation of distance errors). In consideration of the small secondary movements discussed in the preceding section, if subjects actively reached the pointing finger with a motion of the target finger, which they were instructed not to do, they ought to have done better in the active than in the passive task, but this was not the case.

Distance errors versus movement duration

Distance errors and directional biases (*X*, *Y*, and *Z* constant errors) did not increase with movement duration of the target arm in the active or passive conditions. Target arm movement durations, identified using a 2 cm/s criterion for movement onset and end, varied from 400 to about 1,200 ms depending on movement amplitude and subject. There was no evidence that distance errors were related to movement duration as there was no significant correlation between distance errors and target arm movement duration in any condition, for any subject (e.g., Fig. 5, data shown only for the active condition).

Discussion

We re-examined the notion that the position of an articulated body part can be better localized proprioceptively following an active rather than a passive movement. In the active movement condition, two potential sources of kinematic information may be available to the CNS, proprioceptive feedback (re-afference). and a purely central estimate, based on the operations of an internal forward model.

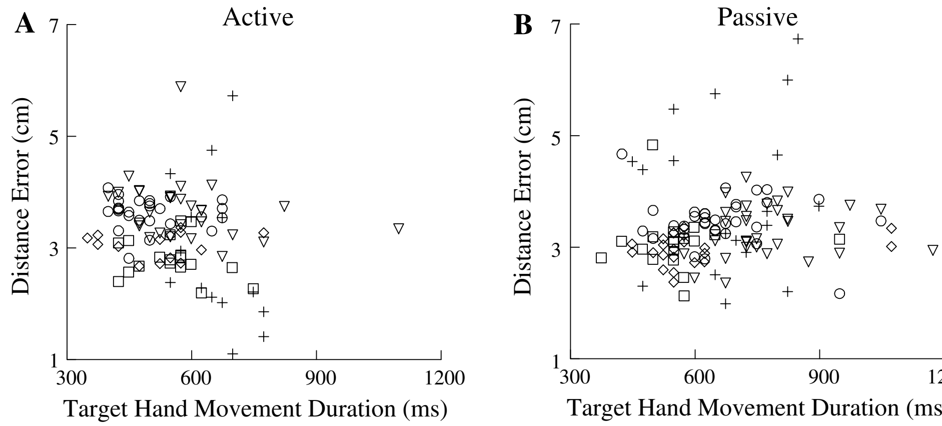

Fig. 5 Distance errors versus target hand movement duration under the active (**a**) and passive (**b**) conditions for five subjects (*each symbol* is for a different subject) in which accurate measures of target hand movement duration were available. *Each point* is data from a single trial. There were no statistically significant correlations ($p > 0.1$) between distance errors and target hand movement durations in any of these subjects

In the passive movement condition, only proprioceptive afferent information (ex-afference) is available. We have shown that, for natural unconstrained 3-D movements of the arm, the tip of its index finger can be localized equally accurately in either condition. Methodological issues, such as the subjects moving the target finger to the pointing finger or differences in workspace locations reached in the active and passive condition, cannot account for these observations as we have shown in the results. Our observations demonstrate unequivocally that proprioceptive afferent information in the passive condition is reliable enough to allow the CNS to determine the position of the index finger with an accuracy that cannot be improved upon in the active condition. This is a new finding whose basic physiological importance stands on its own.

Additionally, our results have several implications for the state-estimation hypothesis. First, proprioceptive sensory activity is clearly not so noisy as to be unreliable, on its own, for the accurate localization of a body part in natural conditions. This dispels one of the arguments made to invoke the existence of an internal forward model-based state estimator of limb kinematics (Wolpert et al. 1995; Wolpert and Ghahramani 2000). Second, while we cannot directly disprove the operation of a state estimator in the active movement condition, our results demonstrate that this does not improve localization accuracy or variability. Moreover, by contrast to the findings of Wolpert et al. (1995), errors were small, had no directional bias, and were unrelated to movement duration. The positive movement duration related bias errors (over-estimate) observed by Wolpert et al. (1995) were interpreted as evidence of the existence of a state-estimation mechanism within the CNS. However, as recently demonstrated by Gritsenko et al. (2007), bias errors of the sort reported by Wolpert et al. (1995) may occur in active and passive movement conditions. They cannot, therefore, be taken as evidence of the operations of a state-estimation process. Consequently, following Occam's razor, there is no need to invoke the existence of an internal model-based state estimator during limb movements.

Supporters of the state-estimation hypothesis may propose that the outputs of the state estimator are not accessible to the conscious proprioceptive localization system; or that once the movement of the target arm is completed, the CNS utilizes only proprioceptive inputs to determine its location. However, in the study of Wolpert et al. (1995), as in ours, proprioceptive localization was effected consciously by a voluntary movement of the pointing arm at the termination of movement of the target arm. Yet, Wolpert et al. (1995) reported an overshoot bias in localization for all movement durations, whereas we found no evidence of such a bias error. Importantly, in our study, localization depended purely on proprioception, whereas in the study of Wolpert et al. (1995), localization was effected by a visual estimation of the position of the unseen limb (i.e., moving a light cursor over the estimated position of the thumb). Errors of transformations between visual and proprioceptive reference frames have been appreciated for some time (e.g., Soechting and Flanders 1989; Darling and Miller 1993). In particular, the transformation of targets represented in a proprioceptive reference frame to a visual reference frame is not accurate (Darling and Miller 1993). The bias error reported by Wolpert et al. (1995) may thus be the result of errors of transformations between proprioceptive and visual representations (see also the discussion in Gritsenko et al. 2007 on this point). In our study, only a proprioceptive frame of reference was involved.

Active versus passive proprioceptive accuracy

Our results are clearly at odds with those of Paillard and Brouchon (1968), especially on the size of the localization errors. The difference in localization accuracy between the two conditions reported in Paillard and Brouchon's study (1968) was rather large. The median value of the localization bias in the active movement condition was ±6 mm and thus without a directional bias. In the passive movement condition, the median value was +22 mm, in the direction of underestimation. A possible explanation for the different findings is that proprioceptive inputs were restricted in Paillard and Brouchon's study due to movement being constrained largely to the shoulder for single dimension (up/down) motion and because during passive movements, the elbow and wrist were resting in a cradle which further constrained their motion.

Others have also reported greater accuracy of proprioceptive localization for active than passive movements (Monaco et al. 2010; Adamovich et al. 1998; Fuentes and Bastian 2010; Gritsenko et al. 2007). However, only one of these studies (Monaco et al. 2010) used an experimental protocol that purely involved proprioceptive localization of one limb by another. While Monaco et al. (2010) state that they found greater localization accuracy for active compared to passive movements restricted to the horizontal plane, the data presented in their Fig. 4 show that there are no differences in absolute errors, or bias (constant) errors, in the active versus passive conditions. The variable error was slightly greater (~4 mm) in the passive condition compared to the active condition, just reaching the 95 % confidence interval. Their results are thus largely in accord with ours. For one of the conditions studied by Gritsenko et al. (2007), their SP-C task (in which subjects stopped a slow right elbow movement in response to a cue and then reported that elbow angle by moving a pointer with the left arm), subjects underestimated the visual perception of their elbow angle after stopping the ongoing movement in response to an auditory cue. This SP-C task resembles that of Wolpert et al. (1995) and ours. While they found that subjects underestimate their elbow angle, they reported no difference between the active and passive movement condition, reminiscent of our results. Their finding that subjects underestimate elbow angle is not consistent with our finding and may be explained by visuo-proprioceptive transformations as explained above. The other studies (Adamovich et al. 1998; Fuentes and Bastian, 2010) and the other tasks studied by Gritsenko et al. 2007) involved either memory of target locations, transformation of proprioceptive to visual frames of reference, or used constrained single-joint movements rather than natural multi-joint movements. Interestingly, Fuentes and Bastian (2010) observed that subjects were better at estimating the position of their fingertip than their elbow angle in the passive condition. This is consistent with the idea that localization of the terminal segment of the arm, rather than joint angles, is the focus of proprioception, at least at the perceptual level. Unfortunately, Fuentes and Bastian (2010) did not investigate proprioceptive localization of the finger tip in an active task. In conclusion, the present study demonstrates that pure proprioceptive localization is very accurate under natural unconstrained conditions, indeed in two subjects as accurate as when vision was allowed. Importantly, there were no differences in variability between active and passive conditions with eyes closed Fig. 4 b, d). If the CNS was using a state-estimation mechanism, then, inherent to this process, variability should have been lower in the active condition.

On the evidence for limb kinematics derived from corollary discharges

The idea of deriving kinematic variables of limb movements from efference copies had been the subject of discussion and experimental work for some two decades prior to the re-emergence of these ideas in the 1990s. The position of the eyes in the orbit is derived directly from the motor commands that move them (Guthrie et al. 1983). By contrast, in the much more complex skeletomotor system, the evidence—including the present report—still strongly favors that proprioception is derived from the activity of sensory receptors (see Matthews 1982, 1988). However, more recently, Gandevia et al. (2006) reported a "sense of movement" which required extreme experimental interventions to reveal. In their study, the wrist muscles of their subjects were deafferented and paralyzed. With efforts of 20–50 % of maximum voluntary contraction, subjects reported imagined changes of wrist angle of 20–30°, except for one subject where the imagined change was larger (~70°). It does not follow, however, that this "sense of movement" contributes to proprioceptive localization mechanisms in normal physiological conditions given the large imagined efforts required to induce these perceptions of movement which would normally move the unloaded limb to extreme flexion/extension. The study of Gandevia et al. (2006) also stands in marked contrast to previous studies of the issue (Goodwin et al. 1972; McCloskey and Torda 1975; Stevens et al. 1976; Stevens 1978). Most notably, during experimentally induced whole-body paralysis, Stevens (1978) stated that "one felt like a solid piece of cement." Importantly, no sensations of movement were reported on attempts to move, though the subject was aware of willing a movement. The state-estimation scheme as proposed may not depend on the "sense of movement" investigated by Gandevia et al. (2006), but is dependent on a central mechanism that ought to be capable of estimating limb position from motor commands with some accuracy. The results of Gandevia et al. (2006) show that such estimates are not very accurate.

Conclusions

The proprioceptive localization of the index fingertip under natural unconstrained conditions is no better when it is moved actively than when moved by an external agent.

Consequently, our results cast doubt on the idea that during active movements, the brain determines kinematic variables based on the operations of a state-estimator weighting internal forward model predictions and proprioceptive feedback signals. The more parsimonious conclusion is that only proprioception is involved.

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