Exp Brain Res (1998) 118:415–420 © Springer-Verlag 1998

RESEARCH NOTE

Annaliese Plooy · James R. Tresilian
Mark Mon-Williams · John P. Wann

The contribution of vision and proprioception to judgements of finger proximity

Received: 19 May 1997 / Accepted: 6 October 1997

Abstract We sought to determine whether an increase in judged egocentric distance created by increasing vergence-specified distance would be negated when participants pointed at their own finger. It was found that ocular position dominates limb proprioception in the judgement of finger distance in the sagittal plane when vision is available. In contrast, an increase in perceived egocentric distance was largely attenuated by the presence of limb proprioception in reduced visual cue conditions. We conclude that the relative contribution of vergence to perceived distance depends upon the strength of the vergence effort signal when there are other cues present. Furthermore, if the distance percept includes a major contribution from retinal cues, then the visual component will dominate the limb proprioception component. If the visual component is largely determined by vergence information, limb proprioception will make a significant contribution and actually dominate when the vergence effort signal is weak. The results extend previous studies that have found a similar relationship between ocular position and limb proprioception in the perception of a finger's location in the coronal plane.

Key words Vergence · Depth perception · Proprioception · Limb position · Pointing · Human

Introduction

Many everyday tasks require the interaction of one hand with an object held in, or located close to, the other hand. Interaction with objects located in pericorporeal space often requires mapping between visually and proprioceptively specified locations (e.g. reaching an unseen hand to a seen target). Furthermore, bimanual tasks may necessitate mapping between the proprioceptive ("felt") location of an unseen limb and a target whose location is specified by both vision and limb proprioception of the other hand. We will refer to this relationship as vision with proprioception to proprioception-alone (VP:P) mapping. Systematic and variable errors that occur when mapping from vision to proprioception (V:P, vision to proprioceptive mapping; Wann 1991) are known to be larger than the errors that occur through VP:P mapping (von Hofsten and Rosblad 1988; Wann 1991; van Beers et al. 1996; Mon-Williams et al. 1997). The improved accuracy in VP:P mapping must be due to the central nervous system combining limb proprioception with visual information in the determination of target location (cf. van Beers et al. 1996). The decrease in pointing error that occurs when proprioception is added to vision is consistent with current models of the nervous system: it is known that a combination of multiple cues of equal reliability (equal variance) can improve performance relative to that obtained using any one cue in isolation (Green and Swets 1966; Bruno and Cutting 1988).

Previous research has shown that, although the proprioceptive system allows accurate perception of limb position in the absence of vision, it may play a relatively minor role when vision is available (Hay et al. 1963, Mon-Williams et al. 1997). The direction of all points in a visual scene can be shifted by placing yoked prisms in front of the eyes: a fact that has long been exploited in studies of visual adaptation (cf. Harris 1965; Welch 1978; Howard 1982). Displacement of visual input using this method has been found to have an effect on a VP:P finger-positioning task, and the effect is dependent upon the amount of visual information available (Mon-Williams et al. 1997). When the scene is fully illuminated and participants are asked to place an unseen finger in the same position as their seen finger, yoked prisms cause the unseen finger to be positioned away from the actual location of the seen finger in the direction of visual dis-

A. Plooy · M. Mon-Williams · J.P. Wann
Department of Psychology, University of Reading,
3, Earley Gate, Reading RG6 6AL, UK

A. Plooy · J.R. Tresilian · M. Mon-Williams (✉)
Department of Human Movement Studies,
University of Queensland, St. Lucia, Queensland 4072, Australia
Fax: +61-7-3365-6877, e-mail: markmw@hms.uq.edu.au

placement. The relative contribution of proprioception to the perception of limb position is found to be very small (approx. 10%) under such conditions. In contrast, when visual information is severely reduced by only providing a small light-emitting diode (LED) on the end of a finger viewed in darkness, the contribution of vision becomes greatly reduced (approx. 10%) relative to proprioception (Stark and Bridgeman 1983; Mon-Williams et al. 1998a). It should also be noted that altering proprioceptive information has been reported to produce reciprocal changes in visual perception. For example, Biguer et al. (1988) reported that proprioceptive inputs from neck vibration in a sparse visual environment produced apparent motion of a stable visual target, and Lackner (1988) reported distortions of body image resulting from enhanced proprioceptive input.

The effect of unyoked prisms in depth perception is more complicated as a number of retinal and extraretinal cues contribute to specified egocentric distance. Furthermore, the relative contribution of the cues varies according to the "confidence" attached to the available information sources by the nervous system. It is well established that vergence angle is used in the estimation of distance and, furthermore, its contribution is increased under reduced-cue conditions (see Foley 1980 for a comprehensive review). This observation raises the question of whether vergence-signalled distance information would override limb proprioception when making judgements of egocentric depth in full-cue and reduced-cue conditions. This question is the analogue of that addressed by Mon-Williams et al. (1997), viz. does visual information about target position override limb proprioception when making judgements of limb location in full- and reduced-cue conditions? It is important to emphasise that the answer to the latter question cannot be transferred directly to the former: it is invalid to extrapolate from previous studies with yoked prisms. In contrast to judgements of visual direction, judgements of egocentric distance rely on a number of interacting retinal and extraretinal cues. It is therefore unclear whether altering vergence-signalled distance information will override limb proprioception when a number of additional (visual) cues are present.

Alteration of vergence-specified distance may be achieved through the introduction of bias to the vergence system (changing the open-loop vergence bias or heterophoria) either by adapting to the presence of a prism over one eye (Owens and Leibowitz 1980), by fixating a close target for an extended period (Shebilske et al. 1983; Heuer et al. 1991), or by briefly introducing a prism over one eye (J. R. Tresilian and M. Mon-Williams,unpublished work). It has been observed that inducing divergent biases results in the expected over-estimation of distance (Ebenholtz and Wolfson 1975; Owens and Leibowitz 1980; Shebilske et al. 1983; Heuer et al. 1991). The current study is concerned with the simplest method of changing vergence-specified distance: the introduction of a prism over one eye. We decided to explore the effect of increasing the vergence-specified distance in a VP:P mapping task by using an ophthalmic prism with its base orientated towards the nose (base-in prism). This manipulation has the effect of changing vergence-specified distance without changing actual target distance. Orientation of the prism with its base outwards (temporal) creates a complex interaction between available visual cues and may actually create an illusion of increased egocentric distance (J. R. Tresilian and M. Mon-Williams,unpublished work). It is not yet clear how the perceptual system weights the various sources of visual and extraretinal distance information. As this experiment was not concerned with distance perception per se, we decided against studying the effect of base-out prism. The advantage of the base-in prism is that the alteration in perceived distance occurs in the direction predicted from the orientation of the unyoked prism. We therefore used base-in prism to explore the effect of increasing vergence-specified distance in full-cue and reduced-cue environments (where limb proprioception has previously been found to "override" available visual information).

Materials and methods

Participants and apparatus

Five unpaid volunteer participants, naive to the purpose of the experiment, were recruited. All participants gave informed consent and the experiment was approved by the University of Queensland ethical committee. All of the participants had normal visual status (all were emmetropes) and none had previously taken part in a "pointing" experiment. The group consisted of three men and two women with an age range of 21–35 years.

The primary apparatus used in experiment 1 consisted of a specially created rectangular viewing box (53 cm long by 13 cm wide by 13 cm high; see Fig. 1). Small holes cut into the top of the viewing box allowed the positioning of either the participants' or the ex-

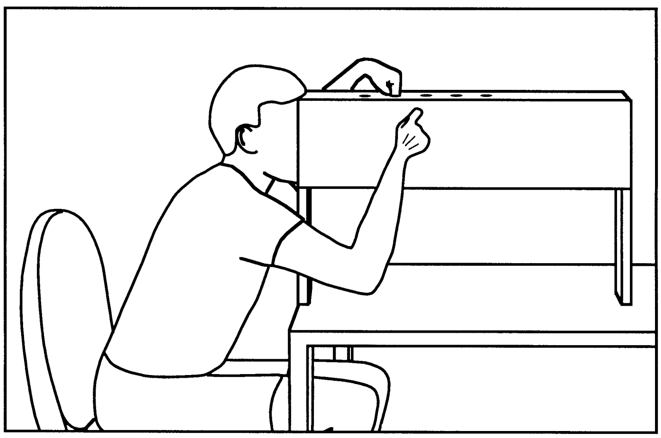

Fig. 1 A schematic of the experimental apparatus. Either the participant's or the experimenter's finger was inserted into one of the target holes located at 15, 20, 25, or 30 cm from the participant. The participant's task was to position the unseen index finger of the right hand such that its tip was placed on the outside of the viewing box at the perceived distance of the target digit. Positional accuracy was measured using an Optotrak 3D optoelectronic movement-recording system

perimenter's finger at 15, 20, 25 or 30 cm away from the eyes. These four distances were chosen so that target distance changed in steps of approximately equal convergence effort[1] (e.g. in steps of 1 MA) from 3 to 6 MA.

Participants viewed the target digit through a pair of trial frames (diameter 3 cm) into which an ophthalmic prism could be placed. The task was to position the unseen index finger of the right hand such that its tip was placed on the outside of the viewing box at the perceived distance of the target digit. Positional accuracy was measured using an Optotrak 3D optoelectronic movement-recording system. This system measures the three-dimensional (3D) position of small infra-red light-emitting diodes (IREDs); it was factory pre-calibrated to a static resolution of IRED position less than 0.2 mm. The system recorded the distance between an IRED placed on the distal end of the index fingernail and another placed next to the target position (defining the positional error). The configuration allowed measurement of the error to within 3 mm. On each trial the system recorded the positions of the IREDs for 0.5 s at a sampling rate of 30 Hz. The position of each IRED was computed as the mean of the samples over the collection period.

Procedure

Baseline measurements were first taken in separate sessions with the participants either pointing at their own seen finger with full vision or pointing at the experimenter's finger with full vision. In the second session, run in complete darkness, the participants pointed at a small LED on the end of their own finger or pointed at a small LED on the end of the experimenter's finger. The order of the trials was alternated within the sessions.

In the actual experimental sessions, the participants binocularly viewed the target through an 8-Δ prism (1 prism dioptre, Δ, is the angle whose tangent is 0.01), placed in front of the right eye "base-in". It should be noted that a prism has a non-linear effect on vergence angle. It is possible to calculate the effect of the prism on registered angle using trigonometry: an 8-Δ base-in prism changes registered vergence distance from 15, 20, 25, and 30 cm to 21, 28, 40, and 51 cm, respectively. In the first experimental session, the participants either: (1) pointed at the experimenter's finger with full vision (condition A) or (2) pointed at their own seen finger with full vision (condition B). The second experimental session was run in complete darkness and participants either: (1) pointed at a small LED on the end of their own finger (condition C) or (2) pointed at a small LED on the end of the experimenter's finger (condition D). Participants were exposed to normal ambient room illumination between individual trials in conditions C and D to ensure that dark adaptation did not occur. Prior to conducting the experiments, we established that the point light used to drive vergence did not create an accommodative stimulus (Mon-Williams et al. 1998b). We verified that the point light did not create an accommodative stimulus on two separate participants (neither of whom were used within the actual experimental procedures). The participants were placed in the dark with the left eye covered and were asked to fixate the pinpoint light source. Accommodation was measured using a modified Canon Autoref R-1 infra-red objective optometer. No information was provided regarding the location of the light, which was randomly placed at 50 cm, 33 cm, and 20 cm from the participants. The location of the target had no influence on the accommodative response and, in all positions, both observers showed accommodation equivalent to distant fixation. Post hoc questioning revealed that both observers had assumed that the light was at the far end of the room on all three recording sessions.

Participants pointed to each target position five times in each condition. The actual digit used as a target (the participant's and the experimenter's) was changed on each trial. Targets were presented to observers in a pseudorandom trial order with the constraint that the same finger position could not occur more than twice consecutively. It was ensured that a prism trial was always followed by presentation of the same powered prism in the opposite orientation (e.g. prism base-in was followed by prism base-out), although only the data from the base-in prism were considered within the analyses for reasons previously outlined. This procedure was used to ensure that physiological adaptation did not occur in response to the prism. It is known that prisms will not alter a person's heterophoria if viewing time is restricted and orientation is sequentially reversed (Schor 1979).

Participants performed the task as follows: they closed their eyes, the experimenter inserted the appropriate finger into the appropriate hole, the observer leant forward to position themselves in the trial frame, opened their eyes and binocularly fixated the finger, positioned their right index finger alongside the left target finger, held the right index finger in this position for a short time (approx 1 s) whilst data were collected, closed their eyes and leant back. The participants were instructed to position their limb as accurately as possible: they were allowed as much time and as many corrections as they judged necessary for accurate positioning.

Analysis of variance was initially used to ensure that the prism produced a significant increase in perceived distance (i.e. the baseline measures were compared with the experimental data). In order to determine the change in pointing response induced by the prism, the normal pointing bias established in the baseline sessions was subtracted from the error found when pointing through the prism for each individual (i.e. the baseline data were subtracted from the experimental data). Analysis of variance was then conducted on the mean prism-induced error to determine the relationship between target distance and overshoot. Preplanned contrasts using Dunn's procedure (Keppel 1982, p. 146) were carried out on the means of interest to study the interaction between the effect of the prism and conditions A and B. Statistical analysis for conditions C and D consisted of calculating coefficient of determination for the mean data points as a function of distance. The effect of the prism on perceived distance was assessed by calculating linear equations of least-square fit across participants.

Results

In common with previous studies (von Hofsten and Rosblad 1988; Wann 1991; Mon-Williams et al. 1998; van Beers et al. 1996), it was found that the participants' baseline pointing responses were less accurate when vision alone was present (a mean error of 3.6 cm overshoot was present across participants) and most accurate when both limb proprioception and vision of the finger was available (an error of 1.57 cm overshoot). These figures refer to the mean baseline error across targets: the relationship between overshoot and target distance was not statistically significant. The participants were relatively inaccurate in the V:P task in the present study (cf. van Beers et al. 1996), but this was probably due to the inexperience of the participants.

The data were first tested to ensure that the prism had the desired effect of increasing perceived egocentric distance. A significant ($P<0.05$) increase in judged target distance was found for every condition and every target location when participants viewed through the prism. The prism-induced error was then calculated by subtract-

[1] It is easiest to describe vergence stimuli in terms of metre angles (MA): this is the reciprocal of distance in meters (the metre angle is the angle through which each eye has rotated from the primary position in order to fixate an object located 1 m away), so that 1 MA corresponds to 100 cm, 2 MA corresponds to 50 cm, etc. One advantage of the metre angle is that it may be readily compared with the dioptre (D). The dioptre is used to describe the power of a refractive lens (or ocular refraction) and is also expressed as the reciprocal of distance in metres.

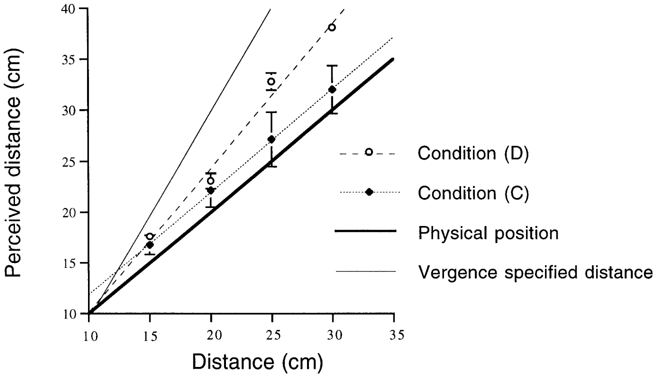

Fig. 2 Physical distance plotted against the distance perceived in the reduced-cue conditions (C and D) with the prism in place. The participants were either pointing at a small LED on the end of their own finger in darkness (C) or pointing at a small LED on the end of the experimenter's finger (D). There is an indication of where physical distance and perceived distance are in perfect correspondence (*thick continuous line*) and the relationship between physical distance and vergence-specified distance is plotted (*thin continuous line*: calculated by trigonometry from an inter-pupillary distance of 6.5 cm). The maximum variable error with any target position for any individual participant was 2.5 cm. Regression analysis described the relationship between physical distance (x) and perceived distance as $1.0x+1.8$ cm ($r^2=1.0$) in condition C and $1.4x–4$ cm ($r^2=0.99$) in condition D. The relationship between perceived distance and vergence angle-specified distance (calculated from trigonometry) in condition D was described by the equation $0.69x+3.6$ cm ($r^2=0.99$). SE bars across participants are shown

ing the baseline data from the experimental data for each individual. Analysis of variance was conducted on these data to determine whether there was an interaction between the amount of overshoot and target distance. No significant interaction was found in conditions A, B, or C, and the overshoot was remarkably similar regardless of target position. It is not clear why a non-linear shift in extraretinal information should produce a constant bias in distance perception (the base-in prism has a greater effect on vergence-specified distance as physical distance increases), but we provide a possible explanation within the Discussion section.

It is known that a reasonably close relationship exists between vergence angle and perceived distance when all other distance cues are removed (Foley and Held 1972; von Hofsten 1976; Foley 1980), and vergence angle was the only distance cue in condition D. This meant that a non-constant bias effect of the prism on distance perception was evident in condition D, and a significant interaction was found between target position and the amount of overshoot ($F_{3,16}=16.01$, $P<0.0001$).

The mean increase in perceived distance created by the prism was found to be 2.7 cm (SE 0.2 cm) for condition A across participants, resulting in an absolute pointing error (taking the normal bias into account) of 6.3 cm. The mean increase in perceived distance for condition B was found to be 3.5 cm (SE 0.8 cm), which meant that the absolute pointing error was 5.07 cm across participants. The difference in prism-induced overshoot between conditions A and B was not statistically reliable, suggesting that the visual information is “overriding” limb proprioception in the perception of egocentric distance.

Figure 2 shows physical distance plotted against the distance perceived in the reduced-cue conditions (C and D) with the prism in place. Figure 2 also provides an indication of where physical distance and perceived distance are in perfect correspondence (the thick continuous line) and plots the relationship between physical distance and vergence-specified distance (the thin continuous line, calculated by trigonometry from an inter-pupillary distance of 6.5 cm). The maximum variable error with any target position for any individual participant was 2.5 cm. Regression analysis described the relationship between physical distance (x) and perceived distance as $1.0x+1.8$ cm ($r^2=1.0$) in condition C and $1.4x–4$ cm ($r^2=0.99$) in condition D. The relationship between perceived distance and vergence angle specified distance (calculated from trigonometry) in condition D was described by the equation $0.69x+3.6$ cm ($r^2=0.99$).

These data indicate that participants were not able to totally ignore available visual information especially when the conflict between visual information and limb proprioception was small. It appears, however, that limb proprioception dominates distance judgements when a large conflict occurs between proprioception and visual information in a sparse visual environment.

Discussion

The reported experiment was designed to address the question of whether vergence information about a visible target's distance would override limb proprioception when making judgements of egocentric distance in full-cue and reduced-cue conditions. For judgements of target direction, it has previously been established that vision will override limb proprioception in full-cue conditions to such an extent that the contribution from the latter is negligible (Hay et al. 1963; Welch 1978; Mon-Williams et al. 1997). In sufficiently reduced-cue conditions, this visual dominance can be eliminated and limb proprioception overrides vision (Mon-Williams et al. 1997). The results of the present experiment show that a similar relationship exists between the visually perceived distance and the distance perceived through limb proprioception. It was found that increasing vergence-specified distance causes an increase in perceived egocentric distance: an increase in perceived egocentric distance (induced by manipulation of vergence angle using a prism) was not attenuated by the presence of limb proprioceptive information in a “full-cue” environment. In contrast, an increase in perceived distance was largely overridden by limb proprioception in a reduced visual environment. These results suggest that the proprioceptive system plays a relatively minor role in the perception of finger distance when full vision is available but is dominant in reduced visual cue conditions.

In the present experiment, the effect of the prism was to increase the apparent distance of a visible target. In reduced-cue conditions without limb proprioceptive information (condition D), the gain of the relationship between perceived distance and vergence angle-specified distance (calculated from trigonometry) was less than 1 (≈0.7) with an intercept greater than 0 (≈3.6 cm). This is consistent with previous results, which have shown that when vergence is the sole or dominant source of distance information, fixated visual targets very close to an observer appear further away than they actually are, whereas more distant targets appear closer (see Foley 1980). The results of the other experimental conditions are more surprising. In the restricted full-cue conditions (A and B) the effect of the prism was to introduce an approximately constant positive bias to the actual physical distance/perceived distance relationship (over the tested range) rather than to increase its gain as would be predicted on the basis of the reduced-cue results. A constant bias was also found in reduced-cue conditions when limb proprioceptive information about target position was available (condition C). Thus an approximately constant bias over the test range was observed when cues to target distance in addition to vergence were available, be these visual (condition A), proprioceptive (condition C) or both (condition B).

These results strongly suggest that retinal, extraretinal and limb proprioceptive cues are combined in the perception of target distance. If we accept this conclusion, then it follows from the results that the relative importance of these cues in determining distance cannot be constant. The results of conditions A and B imply that the relative importance of vergence angle information decreases as the target becomes more distant. Note that with increasing distance the vergence effort is decreased. If vergence effort is used as information about fixation distance (cf. von Hofsten 1976), the results can be interpreted as suggesting that the weaker the vergence effort signal, the less weight is attached to it and the weight given to the retinal cues increases (little importance is attached to limb proprioception when a visual environment is present). The results of condition C suggest that a similar account may also be appropriate here: the constant bias is due to importance being transferred to limb proprioception as the vergence signal becomes weaker.

Thus, conditions A and B (restricted full-cue conditions) are consistent with vision overriding limb proprioception, with the relative contribution of vergence information to the visual percept being dependent upon the strength of the vergence effort signal. Conditions C and D (reduced visual cue conditions) are consistent with limb proprioception overriding the visual percept (which is here determined by the vergence effort signal), with the degree to which proprioception dominates being dependent upon the strength of the vergence effort signal: the stronger this signal the less dominant limb proprioception becomes.

It is well established that a one-to-one relationship exists between visual displacement and perceived direction (e.g. yoked prism causes a predictable change in the perceived location of visual objects relative to a limb). On the other hand, displacement of the visual scene in one eye relative to the other (via an unyoked prism) produces a change in perceived distance but not direction. It follows that a change in the perceived ocular position of one eye causes a corresponding shift in the perception of visual direction (but not distance) when viewing monocularly and a change in distance (but not direction) when viewing binocularly. In contrast to the perception of direction (where visual target position is specified solely by ocular position), the perception of distance is dependent on a variety of additional information sources that are available through vision.

In summary, extraretinal eye-position information is used in the perception of both a visible target's direction and its distance when carrying out a pointing task. We conclude from the results of the reported experiment that the relative contribution of vergence to perceived distance depends upon the strength of the vergence effort signal when there are other cues present. This is true whether these additional cues are of a visual or limb proprioceptive origin. If both visual and limb proprioceptive cues are present, then the effect of having both is not additive: only the visual cues appear to determine performance, with limb proprioception being virtually ignored. This means that, if the distance percept includes a major contribution from retinal cues, then the visual component will dominate the limb proprioception component. If the visual component is largely determined by vergence information, limb proprioception will make a significant contribution and actually dominate when the vergence effort signal is weak.

References

Beers RJ van, Sittig AC, van der Gon JJD (1996) How humans combine simultaneous proprioceptive and visual position information. Exp Brain Res 111:253–261

Biguer B, Donaldson IML, Hein A, Jeannerod M (1988) Neck muscle vibration modifies the representation of visual motion and direction in man. Brain 111:1405–1424

Bruno N, Cutting JE (1988) Minimodularity and the perception of layout. J Exp Psychol Gen 117:161–170

Ebenholtz SM, Wolfson DM (1975) Perceptual aftereffects of sustained convergence. Percept Psychophys 17:485–491

Foley JM (1980) Binocular distance perception. Psychol Rev 87:411–434

Foley JM, Held R (1972) Visually directed pointing as a function of target distance, direction and available cues. Percept Psychophys 72:263–268

Green DM, Swets JA (1966) Signal detection theory and psychophysics. Wiley, London

Harris CS (1965) Perceptual adaptation to inverted, reversed and displaced vision Psychol Rev 72:419–444

Hay JC, Pick HL, Ikeda K (1963) Visual capture produced by prism spectacles. Psychol Sci 2:215–216

Heuer H, Wischmeyer E, Bruwer M, Romer T (1991) Apparent size as a function of vertical gaze direction: new tests of an old hypothesis. J Exp Psychol Hum Percept Perform 17:232–245

Hofsten C von (1976) The role of convergence in visual space perception. Vision Res 16:193–198

Hofsten C von, Rosblad B (1988) The integration of sensory information in the development of precise manual pointing. Neuropsychologia 26:805–821

Howard IP (1982) Human visual orientation. Wiley, New York

Keppel G (1982) Design and analysis: a researcher's handbook. Prentice-Hall, New Jersey

Lackner JR (1988) Some proprioceptive influences on the perceptual representation of body shape and orientation. Brain 111:281–297

Mon-Williams M, Wann JP, Jenkinson M, Rushton K (1997) Synaesthesia in the normal limb. Proc R Soc Lond B Biol Sci B264:1007–1010

Mon-Williams M, Tresilian JR, Plooy A, Wann JP (1998b) Looking at the task in hand: vergence eye movements and perceived size. Exp Brain Res 117:501–506

Owens DA, Leibowitz HW (1980) Accommodation, convergence and distance perception in low illumination. Am J Optom Physiol Opt 57:540–550

Schor CM (1979) The relationship between fusional vergence eye movements and fixation disparity Vision Res 19:1359–1367

Shebilske WL, Karmiohl LM, Proffitt DR (1983) Induced esophoric shifts in eye convergence and illusory distance in reduced and structured viewing conditions. J Exp Psychol Hum Percept Perform 9:270–277

Stark L, Bridgeman B (1983) Role of corollary discharge in space constancy Percept Psychophys 34:371–380

Wann JP (1991) The integrity of visual-proprioceptive mapping in cerebral palsy. Neuropsychologia 29:1095–1106

Welch RB (1978) Perceptual modification. Academic Press, New York