Two wrongs make a right: linear increase of accuracy of visually-guided manual pointing, reaching, and height-matching with increase in hand-to-body distance

Wenxun Li *, Leonard Matin

Clarence H. Graham Memorial Laboratory of Visual Science, Department of Psychology, Columbia University, New York, NY 10027, USA

Abstract

Measurements were made of the accuracy of open-loop manual pointing and height-matching to a visual target whose elevation was perceptually mislocalized. Accuracy increased linearly with distance of the hand from the body, approaching complete accuracy at full extension; with the hand close to the body (within the midfrontal plane), the manual errors equaled the magnitude of the perceptual mislocalization. The visual inducing stimulus responsible for the perceptual errors was a single pitched-from-vertical line that was long (50°), eccentrically-located (25° horizontal), and viewed in otherwise total darkness. The line induced perceptual errors in the elevation of a small, circular visual target set to appear at eye level (VPEL), a setting that changed linearly with the change in the line's visual pitch as has been previously reported (pitch: −30° topbackward to 30° topforward); the elevation errors measured by VPEL settings varied systematically with pitch through an 18° range. In a fourth experiment the visual inducing stimulus responsible for the perceptual errors was shown to induce separately-measured errors in the manual setting of the arm to feel horizontal that were also distance-dependent. The distance-dependence of the visually-induced changes in felt arm position accounts quantitatively for the distance-dependence of the manual errors in pointing/reaching and height matching to the visual target: The near equality of the changes in felt horizontal and changes in pointing/reaching with the finger at the end of the fully extended arm is responsible for the manual accuracy of the fully-extended point; with the finger in the midfrontal plane their large difference is responsible for the inaccuracies of the midfrontal-plane point. The results are inconsistent with the widely-held but controversial theory that visual spatial information employed for perception and action are dissociated and different with no illusory visual influence on action. A different two-system theory, the Proximal/Distal model, employing the same signals from vision and from the body-referenced mechanism with different weights for different hand-to-body distances, accounts for both the perceptual and the manual results in the present experiments.
© 2004 Elsevier Ltd. All rights reserved.

Keywords: Perception and action; Space perception; Perception of elevation; Spatial localization; Sensorimotor behavior

1. Introduction

Our success in reaching for visible objects suggests that the visual information determining where objects are seen also guides manual reaching. However, the possibility that this identity may not hold has received considerable attention in the context of controversy regarding one of two different morphings (Milner & Goodale, 1995; Ungerleider & Mishkin, 1982) of an earlier

---
* Corresponding author. Tel.: +1 212 854 4538/4325; fax: +1 212 854 3609.

E-mail addresses: wl18@columbia.edu (W. Li), matin@columbia.edu (L. Matin).

"two visual system hypothesis" (Held, Ingle, Schneider, & Trevarthen, 1967). [1] We will refer to the three versions of the two-visual systems concept as "$2VS_1$", "$2VS_2$", and "$2VS_3$". Each of the three had its origin in a different time frame. $2VS_1$ was presented in several varieties in the 1960s (Held, 1968; Ingle, 1967; Schneider, 1967; Trevarthen, 1968), beginning with the proposal that a different region in the brain was responsible for locating visual objects ("where") than for recognizing and identifying them ("what"), with spatial localization mediated in the superior colliculus and object recognition and identification in the cerebral cortex (Schneider, 1967, 1969). $2VS_2$ was originally presented in 1982 (Ungerleider and Mishkin) and proposed that object localization/orientation ("where") was mediated in posterior parietal cortex (the dorsal stream) whereas object recognition and identification ("what") was carried out in inferotemporal cortex (the ventral stream). Subsequent neuroanatomical and neurophysiological work has shown that, as proposed by Ungerleider and Mishkin (1982), visual information is conveyed along two major processing pathways from primary visual cortex, one directing signals to inferotemporal cortex and a second to posterior parietal cortex (Baizer et al., 1991). $2VS_3$ was described in Milner and Goodale (1995), and, although in agreement with $2VS_2$ regarding the separation of ventral and dorsal streams as a fundamental bifurcation in cerebral cortex, it rejected the "what–where" distinction regarding function. Instead, $2VS_3$ proposed that the dorsal stream mediates "action" whereas the ventral stream mediates "perception". The three versions continue to coexist separately and as pieces of several current, more inclusive pictures for connecting the egocentric and allocentric perceptions of space, visually guided sensori-motor action, and their neurophysiological substrates. Several of the latter have been described in reviews (Jeannerod, 1997; Rizzolatti, Riggio, & Sheliga, 1994) which indicate that both action and spatial localization are central features of the work of the dorsal system.

One of the major concerns of the present article is with $2VS_3$, which contends that the visual spatial information used for action differs from that employed by perception (Milner & Goodale, 1995). Three lines of evidence have been central to $2VS_3$'s support: (1) A visual agnosic is able to orient a handheld card correctly while posting it in a variably oriented slot but is unable to verbally report or manually match the slot's orientation reliably (Goodale, Milner, Jacobson, & Carey, 1991; Milner & Goodale, 1995). (2) Observers viewing a circle surrounded by a ring of eleven smaller circles report that it appears larger than the identical circle surrounded by a ring of five larger circles (classical Ebbinghaus/Titchener illusion); however, when an observer reaches for the central circle of a three-dimensional version of the illusion with forefinger and thumb, the interfinger aperture before contact does not vary with the surround (Agl-

---

[1] The Three Versions of the Two Visual System Hypothesis: Although there were significant historical antecedents (e.g., Sprague & Meikle, 1965), the initial version of the "two visual system" concept ($2VS_1$) arose in the context of a dissertation at MIT by G.E. Schneider in 1966 that was described in a contribution to a landmark symposium at the Eastern Psychological Association in 1967, and published as a full-length article under the title "Two Visual Systems" (Schneider, 1969). The symposium, "Locating and Identifying: Two Modes of Visual Processing" consisted of four presentations subsequently published in the *Psychologische Forschung* as four articles (Held, 1968; Ingle, 1967; Schneider, 1967; Trevarthen, 1968) with an introduction (Held et al., 1967) that originated the "what"/"where" terminology now in common use as a descriptor for $2VS_1$ and $2VS_2$. Schneider's own work with the golden hamster showed that interrupting a pathway from the retina to the superior colliculus eliminated the ability to orient toward an object but not the ability to identify it, whereas ablating the visual cortex had the opposite effect—eliminating the ability to identify objects without disrupting the ability to orient toward them. He also synthesized a large body of previous work from a number of laboratories on a number of different species and showed that it supported the separation of a neuroanatomical stream concerned with spatially oriented behavior from a stream concerned with behavior related to identifying objects. Each of the articles by the other three symposium participants also presented a synthesis of a significant body of behavioral and neural evidence supporting the existence of "two systems", each from a different point of view; although the four articles are syntheses of different bodies of work, with surprisingly little overlap, and the bifurcations indicated by the four authors somewhat different, each of the four distinguished between two types of visually controlled behavior that were then, and have since, been referred to as outputs from a "*what*" system and a "*where*" system.

The second wave ($2VS_2$) began with the publication of Ungerleider and Mishkin's (1982) article which described experiments on macaque monkeys in which ablation of inferotemporal cortex resulted in failure on an object discrimination task without loss of the ability to localize objects in space whereas ablation of parietal cortex resulted in failure in a spatial localization task without the loss of ability at object discrimination. Thus, these experiments located two visual systems in cerebral cortex of mammals that were separated on a functional basis similar to the earlier cortical/subcortical separation. Subsequent neuroanatomical and neurophysiological work has shown that, as proposed in Ungerleider and Mishkin (1982), visual information is conveyed along two major processing pathways from primary visual cortex, one directing signals to inferotemporal cortex and a second to posterior parietal cortex (Baizer, Ungerleider, & Desimone, 1991) although the two streams are not entirely unconnected (Baizer et al., 1991; Morel & Bullier, 1990; Van Essen & Maunsell, 1983). A considerable literature has since treated this division into ventral and dorsal streams as a fundamental bifurcation in cerebral cortex.

The basis for the third wave ($2VS_3$) is described in Milner and Goodale (1995) in which the authors argue that the ventral and dorsal streams efferent to V1 are not separated in order to serve object discrimination and spatial localization, respectively, but to serve "perception" and "action", respectively. The use of "perception" by Milner and Goodale (1995) is essentially identical to the use of object recognition, identification, and discrimination in the two earlier treatments, and their "action" stream overlaps with many of the features of the "where" stream in the two earlier views. The basis for proposing action as the main function of the dorsal neuroanatomical division emanating from V1 is described in the detailing in Milner and Goodale (1995) of the three lines of supporting evidence for $2VS_3$ noted in the body of the present article. For a fuller description of the history and development of the two visual system hypothesis consult Bousaoud, di Pellegrino, and Wise (1996) and Jeannerod (1997).

ioti, DeSouza, & Goodale, 1995; Milner & Goodale, 1995). (3) Observers with large scotomas resulting from lesions in primary visual cortex are able to point their eyes and fingers toward objects which they report they cannot see (Milner & Goodale, 1995; Perenin & Jeannerod, 1978; Poppel, Held, & Frost, 1973; Weiskrantz, 1986, 1990, 1997; Weiskrantz, Warrington, Sanders, & Marshall, 1974). But the latter two lines have been subjected to a great deal of criticism, [2] and a clearer and simpler experimental analysis of the relation between perception and action is needed.

In order to probe the relation between the uses of visual information for perception and for the visual guidance of action we have worked with a simpler arrangement that lends itself to considerable further development. The four experiments in the present report employ visual induction to generate large, repeatable, and systematic perceptual and manual errors of localization with a very simple visual field consisting of a single long, dim, thin, straight, pitched-from-vertical line in darkness (Li & Matin, 1996, 1998; Matin & Li, 1994a, 1994b, 1994c, 1995, 1999, 2001). [3] This has permitted

---

[2] Controversy Regarding Two of the Empirical Bulwarks of 2VS$_3$: Following the initial reports, support for the perception/action separation of 2VS$_3$ from each of the last two lines of evidence has been clouded by subsequent experiments and controversy that runs the gamut from concerns with artifact and failed replications (although for each line successful replications have been reported) to theoretical treatments leading to experiments with numerous variations of the stimulating conditions.

The original report of the work with the Ebbinghaus/Titchener illusion (Aglioti et al., 1995) has attracted an enormous amount of work since its publication in 1995. The mountain of literature that has accumulated on the matter is indicated by the presence of three critical reviews centered on the illusion that have appeared in one journal (Bruno, 2001; Carey, 2001; Franz, 2001); these three contain 38, 26, and 23 references, respectively, a significant proportion of which are later than the original 1995 report that opened work on the illusion and are related to it (30, 22, and 20 references respectively; we have not attempted to remove the redundancy in the counts). There is no evidence yet of an abatement of work pertinent to the 2VS$_3$ view regarding the relation between perception and action or an abatement of concern with the resolution of problems regarding the interpretation of the work with the illusion; for example, in the 5-day May, 2002 meeting of the Vision Sciences Society (2002), there were 17 presentations on relations between perception and action including several on the illusion in question, and in the 5-day 2002 meeting of the European Conference on Visual Perception (2002), there were 19 presentations centered on relations between perception and action including the illusion and blindsight. In addition, the entire recent 746-page volume in a series (Prinz & Hommel, 2002) is devoted to relations between perception and action with a good deal of material related to work on the illusion, and articles for a special issue on the perception/action problem were recently solicited by the journal Spatial Vision; the special issue has been published with 11 articles (2003) with two mentioning the Ebbinhaus illusion in the title and a number of others dealing with it in text. The work with the Ebbinghaus/Titchener illusion on normal observers involves measurements of differences between perception and action along the dimension of 'size' of the target circle, but, among other points of controversy, the stimulating conditions are sufficiently complex as to have raised concern that they present physical obstacles which lead subjects to modify the aperture between their fingers with no comparable potential impact on perception and that they also provide complications for perception with no comparable potential impact on action; such possible lack of comparability of the conditions for perception and action has left it unclear as to whether the neural mechanisms processing perception of the illusion and action related to it employ fundamentally different 'visual systems' or whether differences that have been reported resulted from the presence of different demands made on perception and on action by the stimulating conditions and hence whether the experimental conditions have not been appropriately comparable for the perceptual and grasping tasks.

Since the early reports of above-chance accuracy of eye movements and arm pointing to visually presented targets by human observers when the striate cortex is absent (Perenin & Jeannerod, 1978; Poppel et al., 1973; Weiskrantz et al., 1974), more than a decade before the perception/action dialogue began, work on 'blindsight' in humans has become the focus of an important controversy (e.g., Campion, Latto, & Smith, 1983; Fendrich, Wessinger, & Gazzaniga, 1992; Weiskrantz, 1986, 1990, 1997). The major dimensions of the controversy revolve around the difficulty of assuring the absence of artifact in the methodology of assessing accuracy in the measured response of spatial localization and in the assessment of absence of cortical tissue. These concerns include the possible influence of entopic scatter of light from a portion of retina severed from primary visual cortex onto retina with intact connections to visual cortex, evidence that postgeniculate lesions permit blindsight but pregeniculate lesions do not, and whether islands of intact primary visual cortex remained in the patients, to note just three. (It is also a controversy that remains important in its own right regardless of its relation to the question of two visual systems, and a considerable stream of articles related to it continue to appear.)

In addition to the problems noted above, significant concerns with the evidence also arise from the fact that two of the main lines of evidence employed to support 2VS$_3$ depend on individual clinical abnormalities that do not readily generalize to the normal population, and that the one line of support that is based on normal observers has been developed around an effect for which the entire magnitude of the illusory effect on perception is small—less than 3 mm; the effect on the grasping effect is also less than 3 mm out of a maximum interfinger aperture distance of about 60 mm while reaching for a disc that ranged in diameter from 27 to 33 mm. Nevertheless, the view that two visual systems—one for perception and one for action—make use of different visual spatial information and do so differently has become a strong theoretical focus for the analysis of visual processing and for attempts at interpreting the separation between the two main streams of information arising from primary visual cortex.

[3] Spatial Induction of Orientation-Dependent Variations in VPEL: The dramatic effects of visual pitch are most clearly observed in the illuminated pitchroom (Matin & Fox, 1989), and include large changes in perceived size, elevation, and orientation of objects viewed against the background of the pitchroom (also see work with the smaller pitchbox in Stoper & Cohen, 1989). The effect on the elevation perceived as eye level (VPEL) of two long, parallel, bilaterally and eccentrically located, single lines is only 15% less at the same pitch than the influence of the entire well-illuminated, and strongly-textured visual field of the pitchroom; the influence of the 1-line stimulus employed in the present experiments is typically about 19% less than the entire pitchroom (Matin & Li, 1994a, 1994b, 1994c). Of further interest is the fact that pitched stimuli are not necessary for the induction of VPEL change; stimuli in the same nodal plane (Matin & Li, 1999, 2001) produce indistinguishable values of VPEL whether they arise from pitched-from-vertical lines or from oblique lines in a frontoparallel plane (Matin & Li, 1994a, 1994b, 1994c, 1999) and all of these are well accounted for by the same neural model (Matin & Li, 2001). In addition, the induction effects on VPEL are nearly independent of position of the eye in the orbit and of the orientation of the head on the body (Li & Matin, 1993; Matin & Li, 1995). Further, the effects of induction on the perception of elevation are not restricted only to the perception of eye level—they are a part of a change in the relation between the entire physical dimension of elevation and perceived elevation (Matin & Li, 1995; Robison, Li, & Matin, 1995).

the perceptual and manual effects of interest to be considerably magnified and dissected with much finer resolution than in previous work. The experimental results are not consistent with the perception/action treatment of $2VS_3$, but are well explained by a different two-system model in which signals from two systems ("proximal" and "distal") are weighted differently for both perceptual localization and for motor behavior at arm's length than they are for motor behavior closer to the body. The signals controlling both perception and manual behavior are very closely related.

2. General methods

2.1. Stimulus display

Visual inducer. The visual stimulus that induced the changes in perception of elevation and in motor behavior consisted of a 144 cm × 0.2 cm (0.01 mL) strip of phosphorescent tape that had received a brief exposure (2 min) to normal room illumination prior to each experimental run. The strip was attached to a plastic bar that was mounted on a modified standalone pitchable blackboard with velcro. Pivots on the two vertical edges of the blackboard's frame allowed rotation around a horizontal axis within the frontoparallel plane of the blackboard at the true eye level of the erect, seated subject and provided the means by which pitch was set. For different conditions of each experiment, the same set of 7 pitches was presented in a different random order: topbackward at −30°, −20°, or −10°, 0° (vertical), and topforward at 10°, 20° or 30°. The subject's head was stabilized by a chinrest. The strip was centered at the intersection between true eye level and a left horizontal eccentricity of 25° of the subject's viewing (left) eye; the right eye was covered by an eye patch. As measured at the normal between the subject's eye and the blackboard, the erect line stimulus (the "inducer") subtended a 50° by 4.5′ visual angle at the viewing distance of 1.4 m. The actual visual angle subtense of the eccentrically-located line underwent some variation with its pitch, in part consequent on change of the blackboard's distance required to maintain the 1.4 m distance along the normal, and in part to the pitch variation itself: it was 47.1° long × 4.3′ wide, 44.1° × 4.0′, and 40.4° × 3.7′ at the pitches of ±10°, ±20°, and ±30°, respectively. [Since the influence of length on VPEL at a given orientation increases with negative acceleration with a space constant of approximately 15°, approaching saturation at the lengths employed here (Matin & Li, 1994a, 1994b, 1994c, 1999, 2001), these variations with pitch are highly unlikely to have exerted any important effects on the phenomena of interest.]

VPEL target. The target employed for the VPEL setting was presented in the median plane of the subject as a backprojected, optically attenuated image of a 0.5 mw He–Ne laser (20′). The laser was mounted horizontally on a vertical track and was attached to a mobile relay rack by a rack and pinion system that permitted variation of the height of the laser beam. The laser's horizontal beam was itself completely invisible under all conditions.

Target for manual response. In Expts. 1–3 the visual target of the manual response was an LED whose light was diffused and masked to produce a 20′ circular, red stimulus; this replaced the laser target and was located within the eye's median plane at the elevation measured as the VPEL for the given subject for the given inducer orientation or at 6° (15 cm for Expt. 2) above VPEL or 6° (15 cm for Expt. 2) below VPEL.

2.2. Manual measuring device

The system measuring finger position and orientation employed a Polhemus 3-SPACE FASTRAK that generates and uses an electromagnetic field to remotely determine the position and orientation (six spatial degrees of freedom) of a small (0.9″ × 0.8″ × 0.6″), lightweight sensing receiver consisting of three collocated search coils that was taped to the distal digit of the pointing index finger. Measurements of the finger position and orientation were used to determine a point of intersection of the finger direction on the pitched surface, and in conjunction with the height and distance of the eye from the pitched surface, were transformed into visual angle deviations from true eye level.

2.3. Subjects

The same four subjects participated in all conditions of Expts. 1 and 2. Five subjects participated in all conditions of Expt. 3, four of them had not participated in Expts. 1 or 2. Eight subjects participated in Expt. 4; this group included the 5 subjects from Expt. 3 along with three who had not participated in any of the earlier experiments. With the exception of one of the authors (WL) who was a subject in all four experiments, the subjects were Columbia undergraduates who were paid an hourly wage for participating; recruitment and the experimental protocol met the requirements of the human subject committee at Columbia University. With the exception of the author-subject, the other subjects were naive about the purposes of the experiments (see Li & Matin, 1996 for some relevant control procedures). The author-subject had served as a subject in a number of related experiments. All subjects were right-handed and had uncorrected vision of 20/20 or vision that was corrected to 20/20 by use of contact lenses. All subjects gave informed consent, signing a form approved by the Columbia University IRB.

3. Expt. 1: Pointing to perceptually mislocalized targets with the finger at eye level in the midfrontal plane or with the fully extended arm

3.1. Procedures for Expt. 1

VPEL setting. In the first session of Expt. 1 the monocularly-viewing subject set the elevation of the laser-generated target to appear at eye level while viewing the visual field consisting of the eccentrically-located pitched-from-vertical inducing line at each of the 7 orientations in otherwise total darkness. The subject sat straddling a stool and faced the blackboard with head position stabilized by a chinrest attached to the front of the stool. The display was viewed with the left eye; the right eye was occluded by an eye patch. The subject was instructed to only look in the straight ahead direction containing the target (median plane of viewing eye). A method of adjustment with hunting was employed for the setting of the laser target to VPEL by the subject. A trial began with the subject's eyes closed. The experimenter then set the laser target either far above or far below the region of uncertainty and instructed the subject to open his/her eyes, fixate the target, and report whether the target needed to be moved up or down in order to appear at VPEL; the subject immediately closed his/her eyes, whereupon the experimenter reset the elevation of the target by a variable amount and instructed the subject to open his/her eyes again and report on the elevation of the target relative to VPEL again. This sequence was repeated until the subject indicated that the target was at VPEL. Four such VPEL settings were made at one pitch before proceeding to a different pitch; the mean of the four was employed as the subject's VPEL for that condition. The order in which measurements with the different pitches were made was separately randomized for each subject. Four VPEL settings were also made in complete darkness at the beginning and the end of the session.

Manual pointing. In the two sessions subsequent to the VPEL measurements each of the four subjects was run in a manual pointing task with three of the pitches in one session and four in the second session. The subject pointed to a visual target with the index finger of the right hand while viewing the target against the pitched 1-line visual field in darkness with the left eye (an eye patch occluded the right eye's view). For an individual pointing trial the experimenter set the 1-line inducing stimulus to one of the 7 pitches and the circular target to the elevation previously measured as the subject's VPEL for that pitch. Two sorts of pointing trials were used: (a) "Midfrontal-plane point": the subject wrapped the right hand around a cylindrical plastic rod that was fixed horizontally within the subject's midfrontal plane at eye level and directed the index finger at the target by rotating it around the rod (inset, Fig. 1a);
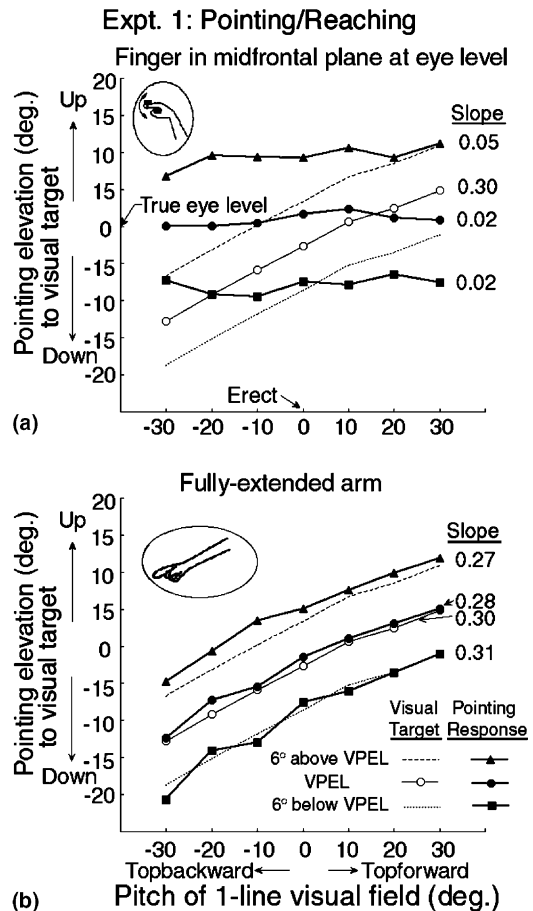

Fig. 1. Experiment 1: Average results for 4 subjects who pointed at a visual target with the finger/hand in the midfrontal plane in panel (a) or with the finger/hand at the end of the fully extended arm in panel (b). Each subject first set a small visual target to appear at eye level (perceptual VPEL setting) in the presence of a variably oriented inducing line in otherwise total darkness (open circles); the VPEL settings are reproduced in both panels (a) and (b). In each panel, in separate sessions, with only the inducer and a visual target visible (20′ circular red LED), the subject pointed to the visual target set at the elevation previously set to VPEL (filled circles), to the visual target relocated 6° above VPEL (filled triangles), or to the visual target relocated 6° below VPEL (filled squares). The elevations of the visual target 6° above and 6° below VPEL are indicated by the dashed and dotted lines, respectively, and are drawn parallel to the VPEL-vs-pitch function that itself is shown as the light solid line connecting the perceptual VPEL settings.

(b) "Fully-extended-arm point": the arm was fully extended from the shoulder straight ahead in front of the body as the subject pointed the finger at the visual target (inset, Fig. 1b). Since the left (viewing) eye was directed straight ahead in order to foveate the visual target, the subject's unseen right (pointing) arm could, in principle, have occluded the view of either the target in the median plane of the left eye or the inducing line at 25° left horizontal eccentricity. With the arm fully extended, occlusion of the visual target would have required a leftward lateral hand/arm movement that extended beyond the midsagittal plane of the body and a much greater

movement to occlude the inducing line. That no such occlusion occurred is clear from the measurements of lateral finger position on each trial. Each pitch occupied 24 trials: the first set of 12 trials involved pointing with the finger/hand in the midfrontal plane at eye level, the second set of 12 trials involved pointing with the fully extended arm. Within a group of 12, there were four blocks of 3 trials, with each block consisting of one trial with the target at VPEL for that pitch, a second with the target 6° above VPEL, and a third with the target 6° below VPEL; the three target locations were sequenced according to a randomized block design. Thus, at a given pitch four of the trials were presented with the target at each of the three elevations.

3.2. Results for Expt. 1

The VPEL settings measured in the first session—the setting by the subject of the elevation of a small target to appear at eye level—increased nearlinearly with the inducing line's pitch, averaging 13° below true eye level for the most topbackward pitch, −30°, and 5° above true eye level for the most topforward pitch, +30° (open circles, Fig. 1a). These values are consistent with previous work (Matin & Li, 1994a, 1994b, 1994c, 2001). The VPEL settings for each individual served as the targets for pointing in the subsequent two sessions. The results for pointing with the finger in the midfrontal-plane point are displayed as the filled circles in Fig. 1a. Although the physical elevation of the observer's VPEL setting—the target of the point—rose with increasing topforwardness of the pitch of the 1-line visual field, the elevation of the midfrontal-plane point remained near horizontal and essentially unchanged [slope of pointing elevation-vs-pitch function = 0.02; $F(6, 18)$ = 0.909, $p > 0.50$]. This result might not be surprising since, although the target's physical elevation varied systematically with the pitch of the 1-line stimulus, it always appeared at eye level, and this constant perception—although generally inaccurate—presumably guided the elevation of the subject's midfrontal-plane point.

However, the same result was not obtained with the fully-extended-arm point (Fig. 1b). Instead, as the elevation of VPEL rose with increasing pitch of the inducing line, the direction of the finger pointing to the visual target at VPEL also rose and remained close to the visual target; the variation in pointing direction was significant [Fig. 1b; $F(6, 18)$ = 57.82, $p < 0.001$], indicating significant departure from a constant pointing direction. Thus, whereas, the nearconstant elevation of the midfrontal-plane point to a fixed elevation visual target is consistent with perception but inaccurate (Fig. 1a), the fully-extended-arm point is not consistent with perception but pointing is nearaccurate throughout the range of the target elevation–inducer orientation combinations.

The experiment was repeated with the target of the manual point set 6° above or 6° below the subject's VPEL for each of the 7 angles of pitch of the 1-line stimulus. Again, for the midfrontal-plane point (Fig. 1a), the finger direction did not change significantly with pitch [$F(6, 18)$ = 1.88, $p > 0.10$, $F(6, 18)$ = 1.49, $p > 0.23$]. And, again, the fully-extended-arm point was nearaccurate throughout the range of pitches (Fig. 1b). Thus, the difference between mislocalization of the midfrontal-plane point and accuracy of the extended-arm point holds over at least a ±6° elevation range above and below VPEL.

3.3. Discussion of Expt. 1

The results of Expt. 1 indicate that the distance of the hand from the subject's body is a critical factor in determining the manual error. However, the midfrontal-plane and fully-extended-arm points involved different constellations of motor behavior: whereas the midfrontal-plane point involved rotation of the index finger around its joint with the hand along with some wrist rotation as the flexed arm between elbow and wrist moved through a small arc with the arm in a nearvertical position near the body, the fully-extended-arm point required the index finger to be extended and in a constant relation to the hand with an unbent wrist and elbow fixed during the point, with joint movement only at the shoulder. Thus, Expt. 1 left open the possibility that differences in the details of the motor behavior are critically involved in the difference between the two sets of results, and Expt. 2 was run in order to determine whether or not this was so.

4. Expt. 2: Manual height matching to a perceptually mislocalized visual target with variable hand-to-body distance

4.1. Procedures for Expt. 2

Manual height matching: The same 4 subjects who participated in Expt. 1 raised or lowered the unseen horizontal hand to match the height of a visual target in the presence of the pitched-from-vertical line in darkness at each of three different hand-to-body distances. In order to constrain the hand to a horizontal orientation and arm motion to the vertical dimension at a fixed hand-to-body distance the following arrangement was employed: The hand held a horizontal wooden platform that was flexibly attached to a rigidly anchored plastic vertical rod and could be moved vertically along the rod with very little resistance and left in a fixed position when the subject was satisfied with the height match (insets, Fig. 2); hand-to-body distance was experimentally varied by relocating the vertical rod to different rod/

Expt. 2: Manual height match

Finger in midfrontal plane

(a)

Finger 20 cm from midfrontal plane

(b)

Finger 40 cm from midfrontal plane

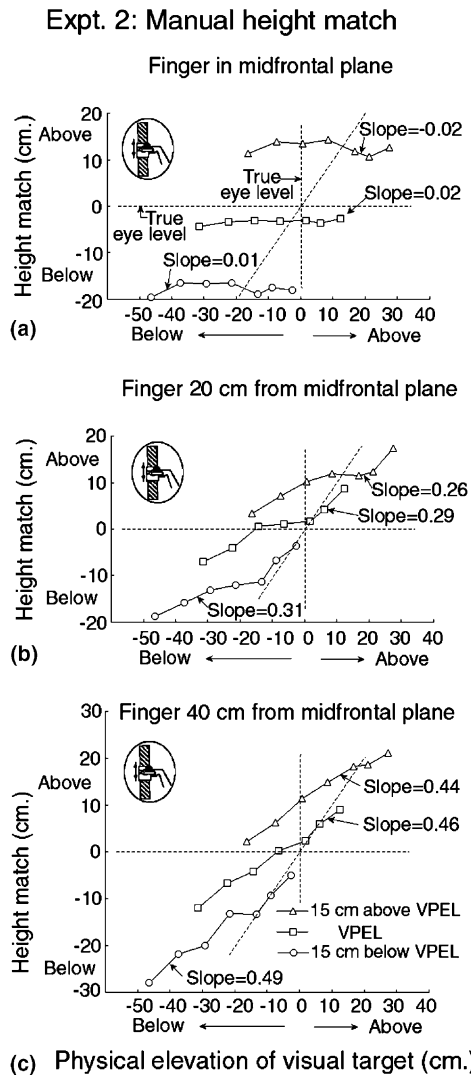**(c)** Physical elevation of visual target (cm.)

Fig. 2. Experiment 2: Each of the same 4 subjects who served in Expt. 1 set the elevation of the hand to match the height of the visual target. The hand was constrained to the midfrontal plane in (a), 20 cm in front of the midfrontal plane in (b), or 40 cm in front of the midfrontal plane in (c). As in Expt. 1 only the pitched 1-line inducer and the 20′ circular red visual target were visible. Each member of a connected set of 7 data points is a result of height-matching under induction by a different orientation of the 1-line pitched-from-vertical inducer. The elevation shown on the abscissa for the target at VPEL was the subject's setting of the target to appear at eye level under induction by the inducer. The manual/visual height match was made in the presence of each of the seven orientations of the 1-line inducer with the visual target of the match at VPEL, at 15 cm above VPEL, or at 15 cm below VPEL. The dashed line in each panel has a slope of 1.00.

body distances. The subjects used the right hand and left eye in performing the manual height match at three different heights of the visual target: 15 cm above VPEL, 15 cm below VPEL, or at VPEL, with the hand at either 0 cm, 20 cm, or 40 cm in front of the subject's midfrontal plane. Measurements were made at each of the 63 combinations of the three target elevations, three hand-body distances, and seven line orientations. Each subject was run in three sessions, with all seven of the pitches run at

a different one of the three finger/hand distances in each session; the three distances were randomly ordered among sessions across the different subjects. Each pitch occupied 12 trials. Within a group of 12, there were four blocks of 3 trials, with each block of 3 consisting of one with the target at VPEL for that pitch, a second with the target 15 cm above VPEL, and a third with the target 15 cm below VPEL; the three target locations were sequenced according to a randomized block design. Thus, at a given pitch four of the trials were presented with the target at each of the three elevations.

4.2. Results for Expt. 2

With the target at VPEL the slope of the height match/target elevation function increased systematically with increasing hand-to-body distance from 0.02 with the finger/hand in the midfrontal plane to 0.29 at 20 cm and to 0.46 at 40 cm (Fig. 2); again, similar results were obtained with the target 15 cm above or below VPEL where the height match settings for a given inducer pitch are displaced from those at VPEL by approximately 15 cm above or below the target at VPEL respectively. These height matching results of Expt. 2 are consistent with the conclusion that the increase in accuracy with distance measured in Expt. 1 is a consequence of the variation in hand-to-body distance [4] and not the particular constellation of motor behavior.

5. Expt. 3: Pointing to perceptually mislocalized targets with the finger at eye level with variable hand-to-body distances

Although the results of Expts. 1 and 2 are entirely consistent, they examined different ranges of distances.

---

[4] In both experiments body-to-target distance was maintained at a constant value (= hand-to-body distance + hand-to-target distance), and so it would be possible to attribute the results of Expts. 1 and 2 either to the variation in hand-to-target distance or hand-to-body distance, or to some linear combination of both. However, note that in Expt. 1 the subject points accurately in the direction of a perceptually mislocalized VPEL target located at twice the distance from the body as the pointing finger at the end of the fully-extended arm, and this is more parsimoniously interpreted in terms of an influence by hand-to-body distance than by hand-to-target distance (Li, Matin, & Semanek, 2003) in which the visual target distance was set at either 50, 140, or 300 cm from the subject's midfrontal plane, each in conjunction with hand-to-body distance set at 0, 20, or 40 cm, although the accuracy of the manual height match increased with hand-to-body distance, the magnitude of the reduction in the height-match error with hand-to-body distance was approximately the same for the three distances of the visual target; thus the continuous, gradual decrease of the manual error with increased hand-to-body distance is due to the distance of the hand from the body and not the distance of the hand to the target.

In Expt. 3 each of 5 subjects pointed to the visual target located at VPEL with the hand constrained at each of the same three distances employed in the height match measurements of Expt. 2.

5.1. Procedure for Expt. 3

VPEL settings were made following the procedure described above for Expt. 1.

Manual pointing. The manual pointing task was essentially identical to that of Expt. 1. Here the subjects pointed to the visual target located at VPEL with the hand constrained at each of the three distances: 0 cm, 20 cm, or 40 cm in front of their midfrontal plane. The hand was set at true eye level at each distance by the experimenter by relocating the horizontal rod that constrained the hand to the correct fixed distance. At each distance the measurements were made with the target at VPEL, at 6° above VPEL, and at 6° below VPEL. The format of Expt. 3 followed that of Expt. 1.

5.2. Results for Expt. 3

The form of the results (Fig. 3) is essentially the same as for the height match in Expt. 2—the slope of the function relating manual elevation to pitch increased with distance: flat functions were measured for the midfrontal plane point (average slope = 0.02, repeating the result of Expt. 1 with a different group of subjects), and the slopes averaged 0.12 and 0.18 with the hand at 20 and 40 cm distance, respectively (averages across the three heights at each distance).

5.3. Discussion of Expts. 1–3

5.3.1. Linearity in Expts. 1–3

Fig. 4 plots the results for the three experiments in equally-scaled dimensionless units, displaying for each distance, the slope of the best-fitting straight line relating the elevation of the manual point or height match to the elevation of the visual target. The results in the three experiments follow very similar linear increases with increase in hand-to-body distance, indicating that the two different types of motor behavior, pointing and height matching, produce errors that are consistent for a given distance of the hand from the body; [5] thus the variation with distance is not specific relative to

---

[5] Each point in Fig. 4 is the slope of the best fit straight line obtained from a plot containing the seven paired values (height of the finger point or height match against the elevation of the visual target) averaged across subjects, one for each of the seven pitches. A slope of 0.00 results from a manual point whose elevation did not change with elevation of the target of the point or height match whereas a slope of 1.00 results from identical variations with inducer pitch of the manual point and VPEL.

the details of the peripheral aspects of the motor behavior, but is a more general property of manual behavior. [6] It can also be concluded that the large difference in accuracy of the manual behavior in Expt. 1 between the midfrontal-plane point and the fully-extended arm point was not an abrupt difference that only held at the extremes of distance, but a gradual change with distance that held for the two different constellations of motor behavior in Expt. 1 as it did for the height match. [7]

---

[6] As displayed in Fig. 4, the results of Expts. 1–3 also make it clear that differences in results that have been reported between experiments involving height-matching (Robison et al., 1995) and extended-arm pointing (Welch & Post, 1996) are not consequences of a difference between the motor behaviors involved in the height-match and extended-arm point procedures, but are due to the difference in distance of the finger/hand from the body employed in those experiments.

[7] We note some summary measures of variability and individual subject consistency: In Expt. 1 the values underlying the averages in Fig. 4 of the slope of the manual elevation/visual target elevation function ranged from −0.06 to 0.18 for the midfrontal-plane point and from 0.60 to 1.14 for the fully-extended-arm point across the four subjects; in Expt. 2 the range across the four subjects was −0.03 to 0.06 at the midfrontal plane, 0.20 to 0.36 at 20 cm, and 0.35 to 0.66 at 40 cm; in Expt. 3 the range across the 5 subjects was −0.03 to 0.12 for the midfrontal plane, 0.18 to 0.54 at 20 cm, and 0.48 to 0.66 at 40 cm; these ranges span the results for the three target elevations: at VPEL, above VPEL, and below VPEL. The subjects displayed a great deal of consistency in their individual manual responses: Thus, the ordering of slopes among individuals of the manual response/pitch functions was generally retained for the 3 target elevations and 2 nonzero distances as indicated by Pearson product-moment correlations (r) between the corresponding slopes at 20 cm and 40 cm of +0.77 and +0.65 in Expts. 2 and 3, respectively; these values of r were significant at $p < 0.003$ (df = 11) and $p < 0.01$ (df = 14), respectively.

The slope in Fig. 4 in each case is built from two numbers: the denominator of the ratio is the slope of the elevation of the visual target vs pitch; the numerator is the slope of the elevation of the manual response to the visual target vs pitch. The following calculation provides a measure of the variability of the perceptual VPEL setting: A standard deviation (SD) was calculated over the 4 trials involved in each VPEL; these individual SDs were then averaged across the 7 pitches for a given subject, and further averaged across all 9 subjects in the two different subject groups in Expts. 1–3; the value of this final average SD, measuring the SD per subject per pitch, was 0.7°. Similar calculations of variability were made for the manual settings: The average SD for manual elevation across the 21 conditions of each experiment was equal to 2.3° and 3.5° at the two hand-to-body distances in Expt. 1, 2.0, 2.0, and 1.9 cm at the three distances in Expt. 2, and 1.3°, 1.6°, and 1.7° at the three distances in Expt. 3. In Expt. 4, the individual slopes for the eight subjects of the manual elevation-vs-pitch function ranged from −0.01 to 0.07 for the midfrontal plane point and from 0.10 to 0.31 for the fully-extended-arm point, with the average SD for the setting of manual elevation across the 7 pitch orientations equal to 1.4° and 2.9°, respectively. Where the results could be examined for individual consistency (different nonzero orientations with the fully-extended-arm point) there was a great deal of consistency, with the order of the manual settings across individuals generally retained across pitches: for example, for manual pointing to horizontal with the extended arm, the correlation (r) of settings between the −10° and −30° inducing lines across the eight subjects was +0.82 ($p < .01$; df = 7).

Expt. 3: Pointing: hand at eye level

(a) Finger in midfrontal plane

(b) Finger 20 cm from midfrontal plane

(c) Finger 40 cm from midfrontal plane
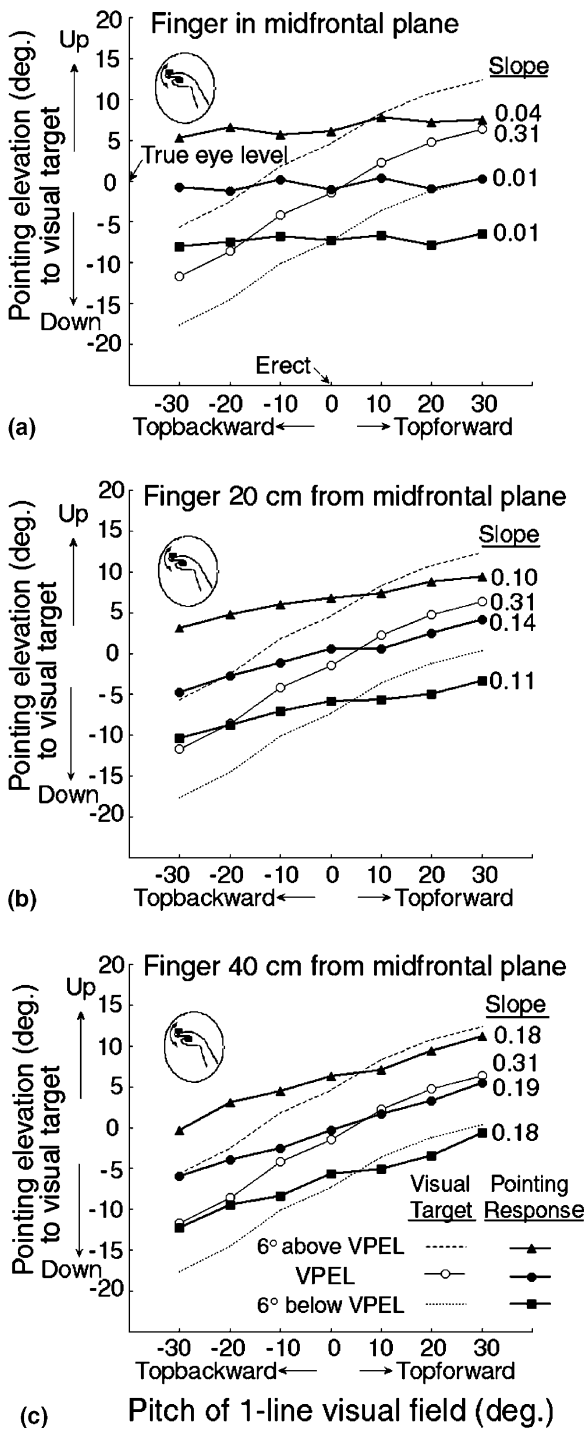
Pitch of 1-line visual field (deg.)

Fig. 3. Experiment 3 employs the same paradigm that was employed in Expt. 1 at each of three different distances of the finger/hand from the body: at the midfrontal plane in panel (a), 20 cm in front of the midfrontal plane in panel (b), and 40 cm in front of the midfrontal plane in panel (c). The results shown are the averages for the 5 subjects. The average perceptual VPEL/pitch results are shown in each panel as the open circles connected by the light solid lines; the elevations of the visual target 6° above and 6° below VPEL are indicated by the dashed and dotted lines, respectively, and are drawn parallel to the VPEL-vs-pitch function.
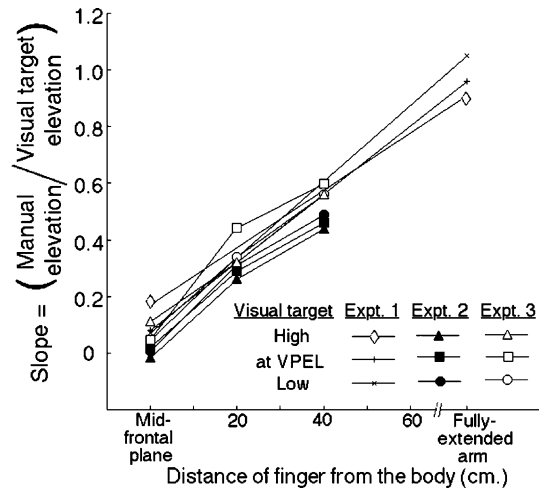

Fig. 4. The average slope of the manual elevation/visual target elevation is displayed as a function of distance of the finger/hand from the midfrontal plane of the body for each condition of Expts. 1–3. The ordinate values are dimensionless and are scaled so that a slope of 0.00 results from a manual point whose elevation did not change with elevation of the target of the point or height match whereas a slope of 1.00 results from identical variations with inducer pitch of the manual point and VPEL. For Expts. 1 and 3, high and low visual targets were 6° above and below VPEL respectively; for Expt. 2, high and low visual targets were 15 cm above and below VPEL respectively. Each plotted value was obtained as follows: The slope of the manual response to the visual target vs pitch function for a given subject was divided by the slope of the visual target vs pitch function; the plotted value is the average value across subjects.

5.3.2. Earlier interpretations of connections between perception and manual behavior related to Expts. 1–3

In our earlier experiments involving manual behavior the height-matching task of Expt. 2 was employed with the hand in the midfrontal plane only, with the target light set at one of 5 equally spaced elevations centered at the VPEL for each of the seven pitches and an inducer consisting of two 66°-long, parallel, bilaterally symmetric lines at ±25° horizontal eccentricity over a ±30° range of pitches (Matin & Li, 1995 [Fig. 5]; Robison et al., 1995). The slope of the function relating the height of the match to the height of the target approximated 1.00 at each pitch and the location of the y-intercept for each pitch fell close to the VPEL for that pitch. In accounting for these results it seemed reasonable at that point to believe that only perception was affected by the inducing stimulus, and that the manual match had been made by a hand/arm that was uninfluenced by the inducer but which closely followed the perceived location of the target to wherever it might be however much perception itself had been in error.

Subsequently, Welch and Post (1996) and Stoper (1997) reported that reaching to touch a visual target in a pitched visual field is more accurate than would be predicted by the error in VPEL alone; in addition, Stoper measured larger errors in manual settings with the hand in the midfrontal plane than with

a less-than-fully-extended arm. [8] Those results indicate that something more than the height-match-closely-follows-perception assumption was required. Welch and Post suggested a basis in either a version of $2VS_3$ (different mechanisms mediate "perception" and "action") or alternatively, that "the presence of visual pitch changed the perceived orientation of the whole body." In a related vein, Stoper suggested that the existence of larger errors with the hand near to the body can be explained by the assumption that the subject makes an error in the judgment of the apparent horizontal in the sagittal plane with the hand closer to the body, and that judgment of the apparent horizontal is not involved when reaching to touch the distant surface containing the visual target.

The results of Expt. 2 that we first presented at meetings in 1999 (Li & Matin, 1999a, 1999b) confirmed the need for greater complexity than the height-match-follows-perception assumption, and at that time we suggested, as had Welch and Post previously, that "...perceived somatosensory space is tilted in the direction of the pitch of the visual field..." Indeed, the interpretation provided a speculative explanation for the height-match results of Expt. 2. The explanation makes use of a "whole-body tilt signal" which (mis)informs the subject that the entire body is tilted and that the horizontal at eye level lies along the line between the VPEL target and the eye. Such a whole-body tilt signal would result in all height-match settings lying along this line. [9]

However, although the whole-body-tilt-signal explanation is sufficient for the height-match results of Expt. 2, it is not adequate to explain the results of Expts. 1 and 3 where the subject is required to point the finger in the direction of the visual target. Something more complicated is required: This becomes particularly apparent when we consider the results of pointing to the perceptually mislocalized target in Expt. 1: Although the subject points nearaccurately to the visual target-set-at-VPEL with the arm fully extended, with the hand/finger in the midfrontal plane at eye level, the subject's finger points along a horizontal line at true eye level that is very different from the eye/VPEL line (Fig. 1a). Since the whole-body-tilt-signal explanation puts the perceived direction of the horizontal along the line between the VPEL target and the eye at all distances, it incorrectly predicts that the subject's finger in the midfrontal plane at eye level should point along that line. Thus, the fact that the subject points in two very different directions with the finger in the midfrontal plane and with the fully-extended arm presents a critical argument against the whole-body-tilt-signal explanation. The results of pointing from different distances in Expt. 3 (Fig. 3) confirmed and extended the results of Experiment 1 and made the argument against the whole-body-tilt-signal explanation even more compelling. Although we recognized the problem by the time of the ARVO and Psychonomic meetings in 1999, it was only some time later—in early 2000—that we developed a viable solution to it. This solution was developed in conjunction with an analysis that led to Expt. 4.

6. Expt. 4: Pointing to the felt horizontal

6.1. Procedure for Expt. 4

Pointing to felt horizontal. The subject set the elevation of the finger/hand to feel horizontal in the presence of each of the seven orientations of the 1-line inducer in otherwise total darkness. This was done separately with the finger/hand in the midfrontal plane at eye level and with the fully extended arm. Pointing-to-the-horizontal measurements also were made in complete darkness prior to and following the measurements made in the presence of the visual inducer.

6.2. Results for Expt. 4

In Expts. 1–3 the VPEL settings measured the influence of the visual inducer on the perception of the visual target alone whereas the pointing and height-match settings measured the influence of the visual inducer on the conjunction of visual perception and manual behavior relative to the visual target. By removing the visual target of the manual point and employing a nonvisual cri-

---

[8] Although Stoper (1997) refers to both the less-than-fully-extended-arm settings and the midfrontal-plane settings as "pointing", his description makes it clear that both were height matches in which the subject adjusted the height of the hand but not its angle, with the hand at a fixed (but unreported) distance from the body. Their settings were not made by orienting the angle of the finger to the desired direction with the hand at a fixed height as was done in all but one of the conditions in our Expts. 1 and 3; in the case of the exception, the fully-extended-arm condition in our Expt. 1, angle setting (or direction setting) was accomplished by varying the arm's height; there the arm was rigid and the index finger pointed in the direction of the target with rotation at the shoulder (no variation in flexion at index finger joints, at the wrist, or at the elbow).

[9] Since the existence of some illusory whole-body signals have been reported to be perceptible (i.e., available for verbal reporting) in other dimensions (Witkin, 1949), our nonsystematic observations on this matter here to the contrary are worth reporting: All of the several hundred observers who have viewed the fully-structured, well-illuminated pitchroom (Matin & Fox, 1986, 1989; Matin & Li, 1992, 1994a, 1994b, 1994c) have manifested a VPEL-vs-pitch function that rises with increasing topforwardness of the rotatable room; they have also invariably described the related illusions involving systematic variation in perceived size of an erect human-as-visual-stimulus viewed against the pitchroom's back surface and of perceived tilt of a freely hanging plumb line as well as a number of other illusions. Although several observers did report that they were disoriented when viewing the pitched room, only a rare observer reported that s/he felt any tilt of her/his own body or any part of her/his body, or any abnormal sensations from her/his own body at any time during the viewing of the stationary pitchroom. Thus, if such a whole-body tilt signal is generated by visual pitch, whatever its nature might be, it appears that it would generally play its role unbeknownst to the subject.
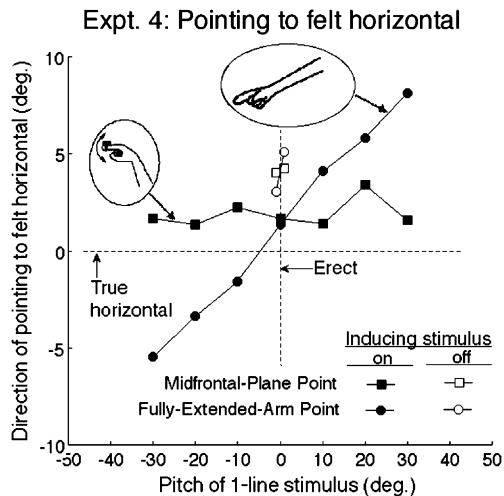
Fig. 5. Expt. 4: Average results for the 8 subjects who pointed to the direction felt to be horizontal with the finger/hand in the midfrontal plane at eye level or with the fully extended arm. In each case the subject viewed the visual field containing only the variably oriented inducing line in otherwise total darkness. Measurements in total darkness before and after those with the inducing line are displayed above the abscissa zero.

terion for manual behavior, Expt. 4 measured the influence of the visual inducer on manual behavior alone: In Expt. 4 the subject set the elevation of the finger/hand to feel horizontal in the presence of the 1-line inducer in otherwise total darkness. Fig. 5 shows that the fully-extended-arm point to the nonvisual criterion manifests an error whose amount changes nearlinearly with inducer orientation and is only slightly less than the error produced by the influence of the visual inducer on the elevation of VPEL; however, the midfrontal-plane point is nearaccurate at all inducer orientations. Thus, the errors and accuracy in pointing to the nonvisual criterion in Expt. 4 (Fig. 5) are in the reverse relation to finger/hand distance relative to the results of pointing and height-matching to a visual target in Expts. 1–3. [10]

7. General discussion

7.1. Two wrongs make a right

These results for Expt. 4 dictate a surprising basis for explaining the systematic variation in accuracy of pointing and height matching to a visible target with distance

of the hand from the body in Expts. 1–3: (a) The midfrontal-plane point/height match to the visual target that appeared to lie on the horizontal (at VPEL) was essentially invariant with pitch at elevations near true horizontal because that was where the finger/hand felt horizontal at all pitches; each set of parallel manual settings to the targets above (or below) VPEL correspond to the feeling of a given felt deviation above (or below) VPEL. (b) But the physical elevation at which the fully extended arm felt horizontal changed with inducer orientation along a function that was close to that followed by VPEL, and so the finger/hand was set close to the VPEL setting and thus to nearaccuracy; again, a similar basis holds for the manual settings to the targets above and below VPEL. This interpretation for both (a) and (b) only assumes that the manual setting by the unseen hand to a visual target is the outcome of a crossmodality match between a visual criterion (VPEL setting) and a nonvisual criterion (finger/hand elevation feels horizontal), as is normally the case without an inducer. *Thus, nearaccuracy at pointing to a perceptually mislocalized visual target with the fully extended arm is a consequence of nearequality* [11] *of the induced errors in visual perception of the elevation of the physical horizontal and in manual localization of the physical horizontal by the extended arm, whereas the systematic errors in the midfrontal-plane point to the same visual target are a consequence of the essential failure of the induction stimulus to induce errors in the manual behavior—instead the midfrontal-plane point to the visual target at VPEL stayed close to the physical horizontal and did not covary with the induced errors in the visual perception of the elevation of the physical horizontal.*

7.2. Proximal/distal model

7.2.1. Modeling perceptual localization

The previous paragraph provides the basis for a quantitative treatment of the results of the four experiments that employs a new development of the model that provided the original account for the effect of visual pitch on VPEL (Matin & Fox, 1986, 1989) and has since served as a basis for subsequent experimental and theoretical work regarding the perception of elevation (Cohen, Stoper, Welch, & DeRoshia, 2001; DiZio, Li, Lackner, & Matin, 1997; Li & Matin, 2001; Matin & Li, 2001). The original account interpreted the influence

---

[10] The variation of the elevation of the manual settings of the extended arm to feel horizontal in Expt. 4 (Fig. 5) differs from Stoper's (1997) view that the subject uses the judgment of apparent horizontal for manual behavior with the arm close to the body but fails to use the judgment of apparent horizontal at all for manual behavior with the arm further from the body. That view also does not account for the distance-dependent differences in pointing to the visible target in Expts. 1 and 3.

[11] The perceptual and motor errors possess the same sign under visual induction. Thus, for example, under induction by topbackward visual pitch the elevation of a visual target at true eye level is perceived to lie above true eye level and the fully-extended arm that is truly horizontal is felt to lie above true horizontal. For this case, in order to appear at eye level (VPEL setting), the visual target is set below true eye level, and, in order to feel horizontal the fully-extended arm is set below true horizontal. Similar relations hold under topforward pitch.

of visual pitch (and subsequently, changes in retinal orientation [12]) on perception of elevation in complex visual fields and in visual fields consisting of 1-line and 2-line inducing stimuli as a consequence of a linear weighted sum of inputs from the visual field and from the body-referenced mechanism. [13] We now refer to these components as originating in the proximal and distal systems of a "Proximal/Distal model" and extend the original model to account for visually guided sensorimotor behavior involving pointing, reaching, and height matching as well as for the VPEL measurements of the perception of elevation: The distal system, D, is referenced with respect to coordinates in the space outside the observer, with input regarding visual pitch, V, as the significant segment of its adequate stimulus. The proximal system, P, is referenced with respect to coordinates attached to the subject's own body and is essentially uninfluenced by visual pitch, with influences from the body-referenced mechanism, B, as of greatest significance. [14]

The earlier model was fitted to several aspects of the VPEL measurements in the pitchroom. This earlier treatment for VPEL continues to apply to the present results here with only a minor modification: The close approximation to linearity of the relation between VPEL and visual pitch (Figs. 1–3) suggests the involvement of linearly additive contributions from the proximal and distal systems, an interpretation expressed by

$$E(B, V) = \alpha_E P(B) + \beta_E D(V), \tag{1}$$

where E represents the physical elevation equal to a VPEL setting, and α_E and β_E represent the relative weights of the inputs from the proximal and distal systems, respectively, with $\alpha_E + \beta_E = 1$. [15] If visual input were the sole influence on VPEL, the slope of the VPEL-vs-pitch function would equal 1.00. Since the slope is a great deal less than 1 (Figs. 1 and 3), it is clear that although direct inputs to the body-referenced mechanism have not been changed by the experimental manipulations, the body-referenced mechanism must play a large role in the VPEL discrimination. Separating B into a component due to its main stimulus and a biasing constant characteristic of the individual observer,

$$B = \alpha_E(B_S + B_{E0}); \tag{2}$$

a similar separation for V produces

$$V = \beta_E(V_S + V_{E0}). \tag{3}$$

Here B_S and V_S are components (angular directions) due to inputs to the visual system and the body-referenced mechanism, respectively, and V_{E0} and B_{E0} are biasing constants affecting VPEL that are related to visual stimulation and stimulation by the body-referenced mechanism, respectively. Eq. (4) introduces the terms from Eqs. (2) and (3) into Eq. (1). Thus,

$$E(B, V) = \alpha_E(B_S + B_{E0}) + \beta_E(V_S + V_{E0}). \tag{4}$$

For the present case, V_S may be taken to be equal to visual pitch measured by the angle that the normal to the pitched surface makes with the horizontal and is specified as θ_i, and B_S may be equated to the normal to the direction of gravity. Thus the zero direction for both V and B is the physical horizontal measured at true eye level. Here, as in the earlier treatment, there is no reason to believe that distance of the finger from the body, Π, influences the VPEL setting, and Π is not introduced into the treatment of E. Since $B_S = 0$,

$$E(B, V) = \alpha_E B_{E0} + \beta_E(\theta_i + V_{E0}), \tag{5}$$

and the slope of the VPEL/pitch function is

$$dE(B, V)/d\theta_i = \beta_E \tag{6}$$

with the y-intercept ($\theta_i = 0$) equal to $\alpha_E B_{E0} + \beta_E V_{E0}$. For the two sets of VPEL results the VPEL-vs- pitch slopes are 0.30 and 0.31 (Figs. 1/2, 3; Expts. 1/2 and 3, respectively). Using 0.3 as the slope value leads to $\alpha_E = 0.7$ and

---

[12] We use the term "retinal orientation" to designate the orientation of the geometric image of the line in the spherical approximation to the eye (Matin & Li, 1992, 1994a, 1994b, 1994c, 2001) under the assumption that this spherical approximation to the eye is erect, and that projection is through a pupil centered in the midfrontal plane of the sphere. The angle specifying "retinal orientation" on this spherical projection is the angle of intersection of the great circle containing the image of the line with the circumference of the midfrontal plane of the spherical eye.

[13] The term 'body-referenced mechanism' was introduced (Matin & Fox, 1989) to refer to the combination of all extraretinal influences on the perception of interest—here the visual perception of vertical—including extraretinal eye position information, extraretinal head orientation information (including information regarding the head relative to the body and the head relative to gravity), other effects of gravity on the body, pressure cues from the surfaces of the body, joint receptors, and the vestibular organ; it includes, in addition, the basic local sign information from the visual target employed to measure the discrimination itself. The term was introduced in order to separate the processing of visual from nonvisual influences on perception, and now on manual behavior as well. It is clear, however, that all of these nonvisual influences do not operate on visual input at a common locus or in a similar fashion. But the term retains its usefulness in the present context.

[14] Differences in processing of neural signals that originate from sources of stimulation near to the body and far from the body have been reported by a number of authors (Berti & Rizzolatti, 2002; Fogassi et al., 1992, 1996; Gentilucci et al., 1988; Graziano & Gross, 1994, 1995, Chap. 67; Grüsser, 1983; Jeannerod, 1997; Mountcastle, 1976; Mountcastle, Lynch, Georgopoulus, Sakata, & Acuna, 1975; Rizzolatti, Berti, & Gallese, 2000; Rizzolatti, Matelli, & Pavesi, 1983; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981).

[15] The symbolism employed here is specific to the present experiments and as uncomplicated as we have been able to make it: For example, although variations in the magnitude and/or direction of the gravitoinertial vector may have effects on B, B is neither parameterized nor indexed on g since, in the present experiments, g is constant and the observer is erect throughout.

$\beta_E = 0.3$. This value of β_E is considerably less than values of 0.56 and 0.63 obtained in the illuminated pitchroom (Matin & Fox, 1986, 1989; Matin & Li, 1992), and also smaller than previously measured with either a 1-line or 2-line inducing stimulus in darkness and at other levels of g (Chelette, Li, Esken, & Matin, 1995; Cohen et al., 2001; DiZio et al., 1997; Matin & Li, 1994a, 1994b, 1994c); its smaller size here is a consequence of the smaller influence of the 1-line inducer in the present experiments relative to the influence of the complexly-structured, fully-illuminated pitchroom, and also to the fact that the value in these previous experiments in the pitchroom is in part a consequence of a contribution by variation of height-in-the-field of the visual inducing stimulus that was correlated with pitch (Chelette et al., 1995; DiZio et al., 1997; Li & Matin, 1990, 2002; Matin & Fox, 1986, 1989). [16] Consequently also, the weighting for the contribution of the body-referenced mechanism, α_E, is somewhat greater in the present experiments compared to the earlier pitchroom measurements where values closer to equality for α_E and β_E were obtained. [17]

7.2.2. Modeling manual localization

The results for manual localization differ from those for VPEL; for pointing to a visual target, reaching to a visual target, height-matching, and for setting the finger to feel horizontal in the absence of a visual target, manual localization is controlled by both visual pitch and finger-to-body distance. Thus the basic relation for manual localization, M, that connects it with the proximal and distal systems is not only parameterized by visual pitch and the body referenced mechanism, but by finger-to-body distance, Π_j, as well:

$$M(B, V, \Pi) = \alpha_M(\Pi_j)P(B) + \beta_M(\Pi_j)D(V), \qquad (7)$$

where $\alpha_M(\Pi_j)$ and $\beta_M(\Pi_j)$ represent weightings for the manual behavior parameterized by Π_j. Similarly to the above development for perception, B and V are each

separated into stimulus and biasing components affecting pointing/reaching and height-matching related to the body-referenced mechanism and the visual influence, respectively; for this purpose, the symbol M (for manual) replaces E. Thus, for the body-referenced mechanism,

$$B = \alpha_M(B_S + B_{M0}); \qquad (8)$$

and for vision,

$$V = \beta_M(V_S + V_{M0}). \qquad (9)$$

Again, since $B_S = 0$ and letting $V_S = \theta_i$,

$$M(B, V, \Pi) = \alpha_M(\Pi_j)B_{M0} + \beta_M(\Pi_j)(\theta_i + V_{M0}), \qquad (10)$$

where B_{M0} and V_{M0} are the biasing constants affecting pointing/reaching and height-matching related to the body-referenced mechanism and the visual influence, respectively; again the zero direction for both V and B is the physical horizontal measured at true eye level. From Eq. (10), the slope of the function for the manual point to the visual target relative to the visual pitch of the inducing line is

$$dM(B, V, \Pi)/d\theta_i = \beta_M(\Pi_j). \qquad (11)$$

Since there is no countervailing contribution from visual input when attempting to point at the horizontal in total darkness, the proximal system operates alone, and the result should be independent of hand-to-body distance, Π_j, as it is in fact: The average elevation for the subject's pointing to the horizontal in total darkness is independent of hand-to-body distance, with settings of 4.2° and 4.1° above true horizontal when pointing from the midfrontal plane and with the extended arm, respectively (Fig. 5). However, when pointing to the horizontal in the presence of the inducing line, $\beta_M(\Pi_j)$ is multiplied by the visual influence contributed by the inducing line (θ_i in Eq. (10)), and so hand-to-body distance, Π_j, should play a role, as it does: As shown in Fig. 5, pointing to the horizontal in the presence of the inducing line depends on hand-to-body distance, varying systematically with the orientation of inducing line pitch for the extended arm, but remaining essentially constant for pointing from the midfrontal plane; the influence of the induction line's presence is also shown in the reduction of the y-intercept toward veridicality relative to the dark value for both hand-to-body distances. Thus, the expectations regarding pointing to the orientation felt as horizontal are in correspondence with both the measurements in total darkness and in the presence of the inducing line at various orientations for the different hand-to-body distances.

When the subject points to the visual target the task is very different than when pointing is to the orientation

---

[16] In the present experiments visual pitch was varied by rotating the frontoparallel plane containing the inducing stimulus around an axis in the stimulus plane. In the earlier experiments referred to in the text above visual pitch was varied by rotating the inducing stimulus around an axis in the frontoparallel plane containing the nodal points of the two eyes; in the ranges of variation employed, the latter is very nearly equal to a combination of vertical translation and rotation around the axis in the stimulus plane.

[17] The slope of the VPEL-vs-pitch function is influenced by the particular composition of individuals in the subject group. Slopes as small as 0.16 and as large as 0.70 have been measured in the past with a long (64°-long) 1-line stimulus for different individuals. Although we have found the correlation between the dark VPEL and the y-intercept of the VPEL/pitch function to be significant in several previous experiments (DiZio et al., 1997; Li & Matin, 2001; Matin & Fox, 1989; Matin & Li, 1994a), it was not significant in either Expt. 1 or 3; however, the number of the subjects involved the correlations were small here, equal to 4 and 5, respectively.

felt as horizontal. We note several important differences: For one thing, pointing to the felt horizontal with the unseen hand does not involve a crossmodality match with an aspect of a stimulus apprehended by vision only. Thus, although the visual input from the inducing line can exert an influence on the two different tasks (pointing to the felt horizontal and pointing to a visual target), carrying out the task of pointing to the felt horizontal does not require the utilization of vision, i.e., it does not require matching the finger's direction or orientation to a target that can only be localized through vision. Secondly, pointing to a visual target in a visual field that is completely dark except for the presence of the inducing line does not require that the subject attend to an aspect of a coordinate system such as "horizontal"; the crossmodality match is a relative one that requires no attention by the subject to the hand's direction in space; it only requires attention to the hand's relation to the visual target, whereas pointing to felt horizontal is a wholly egocentric setting requiring attention to the relation between the hand and a unique direction in space. Thus, the task of pointing to the felt horizontal requires no attention to anything outside the body (note that although gravity emanates from outside the body its effect is felt within the body) although, as for the task of pointing to a visual stimulus, external influences from the gravitational stimulus provide numerous inputs to the body including the vestibular system, the joints, the muscular system, the somesthetic system, and more. It is noteworthy that, in spite of these important differences in pointing to the horizontal under induction and pointing to the visual target-set-to-VPEL under induction, the slopes are similar for each of the two cases as shown in Table 1.

In order to derive actual quantitative predictions for the results of the experiments in which the subject points the finger or height matches to the visual target, it is necessary to obtain values for $\alpha_M(\Pi_j)$ and $\beta_M(\Pi_j)$. We do this by making use of Eqs. (6), (11), and the plot in Fig. 4. Using Eqs. (6) and (11), the ordinate in Fig. 4 can be expressed in terms of the model. Designating the theoretical value of the ratio of slopes on the ordinate as S,

$$S = \beta_M(\Pi_j)/\beta_E. \tag{12}$$

Since it is clear that as plotted in Fig. 4 the results of Expts. 1–3 are linear, a best fit to the linear equation $S = k_1 + k_2\Pi$ utilizing all of the results from Expts. 1–3, was done. The outcome of this fit may be expressed with only a small error resulting from an approximation in Eqs. (13) and (14). For this purpose, in order to normalize hand-to-body distance to a range between 0 and 1, Π_j' was set equal to $\Pi_j/70$ cm, where 70 cm is an approximation to the average maximum finger-body distance. Then the best fit for $\beta_M(\Pi_j')$ is

$$\beta_M(\Pi_j') = 0.05 + 0.9\Pi_j'\beta_E, \tag{13}$$

and since $\alpha_E + \beta_E = 1$ as well as $\alpha_M(\Pi_j') + \beta_M(\Pi_j') = 1$,

$$\alpha_M(\Pi_j') = 0.95 - 0.9\Pi_j'(1 - \alpha_E). \tag{14}$$

Eqs. (13) and (14) yield values for $\alpha_M(\Pi_j')$ and $\beta_M(\Pi_j')$ for the extended arm pointing to the VPEL target ($\Pi_j' = 1$) equal to 0.68 and 0.32, close to the best-fit values to the slopes in the data for Expt. 1 of 0.72 and 0.28. It is worth noting that both the data for pointing to the VPEL with the extended arm and predictions of $\alpha_M(\Pi_t')$ and $\beta_M(\Pi_j')$ from the model are very close to the values of α_E and β_E of 0.7 and 0.3 for VPEL, respectively; these predicted values are thus consistent with the nearaccuracy measured for pointing at the visual target with the fully-extended arm. Eqs. (13) and (14) also yield values of 0.95 and 0.05 for $\alpha_M(\Pi_t')$ and $\beta_M(\Pi_t')$, respectively, for pointing/height matching from the midfrontal plane ($\Pi_j' = 0$), and predicts a slope of 0.05, very close to the best-fit slope of 0.02 for the results of pointing to VPEL from the midfrontal plane in Expt. 1. The slope values obtained for intermediate distances from equations (13) and (14) also correspond well to the results for Expts. 2 and 3. [18]

Thus, the parameters of the model that describe the guidance by the sensorimotor system of manual localization with the extended arm are concordant with the perceptual system's setting of VPEL by virtue of utilizing weightings for inputs from the distal and proximal systems that are nearly identical to those employed by the perceptual system (Fig. 6). This concordance diminishes

---

[18] Utilizing Eq. (10) to form two equations with the derived values of $\alpha_M(\Pi')$ and $\beta_M(\Pi_j')$ along with the y-intercepts from the results of Expt. 1 (0.95° and −2.50° for the midfrontal-plane point and the fully-extended arm point, respectively) provides a solution for B_{MO} and V_{MO}; the values are $B_{MO} = 1.59$ and $V_{MO} = -11.19$. This value of B_{MO} is consistent with the measurements for pointing to the horizontal in total darkness: Although the value of 4.15 for pointing to the horizontal in total darkness might itself appear to serve as a reasonable biasing value for the body-referenced mechanism since it was measured in total darkness without vision, it cannot serve as the appropriate value for B_{MO} in the presence of a visual field; the presence of a visual field reduces the weight for the contribution of the body-referenced mechanism (Matin et al., 1982), and the magnitude of the reduction from 4.15 to 1.59 is consistent with this. On the other hand the value of −11.19 for V_{MO} is larger than anticipated; we note three relevant matters: (1) The parameter values of $\alpha_M(\Pi_t')$ and $\beta_M(\Pi_j')$ calculated for the model involved data from experiments conducted with two different groups of subjects (Expts. 1 and 4), and differences among the individuals in the two groups is likely to have contributed to the actual values. (2) In order to obtain solutions for B_{MO} and V_{MO} it was also necessary to assume that the value of each is identical for the two different hand-to-body distances; it is not clear that this assumption will hold generally. (3) Constant errors such as y-intercepts are not as reproducible as are slope values; although slope values do differ among individuals (footnote 17), the value for a given individual is considerably more stable than the y-intercept.

Table 1
The table contains values of the slopes of the functions that relate the elevation of the pointing finger to the pitch of the inducing line

	Slopes	
	Fully-extended arm point	Midfrontal plane point
Point to horizontal (Expt. 4)	0.23	0.02
Point to visual target at VPEL (Expt. 1)	0.28	0.02
Model's prediction for pointing to visual target at VPEL (Expt. 1)	0.32	0.05

Each row displays the slope for the measurements of the fully-extended arm in the left column and for the hand in the midfrontal plane in the right column. The top row displays the slopes of the best-fitting straight lines to the results (Fig. 5) when the subject attempted to point in the direction of the felt horizontal in the absence of a visual target; the second row displays the slopes of the best-fitting straight lines to the results of pointing to the visual target for the case in which the visual target was set to VPEL (Fig. 1); the third row displays the predictions for the manual behavior in Fig. 1 by the Proximal/Distal model described in Section 7.2.

$$\left[\begin{array}{c} E(B, V) = \alpha_E P(B) + \beta_E D(V) \\ \alpha_E + \beta_E = 1 \end{array} \right]$$

$\alpha_E = 0.70$

$\beta_E = 0.30$

$\beta_M = 0.32$ $\alpha_M = 0.68$

$\beta_M = 0.05$ $\alpha_M = 0.95$

$$\left[\begin{array}{c} M(B,V,\Pi) = \alpha_M(\Pi)P(B) + \beta_M(\Pi)D(V) \\ \alpha_M(\Pi) + \beta_M(\Pi) = 1 \end{array} \right]$$
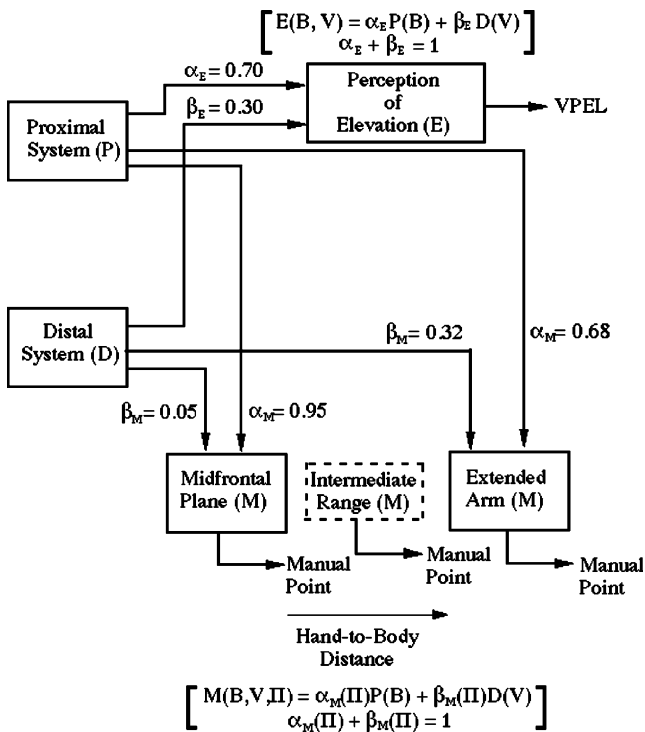
Fig. 6. The figure shows the flow diagram for the Proximal/Distal model described in Section 7.2, displaying the weights for predicting the sensitivity of VPEL to visual induction (top portion), and the weights for predicting the sensitivity of manual pointing to visual induction for the hand in the midfrontal plane and for the fully-extended arm (bottom portion).

as the distance of the finger from the body diminishes; the concordance is minimal in the midfrontal plane where the weighting of the proximal system is maxi-

mized and the weighting of the distal system is minimized. As a result of the identical influences from the visual field on the sensorimotor system guiding manual localization and from the perceptual system determining VPEL, pointing with the arm extended is accurate relative to the physical world in the present experiments. Thus we note again that there is an aspect that appears paradoxical in the predictions of the model in that, although perception mislocalizes the visual target of the manual point, pointing with the extended arm is accurate; i.e., perception and pointing with the extended arm are in agreement—they are both influenced by the orientation of the inducing line and the disparity in errors between them is close to zero. On the other hand, with the finger close to the body (e.g., in the midfrontal plane), pointing is strongly influenced by the proximal system and only minimally influenced by the distal system. Although the proximal system and the visual input maintain reasonably close localizations in a normal environment, under induction by the pitched-from-vertical line, localization by perception is modified. However, because of the small weighting given to the distal system's input, the sensorimotor guidance by the finger-in-the-midfrontal-plane is not substantially modified by the visual inducing stimulus; but since perception has been modified, pointing from the midfrontal plane is in error by approximately the magnitude of the modification of perception as measured by the deviation of VPEL produced by the inducing line.

On this interpretation, then, the variation of manual accuracy with manual distance in pointing to the visual target is the consequence of an orientation-dependent and distance-dependent influence of the visual inducer on the relation between manual and physical coordinates in conjunction with the orientation-dependent influence of the inducer on visual localization. [19] It is not a consequence of a lack of influence of visual induction on manual behavior as proposed in $2VS_3$ (Aglioti et al., 1995; Goodale & Haffenden, 1998). The accuracy in pointing to a target at full arm extension is the result of nearequal error-generating influences by visual induction on visual perception and on action (measured by VPEL and the fully-extended-arm point, respectively) instead of the dissociation between perception and action in processing visual spatial information required by $2VS_3$. Furthermore, the systematic variation with distance in the relation between localization by visual perception and manual pointing/height matching is also not

---

[19] VPEL—the angular measure employed here—does not vary with the viewing distance of the visual field: Thus for any given orientation of a parallel, 2-line, pitched-from-vertical inducing field, VPEL does not change over the distance range from 1/3 meter to 1 meter (Post & Welch, 1996).

due to a lack of visual influence on the manual behavior but instead to the systematic variation of the influence that generates variation in the felt orientation of the finger/hand. In a subsequent set of experiments (Li & Matin, 2004) in which we examined the time course of the decay of the influence on VPEL following removal of either the inducing stimulus, the visual target of the behavior, or both, we have learned that the decay of the influence on perceptual mislocalization is slow (3 min time constant), whereas the decay of the direct influence on the manual behavior is rapid (under a minute), that removing the inducer without removing the visual target eliminates the distance dependence, and that removing the visual target without the inducer leaves the distance dependence in memory to continue influencing the manual mislocalization. In still further subsequent

work (Matin, Li, & Bertz, 2004) we have reported experiments with identical format and analogous results to the present experiments in which the roll-tilt orientation of the hand manifests distance-dependent manual settings to match the orientation of a roll-tilted-from-vertical line mislocalized under the classical rod-and-frame illusion of Witkin and Asch (1948); in this case, with the hand in the midfrontal plane the subject sets the roll-tilt of the hand to true vertical when matching to the line mislocalized as lying at true vertical, but sets the roll-tilt of the hand to accurately match the mislocalized line's roll-tilt orientation with the hand 60 cm from the body. Along with the present distance-dependent results these results suggests distance-based alternatives for explaining two of the main supports for $2VS_3$ noted above. [20, 21]

---

[20] Central to these alternative explanations are the strong, distant-dependent correspondences that exist between the present results and two of the results employed by $2VS_3$ for support: (1) The accurate orientation settings with the extended arm of the visual agnosic coupled with her inaccurate orientation matches with the hand close to the body (Goodale et al., 1991; Milner & Goodale, 1995). (2) The perceptual errors in the Ebbinghaus/ Titchener illusion coupled with the relative accuracy in interfinger aperture in reaching for the illusory stimulus with the extended arm (Aglioti et al., 1995; Milner & Goodale, 1995):

(1) *The visual agnosic DF.* In the present experiments (a) the VPEL setting of the target's elevation, the result of psychophysical measurements (use of verbal report), and (b) the midfrontal-plane point (as well as the midfrontal-plane height match of the target-set-to-VPEL) are both inaccurate in the pitched visual field; these correspond with (a′) DF's inability to verbally report the orientation of the slot accurately, and (b′) her inaccuracy in matching the distant orientation of the slot with that of a handheld card in nearspace, respectively. On the other hand, (c) the fully-extended-arm point in the present experiments is nearaccurate, and this corresponds with (c′) DF's ability to accurately post the handheld card in the slot with a fully-extended-arm reaching movement. In addition, (d) the linear increase of accuracy in pointing to the visual target in the present experiments with increasing distance of the finger from the midfrontal plane (Fig. 4) may be taken to correspond to (d′) the report that DF begins to orient her hand correctly en route to the distal slot (Milner & Goodale, 1995).

This fourfold correspondence suggests analogous arrangements for the mechanisms controlling the two spatial dimensions, elevation and frontal plane orientation, and raises the possibility that DF's accurate orientation of the handheld card during posting is a consequence of an identity or nearidentity of manual and perceptual errors of orientation as it is for the fully extended arm in the present experiments for the dimension of elevation, whereas DF's difficulties are a consequence of damage in cortical areas concerned with space perception and with manual control in nearspace. Our more recent results (Matin et al., 2004) demonstrating similar distance-dependent manual behavior in response to stimuli that are perceptually mislocalized in the roll-tilt dimension provide even clearer correspondences with DF's behavior. These correspondences suggest damage to a cortical region specifically concerned with the control of manual behavior at near distances, with regions controlling manual behavior at large hand-to-body distances left intact.

(2) *The Ebbinghaus/Titchener illusion.* Here we suggest that (a″) the inaccuracy of the psychophysical measurements of the perception of the size of the central circle in the Ebbinghaus/Titchener illusion may be taken to correspond with (a) the mislocalization of VPEL measured psychophysically. In a subsequent report, (b″) when the subjects gave a manual estimate of disk size in darkness prior to reaching they "…were strongly biased in the direction of the illusion (Goodale & Haffenden, 1998)"; this may be taken to correspond with (b) the inaccuracy of the midfrontal-plane point and height match in the present experiments. In both the earlier and the later report (c″) the interfinger aperture during the subject's reach for the central circular disc as the hand approached the disc that is about to be grasped was relatively accurate in suggested correspondence with (c) the accuracy of the fully-extended-arm point in the present experiments, and (d″) the fact that the interfinger aperture maximum is about twice the disc size and the aperture begins to conform to the true size of the disc as the hand approaches the target may be taken to correspond to (d) the linear increase of accuracy in pointing to the visual target in the present experiments with increasing distance of the finger from the midfrontal plane (Fig. 4).

Thus, although $2VS_3$ suggests that the accuracy in setting the aperture between the fingers is greater when approaching the target than might be predicted from the magnitude of the perceptual illusion because the action system was not influenced by the inducer generating the illusion, the inference we draw from the fourfold correspondence with the present results is that the increased approximation to accuracy is a consequence of the induction stimulus for the illusion also inducing a manual error that is closer to matching the perceptual error as the hand approaches the object to be grasped. This interpretation is exactly the opposite of that based on the $2VS_3$ theory; instead of 'no influence on the action system' the suggestion from analogy with the present experiments is that, for the extended arm, the error-generated influence of the inducer on the action system essentially matches the error made by the perceptual system.

[21] We note that Post, Welch, and Olson (2004) have also reported measurements of manual behavior induced by the tilted frame of Witkin and Asch although, since the measurements were made at only one hand-to-body distance, they could not be used to draw inferences regarding hand-to-body distance-dependence. They used a different procedure for measuring the effect than was employed by Matin et al. (2004): Instead of directly measuring the roll-tilt orientation of the hand, they required the subject to point successively at each end of the perceptually mislocalized rod. From these measurements calculations were made that indicated a manual roll-tilt halfway between the true rod orientation and the orientation that corresponded to the magnitude of the perceived illusion; the authors suggest that these results indicate a "partial dissociation of vision and action."

Acknowledgment

References

Aglioti, S., DeSouza, J. F. X., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology, 5*, 679–685.

Baizer, J. S., Ungerleider, L. G., & Desimone, R. (1991). Organization of visual inputs to the inferior temporal and posterior parietal cortex in macaques. *Journal of Neuroscience, 11*, 168–190.

Berti, A., & Rizzolatti, G. (2002). Coding near and far space. In H. Karnath, A. D. Milner, & G. Vallar (Eds.), *The cognitive and neural bases of spatial neglect* (pp. 119–129). New York: Oxford University Press.

Bousaoud, D., di Pellegrino, G., & Wise, S. P. (1996). Frontal lobe mechanisms subserving vision-for-action versus vision-for-perception. *Behavioral Brain Research, 72*, 1–15.

Bruno, N. (2001). When does action resist visual illusions? *Trends in Cognitive Sciences, 5*, 379–382.

Campion, J., Latto, R., & Smith, Y. M. (1983). Is blindsight an effect of scattered light, spared cortex, and near-threshold vision? *Behavioral and Brain Sciences, 6*, 423.

Carey, D. P. (2001). Do action systems resist visual illusions? *Trends in Cognitive Sciences, 5*, 109–113.

Chelette, T., Li, W., Esken, R., Matin, L. (1995). Visual perception of eye level (VPEL) under high g while viewing a pitched visual field. *Annual Meeting of Aerospace Medical Association*, A55.

Cohen, M. M., Stoper, A. E., Welch, R. B., & DeRoshia, C. W. (2001). Effects of gravitational and optical stimulation on the perception of target elevation. *Perception and Psychophysics, 63*, 29–35.

DiZio, P., Li, W., Lackner, J. R., & Matin, L. (1997). Combined influences of gravitoinertial force level and visual field pitch on visually perceived eye level. *Journal of Vestibular Research, 7*, 381–392.

Fendrich, R., Wessinger, C. M., & Gazzaniga, M. S. (1992). Residual vision in a scotoma: Implications for blindsight. *Science, 258*, 1489–1491.

Fogassi, L., Gallese, V., di Pelligrino, G., Fadiga, L., Gentilucci, M., Luppino, G., et al. (1992). Space coding by premotor cortex. *Experimental Brain Research, 89*, 686–690.

Fogassi, L., Gallese, V., Fadiga, L., Luppino, G., Matelli, M., & Rizzolatti, G. (1996). Coding of peripersonal space in inferior premotor cortex (area F4). *Journal of Neurophysiology, 76*, 141–157.

Franz, V. H. (2001). Action does not resist visual illusions. *Trends in Cognitive Sciences, 5*, 457–459.

Gentilucci, M., Fogassi, L., Luppino, G., Matelli, M., Camarda, R., & Rizzolatti, G. (1988). Functional organization of inferior area 6 in the macaque monkey. I. Somatopy and the control of proximal movements. *Experimental Brain Research, 71*, 475–490.

Goodale, M. A., & Haffenden, A. (1998). Frames of reference for perception and action in human visual system. *Neuroscience and Biobehavioral Reviews, 22*, 161–172.

Goodale, M. A., Milner, A. D., Jacobson, L. S., & Carey, D. P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature, 349*, 154–156.

Graziano, M. S. A., & Gross, C. G. (1994). Mapping space with neurons. *Current Directions in Psychological Science, 3*, 164–167.

Graziano, M. S. A., & Gross, C. G. (1995). The representation of extrapersonal space: A possible role of bimodal, visual-tactile neurons. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 1021–1034). Cambridge, MA: MIT Press.

Grüsser, O. J. (1983). Multimodal structure of the extrapersonal space. In A. Hein & M. Jeannerod (Eds.), *Spatially oriented behavior* (pp. 327–352). New York: Plenum Press.

Held, R. (1968). Dissociation of visual functions by deprivation and rearrangement. *Psychologische Forschung, 31*, 338–348.

Held, R., Ingle, D., Schneider, G. E., & Trevarthen, C. B. (1967). *Psychologische Forschung, 31*, 42.

Ingle, D. (1967). Two visual mechanisms underlying the behavior of fish. *Psychologische Forschung, 31*.

Jeannerod, M. (1997). *The cognitive neuroscience of action*. Cambridge, MA: Blackwell.

Li, W., & Matin, L. (1990). Perceived eye level: Sensitivity to pitch of a vertical 2-line stimulus grows with eccentricity but is biased by elevation. *Investigative Ophthalmology and Visual Science, 31*(Suppl.), 84.

Li, W., & Matin, L. (1993). Eye and head position, visual pitch and perceived eye level. *Investigative Ophthalmology and Visual Science, 34*, 1311.

Li, W., & Matin, L. (1996). Visually perceived eye level is influenced identically by lines from erect and pitched planes. *Perception, 25*, 831–852.

Li, W., & Matin, L. (1998). Change in visually perceived eye level without change in perceived pitch. *Perception, 27*, 553–572.

Li, W., & Matin, L. (1999a). Two-dimensional manual mapping of visual space: Changes induced by a pitched-from-vertical line. *Investigative Ophthalmology and Visual Science, 40*(4), S413.

Li, W., & Matin, L. (1999b). The accuracy of finger pointing under illusory displacement depends on its distance from the body. *40th Annual Meeting of the Psychonomic Society*, 106.

Li, W., & Matin, L. (2001). Influences of visual pitch and visual yaw on visually perceived eye level (VPEL) and straight ahead (VPSA) for erect and rolled-to-horizontal observers. *Vision Research, 41*, 2873–2894.

Li, W., & Matin, L. (2002). Separate and combined influences on visually perceived eye level of visual pitch and height-in-the-field of a 2-line stimulus. *Investigative Ophthalmology and Visual Science, 43/4*, 191.

Li, W., & Matin, L. (2004). The time course of hand-to-body distance dependence and memory dependence of manual pointing and height-matching accuracy to a mislocalized visual target [Abstract]. *Journal of Vision, 4*(8), 838a, Available from http://journalofvision.org/4/8/838/, doi:10.1167/4.8.838.

Li, W., Matin, L., & Semanek, D. (2003). Accuracy in manually matching the height of a perceptually mislocalized visual target increases with hand-body distance as does manual pointing [Abstract]. *Journal of Vision, 3*(9), 382a, Available from http://journalofvision.org/3/9/382/, doi:10.1167/3.9.382.

Matin, L., & Fox, C. R. (1986). Perceived eye level: Elevation jointly determined by visual pitch, EEPI, and gravity. *Investigative Ophthalmology and Visual Science, 27*(Suppl.), 333.

Matin, L., & Fox, C. R. (1989). Visually perceived eye level and perceived elevation of objects: Linearly additive influences from visual field pitch and from gravity. *Vision Research, 29*, 315–324.

Matin, L., & Li, W. (1992). Visually perceived eye level: Changes induced by pitched-from-vertical 2-line visual field. *Journal of Experimental Psychology: Human Perception and Performance, 18*, 257–289.

Matin, L., & Li, W. (1994a). The influence of the orientation of a stationary single line in darkness on the visual perception of eye level. *Vision Research, 34*, 311–330.

Matin, L., & Li, W. (1994b). Spatial summation among parallel lines across wide separation (50°): Spatial localization and the Great Circle Model. *Vision Research, 34*, 2577–2598.

Matin, L., & Li, W. (1994c). Mirror symmetry and parallelism: Two opposite rules for the identity transform in space perception and their unified treatment by the Great Circle Model. *Spatial Vision, 8*, 469–489.

Matin, L., & Li, W. (1995). Multimodal basis for egocentric spatial localization and orientation. *Journal of Vestibular Research, 5*, 499–518.

Matin, L., & Li, W. (1999). Averaging and summation of influences on visually perceived eye level between two long lines differing in pitch or roll-tilt. *Vision Research, 39*, 307–329.

Matin, L., & Li, W. (2001). Neural model for processing the influence of visual orientation on visually perceived eye level (VPEL). *Vision Research, 41*, 2845–2872.

Matin, L., Li, W., & Bertz, J. (2004). Distance-contingent accuracy of manual matches to line orientations misperceived under the 2-line rod-and-frame illusion [Abstract]. *Journal of Vision, 4*(8), 380a, Available from http://journalofvision.org/4/8/380/, doi:10.1167/4.8.380.

Matin, L., Picoult, E., Stevens, J. K., Edwards, M. W., Jr., Young, D., & MacArthur, R. (1982). Oculoparalytic illusion: Visual-field dependent mislocalizations by humans partially paralyzed with curare. *Science, 216*, 198–201.

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. New York: Oxford University Press.

Morel, A., & Bullier, J. (1990). Anatomical segregation of two cortical visual pathways in the macaque monkey. *Visual Neuroscience, 4*, 555–578.

Mountcastle, V. B. (1976). The world around us: Neural command functions for selective attention. *Neurosciences Research Program Bulletin, 14*, 1–47.

Mountcastle, V. B., Lynch, J. C., Georgopoulus, A., Sakata, H., & Acuna, C. (1975). Posterior parietal association cortex of the monkey: Command functions for operations within extrapersonal space. *Journal of Neurophysiology, 38*, 871–908.

Perenin, M. T., & Jeannerod, M. (1978). Visual function within the hemianopic field following early cerebral hemidecortication in man—I. Spatial localization. *Neuropsychologica, 16*, 1–13.

Poppel, E., Held, R., & Frost, D. (1973). Residual visual function after brain wounds involving the central visual pathways in man. *Nature, 243*, 295–296.

Post, R. B., & Welch, R. B. (1996). The role of retinal versus perceived size in the effects of pitched displays on visually perceived eye level. *Perception, 25*, 853–859.

Post, R. B., Welch, R. B., & Olson, K. E. (2004). Persistent vision–action dissociation with the rod-and-frame effect [Abstract]. *Journal of Vision, 4*(8), 837a, Available from http://journalofvision.org/4/8/837/, doi:10.1167/4.8.837.

Prinz, W., & Hommel, B. (2002). *Common mechanisms in perception and action. Attention and performance* (Vol. XIX). New York: Oxford University Press.

Rizzolatti, G., Berti, A., & Gallese, V. (2000). Spatial neglect: Neurophysiological bases, cortical circuit and theories. In F. Boller, J. Grafman, & G. Rizzolatti (Eds.). *Handbook of neuropsychology* (Vol. 1, pp. 503–537). Amsterdam: Elsevier.

Rizzolatti, G., Matelli, M., & Pavesi, G. (1983). Deficits in attention and movement following the removal of postarcuate (area 6) and prearcuate (area 8) cortex in macaque monkeys. *Brain, 106*, 655–673.

Rizzolatti, G., Riggio, L., & Sheliga, B. M. (1994). Chapter 9 in Conscious and nonconscious information processing. In Umilta, C., & Moscovitch, M. (Eds.) *International symposium on attention and performance* (Vol. 15, p. 231).

Rizzolatti, G., Scandolara, C., Matelli, M., & Gentilucci, M. (1981). Afferent properties of periarcuate neurons in macaque monkeys. II. Visual responses. *Behav. Brain Res., 2*, 147–163.

Robison, E., Li, W., & Matin, L. (1995). Manual matches to the elevation of visually mislocalized targets. *Investigative Ophthalmology and Visual Science, 36*, S358.

Schneider, G. E. (1967). Contrasting visuomotor functions of tectum and cortex in the golden hamster. *Psychologische Forschung, 31*, 52–62.

Schneider, G. E. (1969). Two visual systems. *Science, 163*, 895–902.

Sprague, J. M., & Meikle, T. H. (1965). The role of the superior colliculus in visually guided behavior. *Experimental Neurology, 11*, 115–146.

Stoper, A. (1997). Environmental pitch and three type of pointing. *Perception, 26*(abst., ECVP suppl.), 99.

Stoper, A., & Cohen, M. M. (1989). Effect of structured visual environments on apparent eye level. *Perception and Psychophysics, 46*, 469–475.

Trevarthen, C. B. (1968). Two mechanisms of vision in primates. *Psychologische Forschung, 31*, 299–337.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT press (chapt. 18).

Van Essen, D. C., & Maunsell, J. H. R. (1983). Hierarchical organization and functional streams in the visual cortex. *Trends in Neuroscience, 6*, 370.

Vision Sciences Society (2002). Abstracts of 2nd Annual Meeting of Vision Sciences Society. *Journal of Vision*, *2*(7), Available from http://journalofvision.org/2/7/, doi:10.1167/2.7.

Weiskrantz, L. (1986). *Blindsight: A case study and implications*. Oxford: Oxford University Press.

Weiskrantz, L. (1990). Outlooks for blindsight: Explicit methodologies for implicit processes. *Proceedings of Royal Society of London B, 239*, 247–278.

Weiskrantz, L. (1997). *Consciousness lost and found*. Oxford: Oxford University Press.

Weiskrantz, L., Warrington, E. K., Sanders, M. D., & Marshall, J. (1974). Visual capacity in the hemianopic field following a restricted occipital ablation. *Brain, 97*, 709–728.

Welch, R. B., & Post, R. B. (1996). Accuracy and adaptation of reaching and pointing in pitched visual environments. *Perception and Psychophysics, 58*, 383–389.

Witkin, H. A. (1949). Perception of body position and of the position of the visual field. *Psychological Monograph, 63*(7), 1–46.

Witkin, H. A., & Asch, S. E. (1948). Studies in space perception. IV. Further experiments on perception of the upright with displaced visual fields. *Journal of Experimental Psychology, 38*, 762–782.