Exp Brain Res (1996) 110:482–486

RESEARCH NOTE

**David P. Carey · Kevin Allan**

# A motor signal and "visual" size perception

Received: 30 January 1996 / Accepted: 30 March 1996

**Abstract** Recent models of the visual system in primates suggest that the mechanisms underlying visual perception and visuomotor control are implemented in separate functional streams in the cerebral cortex. However, a little-studied perceptual illusion demonstrates that a motor-related signal representing arm position can contribute to the visual perception of size. The illusion consists of an illusory size change in an afterimage of the hand when the hand is moved towards or away from the subject. The motor signal necessary for the illusion could be specified by feedforward and/or feedback sources (i.e. efference copy and/or proprioception/kinesthesis). We investigated the nature of this signal by measuring the illusion's magnitude when subjects moved their own arm (active condition, feedforward and feedback information available), and when arm movement was under the control of the experimenter (passive condition, feedback information available). Active and passive movements produced equivalent illusory size changes in the afterimages. However, the illusion was not obtained when an afterimage of subject's hand was obtained prior to movement of the other hand from a very similar location in space. This evidence shows that proprioceptive/kinesthetic feedback was sufficient to drive the illusion and suggests that a specific three-dimensional registration of proprioceptive input and the initial afterimage is necessary for the illusion to occur.

**Key words** Visual perception · Proprioception · Efference copy · Two visual systems · Emmert's law · Human

## Introduction

A number of experiments have demonstrated that the ability to judge the true size of an object breaks down as visual cues to distance are eliminated (e.g. Holway and Boring 1941). Many theorists interpret this "size constancy" as reflecting a size-distance invariance mechanism that uses veridical distance information and the visual angle subtended on the retina to compute an estimate of actual target size. A commonly referred to demonstration of size-distance invariance was described by Emmert in 1881. If an afterimage of a visual target is produced, "projecting" the afterimage onto distant surfaces causes the observer to perceive the afterimage as larger than if the afterimage is projected onto a near surface (see Fig. 1). Such a demonstration shows that perceived size is a function of the visual angle subtended on the retina by an object, and the distance of the object itself. When referring to afterimages, this relationship is

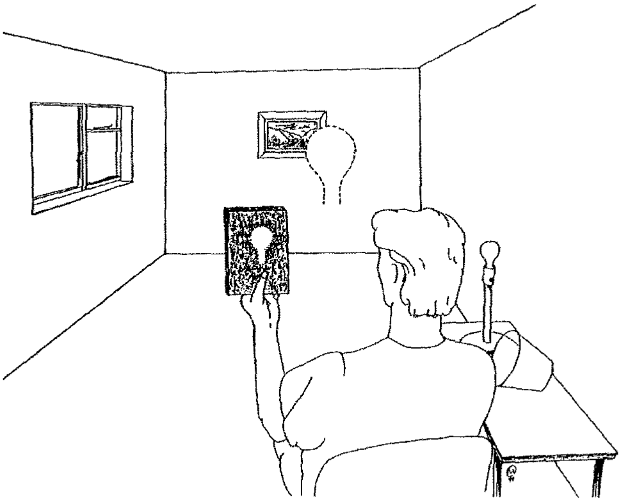

**Fig. 1** Emmert's Law. The distance where the afterimage of the lightbulb appars to fall dramatically influences the perception of its size

---

D.P. Carey (✉)[1] · K. Allan
School of Psychology, The University of St. Andrews,
St. Andrews, Fife, Scotland KY16 9JU, UK

*Present address:*
[1] Department of Psychology, University of Aberdeen,
Kings College, Old Aberdeen, Scotland AB24 2UB, UK;
e-mail: d.carey@abdn.ac.uk

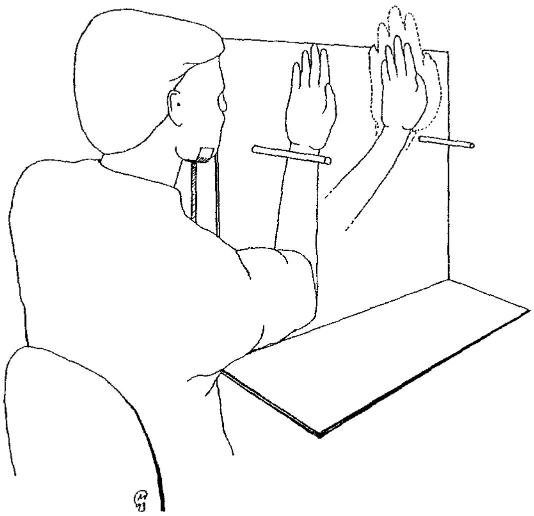

**Fig. 2** The illusion. Moving the hand away in complete darkness results in a percept of a larger image. We used this apparatus to control the distances moved by the subject in active and passive trials. In half of the trials the hand was moved to the near dowel from the far dowel

called Emmert's law (see Edwards and Boring 1951 for further discussion).

In a typical Emmert's law demonstration, the distance of the target is usually specified by visual cues in the testing environment such as linear perspective, occlusion, stereopsis, and the retinal image size of familiar objects. Experiments by Taylor (1941) and Gregory et al. (1959), however, suggest that non-visual signals can also specify target distance in situations similar to the demonstration of Emmert's law. Taylor described illusory changes in the size of an afterimage of a hand-held card, viewed in complete darkness, which occurred when subjects either moved their head away from the card or moved the card away from their head. If the distance of the card was increased, the card's afterimage appeared to increase in size, while a decrease in distance resulted in a decrease in perceived size (Fig. 2 illustrates the illusion using hand movements without a card). The similarity of the illusion to classic Emmert's law demonstrations was noted, and Taylor provided some evidence for the suggestion that these effects were mediated by changes in the degree of vergence of the two eyes (well established as a cue to distance; see Erkelens et al. 1989). Gregory et al. (1959) reproduced the head movement effects that Taylor (1941) described and also reported some "curious phenomena" when afterimages of the hand itself were obtained. This group noted, as did Taylor, that what is unusual about these demonstrations is that changes in target distance *could not have been specified by visual cues, since the afterimages were always viewed in complete darkness*. Nevertheless, the perceived size changes were appropriate, given the fact that the retinal image size of the card's afterimage did not change, while the distance of the card did.

This illusion has been described as a special case of Emmert's law (Dwyer et al. 1990), which most investigators interpret in terms of size perception and constancy. However, this type of interpretation necessarily implies that a motor-related signal about the distance of a hand-held target (or the hand itself) can influence the perceived size of that target in the same manner as a visual signal. Given the recent functional description of two cortical visual systems in primates advanced by Goodale and Milner (Goodale and Milner 1992; Milner and Goodale 1995) and the earlier model proposed by Ungerleider and colleagues (Ungerleider and Mishkin 1982), the notion of a motor signal contributing to size perception and constancy is peculiar. That is, size perception and constancy mechanisms are typically relegated to ventral stream areas such as V4 and inferotemporal cortex (e.g. Cohen et al. 1994; Humphrey and Weiskrantz 1969; Ungerleider et al. 1977). Non-visual signals about eye, limb and head position are usually found in areas of the dorsal stream of visual cortex, where such signals enable the localization of targets in space and/or the guidance of movement, and not perceptual identification or constancy (e.g. Anderson et al. 1990; Colby et al. 1993; Galletti et al. 1993).

As a first step in re-examining the mechanism behind this illusion, we have adapted Taylor's paradigm in order to reveal the nature of the non-visual signal responsible for illusory size changes in the afterimage. The two possible sources of information which could specify limb position are feedforward, efference copy sources or feedback information from proprioception. The role of these motor signals has been studied rather differently in two domains of motor control research. The study of feedforward signals has been emphasised in the eye movement literature, where efference copy is thought to have a vital function in maintaining a percept of the world unaffected by eye movements themselves (exemplified by studies of the effects of eye paralysis with curare on the perceptual consequences of attempted eye movements; see Matin 1976; although see Brindley et al. 1976 for alternative findings). In contrast, the study of feedback signals has been emphasised in the arm movement literature (Jeannerod et al. 1979; Steinbach 1987).

The present study represents a rare attempt to investigate the link between signals related to arm movement and their effects on the attributes of a visual percept. Although there have been previous demonstrations of arm signals influencing the perceived attributes of a visual stimulus, these studies typically involve manipulations of proprioceptive information exclusively, and produce changes in the perceived location of a visual stimulus (e.g. Dizio et al. 1993; Roll et al. 1991). In this investigation we manipulated the availability of feedforward information in order to determine whether or not such information is necessary for the illusory size changes to occur.

## Materials and methods

### Subjects

Eight male and five female subjects participated as volunteers. One woman and one man were left-handed. Subjects used their dominant hand (defined as the writing hand) in all but the last two trials.

### Apparatus and procedure

Subjects spent an initial 5-min period in a completely darkened room. For all practice and experimental trials, subjects were required to hold their dominant hand against one of the two horizontal dowels of the apparatus shown in Fig. 2. The distance between the two dowels was fixed at 35 cm. At a signal given by the experimenter, a high-intensity flash of light (from a Cullmann DC36 photoflash) was directed towards the hand from behind the subject's head (at a distance of approximately 35–40 cm). The flash produced a powerful and vivid positive afterimage of the hand, which persisted for several seconds. In half the trials, the subjects were required to move their hand in a smooth and continuous fashion, while carefully observing the afterimage for any changes. In the other half of the trials, the experimenter supported the outstretched hand at the wrist and moved the subject's limb in a similar fashion. For these "passive" motion trials, subjects were repeatedly instructed not to help or hinder the motion, but to remain completely relaxed and concentrate on the appearance of the afterimage. This type of manipulation has been used in previous studies of motor control in order to attenuate efferent signals about limb position while leaving afferent signals relatively intact (e.g. Paillard and Brouchon 1974). (The possibility of some motor command being issued could not be completely excluded by this manipulation. However, at least the magnitude of such signals should have been dramatically attenuated in the passive trials.) Half of each of the passive and active trial sets were from the far dowel towards the near dowel (towards trials) and the other half were from the near dowel to the far dowel (away trials). When the movements originated at the near dowel, subjects placed their wrist against the distal side of the dowel, while for far dowel trials, the wrist was placed against the proximal side of the dowel.

Subjects received three practice trials before testing began. All subjects were exposed to an afterimage of their static hand on the first of these trials, in order to familiarize themselves with the appearance of the afterimage, and to use as a standard against which afterimage clarity on experimental trials could be rated. The second practice trial required the subject to remain relaxed while the experimenter moved the limb as slowly and smoothly as possible away from the subject (from the near dowel to the far dowel). On this trial, the subject was instructed (before and after the trial) to report any changes in the afterimage during the movement. Subjects were encouraged not to hinder or help the experimenter in any way during such trials. The third practice trial required subjects to make an active towards movement of their arm (far dowel to near dowel). After this trial subjects were told that size change (or lack thereof) was the measure of interest for report. Twelve of our thirteen subjects reported size changes on at least one of the two practice trials involving arm movement, before size change was actually named as the measure of interest.

The subject was required to make two subjective ratings about the afterimage. The quality of the afterimage was defined as the clarity of the initial afterimage before any motion of the arm was initiated (by subject or experimenter). If the afterimage was similar in clarity and vividness to that produced on the first practice trial, subjects were instructed to rate it as "5". If the afterimage was less clear, quality ratings were to be less than 5; more vivid initial afterimages were given ratings higher than 5. The purpose of this measure was to attempt to ensure that perceived size changes in the afterimage (as a function of active/passive or towards/away) were not due to poorer, initially obtained afterimages. Size change was reported as a percentage of the size of the afterimage obtained on each trial before the hand began to move. Subject were told to report 100% if no size change was obtained, 200% if the afterimage appeared to double in size or 50% if the afterimage halved in size.

Two final trials were included, where subjects were asked to place their dominant hand behind (distal to) their non-dominant hand, which was positioned against the near dowel. Once an afterimage of the non-dominant hand had been obtained, the subject was required to move their dominant hand actively to the far dowel. These two trials were included to demonstrate *whether or not the illusion depends upon motion of the same hand from which the afterimage was obtained.*

## Results

Subjects did not report any systematic bias in afterimage quality, although they were capable of distinguishing between more or less vivid initial afterimages. The medians and inter-quartile ranges (in brackets) did not suggest any obvious biases across active/passive or towards/away conditions in the generation of the initial afterimage of the hand [active 5.00 (2.00); passive 5.00 (1.00); towards 5.50 (1.00); and away 5.00 (1.875)]. These data were not analysed further.

If the subjects' perception of size change depended on a feedforward signal, then reported size changes in the obtained afterimage would be diminished or abolished in the passive trials. Median size estimates of the afterimages as a function of displacement type (active/passive) and direction of movement (towards/away) appear in Fig. 3. A Friedman two-way analysis of variance by ranks for away active/passive, and towards active/passive conditions was performed on the raw data. This analysis revealed that the ranks of the four conditions were not equal ($\chi^2$=58.44, $P$<0.0001). A nonparametric multiple-comparisons procedure suggested by Siegal and Castellan (1988) showed that size estimates for both away conditions were significantly larger than for both towards conditions, but passive and active conditions within towards and away did not differ in their mean ranks. In other words, there was no difference in the magnitude of the obtained illusion in passive compared with active conditions.

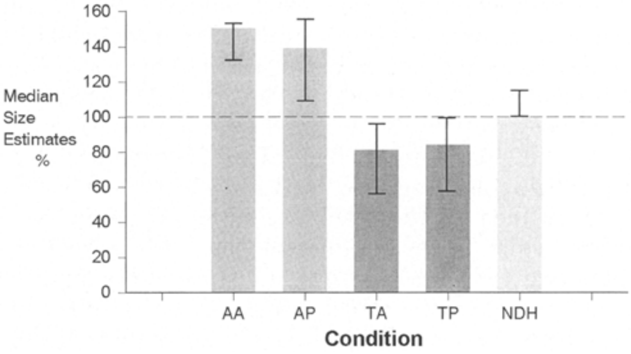

**Fig. 3** Median size change estimates from 13 subjects. *Error bars* represent inter-quartile ranges. In the non-dominant hand condition (*NDH*), an afterimage of the non-dominant hand was obtained, and the dominant hand was subsequently moved (*AA* Away active, *AP* Away passive, *TA* towards active, *TP* Towards passive)

In most subjects the magnitude of the illusion tended to be larger in away conditions, but this may be an artefact of our scale having a lower boundary of zero, but no upper boundary. We saw no trend for the magnitude of the illusion to increase or decrease over the session, although on some trials the illusion did not occur (even if the subjects had reported size changes on previous trials). Finally, we obtained no evidence for the illusion occurring in the condition where the afterimage of the non-dominant hand was obtained before movement of the dominant hand.

## Discussion

There are two main findings from this experiment. The first is that a proprioceptive signal is sufficient to produce the illusion. The second, perhaps more puzzling finding, is the nulling of the illusion when the dominant hand is moved once an afterimage of the non-dominant hand was obtained. Davies (1973) has suggested that there may be a register between hand position signals and the position of an afterimage of the same hand. He showed that after obtaining an afterimage of both hands (held adjacent to one another in the field of view), withdrawing one hand resulted in perceptual disruptions specific to the appropriate part of the afterimage. Accordingly, the nulling of the illusion in the non-dominant hand trials may have resulted from the close initial spatial register of each hand prior to movement, leading to ambiguity about the identity of the afterimage of the hand. Alternatively, proprioceptive information may specify the distance of the non-dominant hand as the distance of the afterimage projection plane. Because the projection plane of the afterimage (so defined) does not change on these trials, no change in the percept of the afterimage occurs. Another (perhaps less likely) possibility is that the systems responsible for the illusion contain information about the perceptual effects of occlusion (i.e. the non-dominant hand occluded the view of the moving dominant hand in hand-visible conditions).

The functional and neuropsychological significance of a proprioceptive signal contributing to visual perception/size constancy requires explanation. Most published studies associate these mechanisms with the ventral stream of areas in visual cortex. Our data suggest that proprioceptive signals are available in these temporal regions, that dorsal stream regions are contributing to size perception/constancy (e.g. Wyke 1960) or that interactions between the two streams are responsible for the illusion. Dorsal visuomotor systems need information about target size and distance in order to program movements. For example, subjects scale the size of their grip for targets they are attempting to grasp well in advance of contact, even if they have never previously seen the target (Jakobson and Goodale 1991; Jeannerod 1981). Sensorimotor systems responsible for such acts are able to extract real size from retinal image size and distance information, which can be supplied by stereopsis, vergence, linear perspective and other such cues. Goodale et al. (1991) have suggested that such computations can be performed by dorsal stream mechanisms exclusively (see also Jeannerod and Rossetti 1993). Nevertheless, it is unlikely that information about the retinal size of the afterimage is maintained in the human equivalent of the "dorsal stream" given what is known about the temporal properties of single units in this channel (Ingling and Grisby 1990; Merigan and Maunsell 1993; Milner and Goodale 1995). That is, magnocellular units (which contribute most of the visual imput to the dorsal stream) show transient responses to visual stimuli, and would be unlikely to sustain the afterimage for the several-second duration of the experimental trials.

An important remaining question is related to the report by Taylor (1941) that eliminating vergence movements attenuated the illusion in the majority of his subjects. His data suggest that when a fixation point prevented changes in vergence, the illusion did not occur. However, pilot observations in our laboratory (using infrared video recordings from 13 naive subjects and an infrared Dr. Bouis Oculometer in two other subjects) suggest no clear relationship between vergence and hand movements made using our apparatus (see Fig. 2) in complete darkness. These hand movements were of the same extent as those which reliably produced illusion effects in the experiment reported here. Eye movement recordings made using search coils by Erkelens and his colleagues also suggest poor vergence and pursuit eye movements to targets moved in darkness (Erkelens et al. 1989; Koken and Erkelens 1993). Of course, the presence of an initial visual target superimposed on a proprioceptive signal which subsequently moves might result in changes in vergence. This issue warrants further investigation, perhaps by recording eye movements with a search coil during trials on which the illusion is (or is not) obtained.

This investigation establishes that a proprioceptive signal about arm position can influence the perceived size of an afterimage. From the present data the functional significance of this non-visual signal and its dramatic effect on size perception cannot be deduced. Its presence is a puzzle which deserves further consideration at the psychological, neuropsychological and even neurophysiological levels. It may require reinterpretation of the illusion in terms quite different from those used in traditional size constancy. In any case, given the lack of evidence for proprioceptive signals in areas of visual cortex associated with constancies and perception, this illusion remains to be explained.

**Acknowledgements** We would like to thank Susan Lederman and Barrie Frost for introducing us to this fascinating illusion. Jackie MacPherson, Paul Gardner, David Milner and Martin Church provided technical/graphical advice and assistance. D.P.C. was supported by a Teaching/Research Fellowship from the University of St. Andrews. K.A. was supported by a British Medical Research Council Studentship. Mel Goodale, David Perrett, Martin Steinbach and Vincent Walsh provided helpful comments on an earlier draft of this manuscript.

## References

Anderson RA, Bracewell RA, Barash M, Gnadt JW, Fogassi L (1990) Eye position effects on visual, memory and saccade-related activity in areas LIP and 7a of macaque. J Neurosci 10:1176–1196

Brindley GS, Goodwin GM, Kulikowski JJ, Leighton D (1976) Stability of vision with a paralyzed eye (abstract). J Physiol (Lond) 258:65P–66P

Cohen L, Gray F, Meyrignac C, Dehaene S, Degos JD (1994) Selective deficit of visual size perception – 2 cases of hemimicropsia. J Neurol Neurosurg Psychiatry 57:73–78

Colby CL, Duhamel J-R, Goldberg ME (1993) The analysis of visual space by the lateral intraparietal area of the monkey: the role of extraretinal signals. In: Hicks TP, Molotchnikoff S (eds) The visually responsive neuron: from basic neurophysiology to behavior. (Progress in Brain Research, vol 95) Elsevier, Amsterdam, pp 307–316

Davies P (1973) Effects of movements upon the appearance and duration of a prolonged visual afterimage. 1. Changes arising from the movement of a portion of the body incorporated in the afterimaged scene. Perception 2:147–153

Dizio P, Lathan CE, Lackner JR (1993) The role of brachial muscle-spindle signals in assignment of visual direction. J Neurophysiol 70:1578–1584

Dwyer J, Ashton R, Broerse J (1990) Emmert's law in the Ames room. Perception 19:35–41

Edwards W, Boring E (1951) What is Emmert's law? Am J Psychol 64:416–422

Erkelens CJ, Van der Steen J, Steinman RM, Collewijn H (1989) Ocular vergence under natural conditions. I. Continuous changes of target distance along the median plane. Proc R Soc Lond [Biol] 236:417–440

Galletti C, Battaglini PP, Fattori P (1993) Parietal neurons encoding spatial locations in craniotopic coordinates. Exp Brain Res 96:221–229

Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. Trends Neurosci 15:20–25

Goodale MA, Milner AD, Jakobson LS, Carey DP (1991) A neurological dissociation between perceiving objects and grasping them. Nature 349:154–156

Gregory RL, Wallace JG, Campbell FW (1959) Changes in the size and shape of visual after-images observed in complete darkness during changes of position in space. Q J Exp Psychol 11:54–55

Holway AH, Boring EG (1941) Determinants of apparent visual size with distance variant. Am J Psychol 54:21–37

Humphrey NK, Weiskrantz L (1969) Size constancy in monkeys with inferotemporal lesions. Q J Exp Psychol 21:225–238

Ingling CR Jr, Grigsby SS (1990) Perceptual correlates of magnocellular and parvocellular channels: Seeing form and depth in afterimages. Vision Res 30:823–828

Jakobson LS, Goodale MA (1991) Factors affecting higher-order movement planning: a kinematic analysis of human prehension. Exp Brain Res 86:199–208

Jeannerod M (1981) Intersegmental coordination during reaching at natural objects. In: Long J, Baddeley A (eds) *Attention and performance IX*. Erlbaum, Hillsdale, NJ, pp 153–168

Jeannerod M, Rossetti Y (1993) Visuomotor coordination as a dissociable visual function: experimental and clinical evidence. Baillieres Clin Neurol 2:439–460

Jeannerod M, Kennedy H, Magnin M (1979) Corollary discharge: its possible implications in visual and oculomotor interactions. Neuropsychologia 17:241–258

Koken PW, Erkelens CJ (1993) Simultaneous hand tracking does not affect human vergence pursuit. Exp Brain Res 96:494–500

Matin L (1976) A possible hybrid mechanism for modification of visual direction associated with eye movements – the paralyzed eye experiment reconsidered. Perception 5:233–239

Merigan WH, Maunsell JHR (1993) How parallel are the primate visual pathways? Annu Rev Neurosci 16:369–402

Milner AD, Goodale MA (1995) The visual brain in action. Oxford University Press, Oxford

Paillard J, Brouchon M (1974) A proprioceptive contribution to the spatial encoding of position cues for ballistic movements. Brain Res 71:273–284

Roll R, Velay JL, Roll J-P (1991) Eye and neck proprioceptive messages contribute to the spatial coding of retinal input in visually oriented activities. Exp Brain Res 85:423–431

Siegal S, Castellan NJ Jr (1988) Nonparametric statistics for the behavioral sciences, 2nd edn. McGraw-Hill, New York

Steinbach MJ (1987) Proprioceptive knowledge of eye position. Vision Res 27:1737–1744

Taylor FV (1941) Change in siz of the after-image induced in total darkness. J Exp Psychol 29:75–80

Ungerleider LG, Mishkin M (1982) Two cortical visual systems. In: Ingle DJ, Goodale MA, Mansfield RWJ (eds) *The analysis of visual behavior*. MIT Press, Cambridge, MA, pp 549–585

Ungerleider LG, Ganz L, Pribram KH (1977) Size constancy in rhesus monkeys: effects of pulvinar, prestriate, and inferotemporal lesions. Exp Brain Res 27:251–269

Wyke M (1960) Alterations of size constancy associated with brain lesions in man. J Neurol Neurosurg Psychiatry 23:253–261