Illusions of visual orientation: comparisons between perceptual and visuo-motor tasks

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ILLUSIONS OF VISUAL ORIENTATION: COMPARISONS BETWEEN PERCEPTUAL AND VISUO-MOTOR TASKS

Richard Thomas Dyde

Abstract

The Milner and Goodale (1995) model of dual cortical visual systems suggests that, in the primate cortex, separate neural substrates dominate the tasks of visual perception and visuo-motor control. This model derives from a number of independent sources of evidence: anatomical, physiological and behavioural. Neuropsychological evidence in humans suggests that visual perception and visuo-motor control can be selectively impaired through damage to the ventral and dorsal visual streams respectively. Evidence has emerged that in the healthy human visual cortex, differentiable effects of visual illusions can be found between the two measures of perception and visuo-motor control. This evidence has been cited to support the Milner and Goodale (1995) model. The series of studies reported in this dissertation used a similar, but methodologically revised application of the illusion paradigm in the novel domain of orientation. Using two types of visual illusions, the simultaneous tilt illusion (STI) and the rod-and-frame illusion (RFI), a series of studies found patterns of association, dissociation and interaction that strongly support the Milner and Goodale model. The critical issue, in terms of predicting the pattern of effects across perception and visuo-motor control tasks, was found to be the siting of the causal mechanisms underlying the illusion employed.

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Declaration

I confirm that this thesis conforms with the prescribed word length for the degree for which I am submitting it for examination.

I confirm that no part of the material offered has been previously submitted by me for a degree in this, or any other, University. If material has been generated through joint work, my independent contribution has been clearly indicated. In all other cases material from the work of others has been acknowledged and quotations and paraphrases suitably indicated.

Signed:...

Date: 24th September 2001

Acknowledgements

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My thanks go to David Milner for his generous support and guidance.

Dedication

To Alice and Harry, Robert, Samuel, Lucy and Kate.

Oh! I have slipped the surly bonds of earth
And danced the skies on laughter-silvered wings;
Sunward I've climbed, and joined the tumbling mirth
Of sun-split clouds - and done a hundred things
You have not dreamed of…

Chapter 1: Introduction

The perception .vs. action model

The Milner and Goodale (1995) model of dual visual systems stems from the suggestion that, although the most compelling aspect of human vision is that of our conscious visual experience, the evolutionary pressures that have shaped the development of vision were first concerned not with understanding the visual world, but responding effectively to stimuli within it. Thus the earliest pressures which dictated the development of vision were identical to those which shaped the evolution of all aspects of animal species: the need to survive long enough to reproduce. Although auditory, olfactory and somatosensory systems contribute significantly to achieving this goal, vision provided the ability to deliver essentially instantaneous discriminatory information about the most distal stimuli. Thus vision provided a unique source of environmental information, to both predator and prey.

In many animals the relationship between visual processes and behaviour is most simply explained in terms of two basic behaviours: the need to guide the host towards those elements that assist survival and away from those elements which threaten it. This can be achieved by a relatively straightforward relationship between visual and motor systems and it has been proposed that, in relatively unsophisticated visuo-motor systems the visual processes for resource acquisition and threat avoidance, may be regarded as being independent (Ingle, 1973).

With the development of the primate cortex came, most notably, the emergence of associative and executive functions. The relationship between stimulus and behaviour was now mediated by processes which involved mapping sensory input against internal representations of the world. The advantage of this additional processing was the development of adaptive behaviour. Thus genetic survival was now not solely reliant on the effectiveness of 'reflexive' systems, but an ecological advantage was to be obtained through the sophistication with which flexible and 'conscious' responses were applied.

However, primate cortex evolved from earlier, less sophisticated, structures and thus the phylogenetically older centres linking sensory processing and motor response are likely to have remained intact unless there was some evolutionary advantage in these being replaced. There may be no advantage, and potentially significant disadvantages, in mediating all visually-guided behaviours via the more complex mechanisms of associative and executive function. Thus it is suggested that visual processing subserves more than one outcome and in the more developed cortex that visual processing for perception and processing for action may be differentiable.

Ungerleider and Mishkin (1982) developed the earlier work with hamsters by Schneider (1969) and suggested that in monkeys, two differentiable streams projecting from early cortical vision could be identified. The ventral stream projects ultimately to inferotemporal cortex (IT) with the dorsal stream projecting to the posterior parietal cortex (PPC). Ungerleider and Mishkin's account of the physiological difference between these separate anatomical structures was the dominance of the ventral stream in visual discrimination and the dorsal stream in visual localisation: the 'what and where' model of the dual visual streams. However studies examining the characteristics of cells in the terminal areas of these two streams (IT and PPC) point to an alternative explanation of their function.

Cells in PPC seem to be associated with the form of response made to a stimulus, suggesting a relationship between vision and specific visuo-motor processing e.g. the finding that temporarily inhibiting the processing of cells of specific regions within the posterior parietal cortex results in reversible errors in hand shaping during visually guided grasping in monkeys (Gallese, Fadiga, Fogassi, Luppino and Murata, 1997). The most compelling evidence for similar processes in the proposed homologue of the dorsal stream in humans comes from neuropsychological evidence. This work originated from studies by Balint in the early part of this century (Balint, 1909). Later, more detailed examination of the syndrome of optic ataxia showed that deficits could be confined to specific effector systems. As further studies investigated damage centred within the PPC it emerged that this complex seemed linked with different elements of prehension that could be selectively impaired: localisation of targets (Tzavaras and Masure, 1976) wrist/hand orientation (Perenin, Vighetto, Maugiere and Fischer, 1979; cited in Milner and Goodale, 1995), grip formation (Damasio and Benton, 1979) and selection of grasp points (Goodale, Meenan, Buelthoff, Nicolle, Murphy and Ricacot, 1994). It appeared therefore that this area was intimately involved not only in coding target position in visual space, but in processing all the characteristics of the object which would enable a successful grasp to be performed: location, size/shape and orientation.

In contrast, the properties of many cells within IT in the monkey appear to show substantial invariance in their responses (Tanaka Saito, Fukada and Moriya, 1991).

The patterns of specificities they do show indicate that they may be more bound to the enduring characteristics associated with the stimulus 'value' (Milner and Goodale, 2000). They show less sensitivity to manipulation of stimulus size and distance from the observer (e.g. Perrett, Rolls and Caan, 1982) and the large receptive field sizes of IT neurones also reduce their specificity in terms of the location of stimuli within the visual array (Gross, 1973; Desimone, Schein, Moran and Ungerleider,1985). These characteristics seem less tied to the processing of the contemporaneous instance of the viewed stimulus (coded within absolute space), than with mapping the stimulus onto persistent internal models of the visual world. As such it has been suggested that IT neurones express the qualities which would allow the formation of visual percepts.

In human patients it was only when the rare conditions association with damage isolated to the ventral stream itself were examined that the processing of this stream could be studied specifically. Visual form agnosic patient 'DF' has damage which, though diffuse, appears to have left the primary visual and inferotemporal cortices relatively intact, but bilateral damage in the area of the occipito-temporal regions has essentially deafferented the projections between the early visual centres and IT. She has been extensively tested over two decades and has been shown in a number of cases to exhibit a near mirror image of pattern of deficits and preserved abilities present in the optic ataxia syndrome. She shows 'visually guided' grasp formation that takes size and orientation of targets into account (Carey, Harvey and Milner, 1996) and appropriate selection of grasp points (e.g. Goodale, Meenan, Buelthoff, Nicolle, Murphy and Ricacot, 1994) whilst in measures of perception she seems able to make only coarse visual discriminations.

The presence of a doubly-dissociative pattern of deficits and abilities in action and perception between optic ataxia and visual form agnosia, is cited as strong evidence to support the proposal that visuo-motor control and visual perception rely on separable neural substrates in the human cortex. The siting of damage in the dorsal and ventral visual streams of the two syndromes supports the suggestion that the former is dominant in goal directed acts whereas the latter dominates in the formation of conscious visual perception.

Evidence has also been emerging to suggest that in the healthy cortex a similar pattern of different effects may be present. These studies have used visual illusions comparing their effect on visuo-motor and perceptual measures. The underlying assumption has been that the internal models of the visual world, which drive the perceptual processes, are predicated on associative mechanisms that are strongly influenced by visual context. 'Action' responses, on the other hand, are dominated by the processes of visuo-motor mechanisms which operate within an egocentrically coded reference frame, and are largely immune to illusory effects of context.

This dissertation focuses on the application of the visual illusion paradigm within the context of the Milner and Goodale (1995) model of visual processing. Studies utilising the illusion paradigm have, up until recently, centred on the domains of size, shape and location. However it is suggested that illusions of visual orientation should exhibit similar patterns of different effects across perception and action. This hypothesis is derived from neuropsychological evidence suggesting that orientation processing for action and perception are reliant of separate neural substrates.

Neuropsychological evidence for dissociation of processing of visual orientation

Optic ataxia typically follows damage to the posterior parietal cortex, especially in and around the intraparietal sulcus. Perenin and Vighetto (1988) examined unilateral optic ataxic patients in a number of tasks, one of which involved a comparison of visuo-motor and perceptual report of visual orientation. In the visuo-motor task patients were presented with a disk with a central elongated slot and subjects were instructed to pass their hand through the slot which could be presented in a number of orientations (figure 1.1).

The study reported that there was some asymmetry in terms of motor and visuo-motor deficits and the lesion lateralisation: left hemisphere lesions resulting in errors with both ipsi-lesional and contra-lesional hands. However the most notable result was responses to the target disk in contra-lesional visual space using the ipsi-lesional hand, where consistently higher errors are reported in terms of hand orientation in comparison to responses in the ipsi-lesional visual hemifield (indicated by the shaded and open bars in figure 1.2 respectively). In a parallel test, a sub-set of the group performed a forced-choice response to similar stimuli of varying orientations. Although patients still showed some deficits in this perceptual measure, the results seemed to indicate a larger deficit in the visuo-motor response than that in the perception measure.

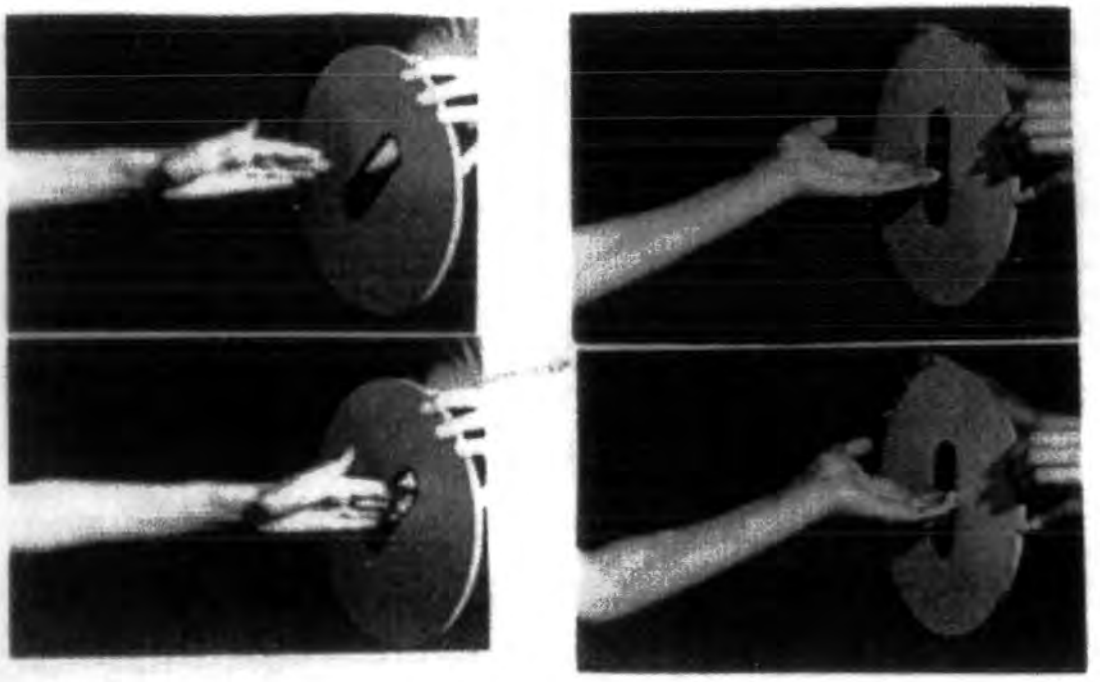

Figure 1.1: Perenin and Vighetto (1988). The two images in the left-hand column show a successful response by a subject in 'posting' the hand through the target slot. The two images in the right-hand column show a patient incorrectly orienting their hand to pass through the target slot.

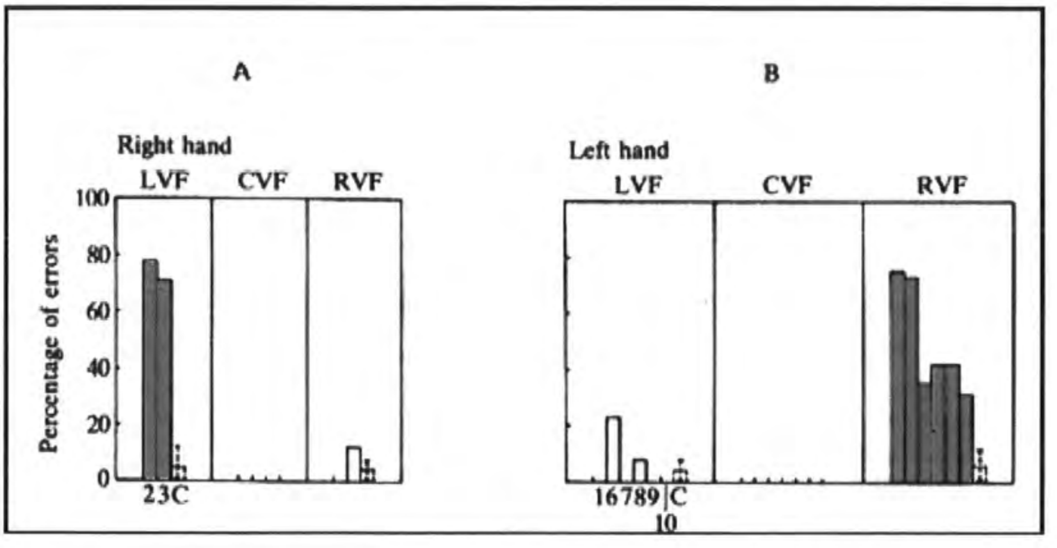

Figure 1.2: Perenin and Vighetto (1988). Distribution of orientation errors of the hand across different combinations for 2 right-hemisphere damaged (A) and 5 left-hemisphere damaged (B) patients and for the control group (C) during the hand orientation test (above). LVF = left visual field; CVF = central visual field; RVF = right visual field. The numbers on the x-axis indicate subject identifiers; c = control subject.

A potential criticism of this interpretation is that the forced choice (matching) response employed in the perceptual measure could be regarded as considerably easier to perform than the posting task, and yet still returned a relatively high level of errors in both ipsi-lesional and contra-lesional visual space. The visuo-motor response allowed for considerably more degrees of freedom to produce an erroneous response. The authors report, however that not all patients showed matching errors, and where errors occurred in matching these did not correlate with the posting errors. Also the matching errors were only seen with tachistoscopic exposure and perceptual deficits could not account for the hand specificity of posting errors seen in several patients. Therefore the results can be interpreted as indicating a greater deficit in the use of visual orientation processing to guide a visuo-motor response, than would be expected from the rate of error found in the perceptual measure. As such it represents evidence for a dissociation of orientation processing between visuo-motor and perceptual responses.

In a single case study involving the visual form agnosic patient 'DF' Goodale, Milner, Jakobson and Carey (1991), replicated an earlier study by Milner, Perrett, Johnston, Benson, Jordan and Heeley (1991). Both these studies used a similar paradigm to the one applied by Perenin and Vighetto (1988). In two perceptual measures (forced choice visual comparison of orientations, and tilting a hand-held card to match a presented orientation) 'DF' showed gross impairments in her ability to make perceptual reports of target orientation. However when 'posting' the card through a slotted disk, her performance was indistinguishable from an age-match control (figure 1.3)

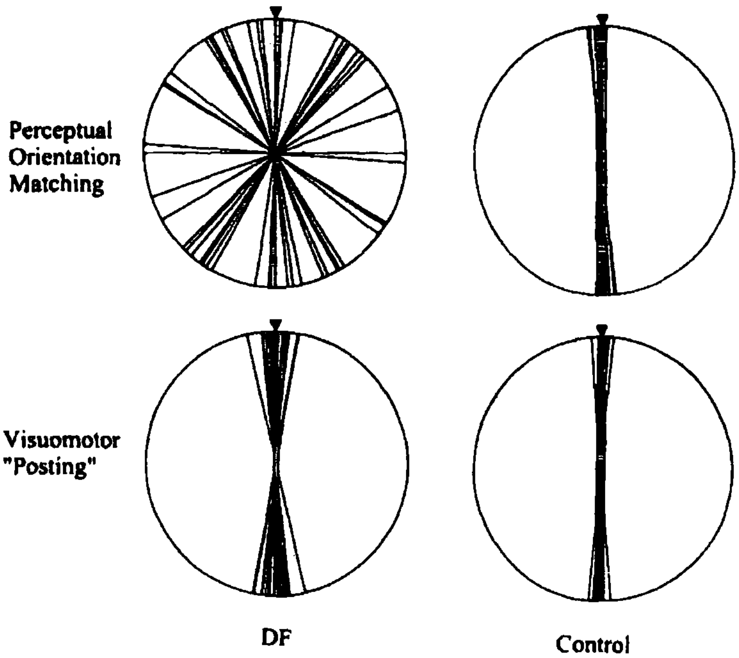

Figure 1.3: Goodale *et al* (1991) polar plots (normalised to vertical) of subjects 'DF' and an age-matched control in the matching and 'posting' responses to target stimuli of varying orientations. 'DF' shows gross errors in the perception measure (top left) but performs at a level comparable to the control in the posting measure (bottom left). Illustration from Milner and Goodale (1995).

The results reported by Goodale *et al* (1991) and Milner *et al* (1991) suggest clear evidence for the opposite dissociative pattern between orientation processing for a perceptual and a visuo-motor task in visual form *agnosia* to that reported by Perenin and Vighetto (1988) for optic ataxic patients. From the siting of the damage associated with the two syndromes this would suggest that, in the domain of orientation, there is evidence to support differential influence of dorsal and ventral stream processing on action and perception measures.

It may be possible, therefore, to apply the visual illusion paradigm in the domain of orientation for subjects with intact visual cortices. The Milner and Goodale (1995) model would predict that an action measure would be largely immune to the effects of an illusion of tilt, whereas perception measures should show reliable effects. However, before the illusion paradigm is applied in this new domain, an examination of the paradigm itself is required. There have been strong suggestions that dissociative patterns found in studies using illusions may be contaminated by artefacts associated, not with differences between cortical processing, but with the paradigm itself.

The perception .vs. action model and the visual illusion paradigm

Carey (2001) has recently reviewed the studies that have examined visual illusions and the Milner and Goodale (1995) perception .vs. action model over the last 5 years. He concluded that the evidence overall, although favouring the suggested resistance to illusory effects in visuo-motor responses, was equivocal. Carey proposed that a 'second phase' had begun in terms of this area of research. Factors such as control conditions, statistical analyses, unintended effects of illusion inducing elements, and attentional biases associated with the method itself should be critically examined. In doing so the pattern of results that have been reported since the Aglioti, De Souza and Goodale (1995) study may be effectively synthesised.

The aim of this initial summary is to determine whether there is any consistent pattern of effects to be found in studies that have made widely differing theoretical inferences: ranging from strong support to strong criticism for the perception vs. action model and its application to healthy subjects. Many studies seem to suggest that there may be a need to qualify, rather than negate, the model's primary tenets. Additionally, this summary aims to identify the methodological issues that must be addressed to ensure that valid comparisons are made across the disparate measures of perception and visuo-motor control. In order to achieve this secondary goal, a detailed examination of both the experimental methods and statistical analyses is necessary to determine whether the 'devil is in the detail'.

<u>Early evidence for dissociative patterns using the visual illusion paradigm</u>

Bridgeman, Hendry and Stark (1975) reported that conscious visual perception was blocked during saccadic eye movements. In particular, they found that small displacements of stimuli were suppressed, an effect first noted by Ditchburn (1955). This effect was examined further by Bridgeman Lewis, Heit and Nagel (1979) who examined pointing to targets shifted during this 'saccadic suppression'. They reported that positional data concerning a target's movement appeared to be accessible to mediate this visuo-motor response in spite of there being no apparent perceptual awareness of stimulus movement. A similar finding to Bridgeman *et al* (1979) was contemporaneously reported by Prablanc, Echallier, Komilis and Jeannerod (1979).

The paradigm was later modified and extended by Goodale, Pelisson and Prablanc (1986), who found that ballistic pointing responses took account of saccade-locked shifts in target displacement in a way that suggested a smooth and continuous updating of the pointing act. Furthermore, they reported that even in a forced-choice response aimed at recording subjects' perception of the movement, that subjects could not reliably discriminate between trials which involved a saccade-locked displacement and those that did not.

These findings suggested an absence of access by the perceptual mechanisms to the visual processing of the displacement that appeared to be nevertheless available to the ocular-motor and skeletal-motor systems. These studies gave credence to the suggestion that, in subjects with intact visual cortices, the perceptual experience of target displacements and the visuo-motor systems that were guiding motor responses were reliant on separable processes. It appeared, therefore, that the mechanisms dedicated to maintenance of a stable perception of the visual scene (in this case during saccadic suppression) appeared to assume the absence of displacement information, but that this same information was available to the visuo-motor systems which in turn adjusted a motor act to take account of it.

In a subsequent study Bridgeman, Kirch and Sperling (1981) compared apparent and actual displacement of stimulus position by use of stroboscopic induced motion through the Roelofs effect (Roelofs, 1935, see appendix A, figure a1). The study aimed to show that a motor response (adjustment of a pointer) would be dominated by the actual stimulus position, rather than an illusory displacement caused by the shift of the background frame. The results showed that an induced displacement did not influence a pointing response in the direction of the (illusory) perceived displacement. Furthermore an actual displacement, accompanied by an illusory perceptual shift in the same direction (leaving a residual illusory percept of no displacement) induced in the visuo-motor task responses that reflected the actual change in position, albeit with consistent biases towards the stimulus' original position. The authors cautiously interpreted their results as "...an intermediate between the hypothesis of independence of information in the two visual systems...[and]...a unified visual system..." (Bridgeman *et al* 1981, p. 339). Potential criticisms of the study include the fact that the study separated the titration of illusion magnitude for each subject (computed from only 3 trials) and the pointing trials into two separate stages, with no confirmation that the illusory magnitudes in each subject remained constant during the extensive number of trials (360). If there are changes over time in the magnitude of illusion this could lead to potential biases in the data especially as the results were based on the performance of only 2 subjects. Also the 'pointing' task itself was not a ballistic prehensive response to a stimulus position, but used a mechanical pointer mounted under the stimulus display which was adjusted using a lever to indicate the observers' response. In other words, it may fall short of what is usually considered a fully 'goal directed act' (in the Milner and Goodale, 1995, nomenclature). Lastly and perhaps most importantly, there were considerable delays between stimulus offset and response. These latencies were not quantified, but may have involved a number of seconds. It is known that the egocentric coding of position decays rapidly (Wong and Mack, 1981; Elliot and Madalena, 1987; Westwood, Heath and Roy, 2000) and that illusory effects are 're-introduced' in 'action' measures when such delays are imposed (e.g. Gentilucci, Chieffi, Daprati, Saetti and Toni, 1996; Hu and Goodale, 2000). The combination of these factors is likely to have reduced any dissociation between the "judgement" and "pointing" responses. However the study seemed to support the predictions of a separation of visual coding for perception and a quasi-pointing task, and indicate that there may be separable processing for the two domains, but falls short of a unequivocal dissociation between the two.

<u>Development of the Bridgeman illusion paradigm</u>

Wong and Mack (1981) utilised a related design using an elliptical 'frame' and an effect similar to the Roelofs effect, measuring the saccadic responses to briefly presented stimuli. The method involved purely perceptual shifts in the stimulus (induced through shifting the frame with the target remaining stationary), complementary shifts (with frame and stimulus moving in the same direction) and opponent shifts where frame and stimulus moved in opposite directions (see appendix A, figure a2). Stimuli were briefly flashed on a second (post shift) presentation for a duration that was judged to be shorter than the latency of the saccade (100 ms). In all three manipulations saccades centred on the veridical position of the stimulus, in spite of perceptual reports that concurred with the predicted illusory effects of the frame shift. Even in the condition where perceptual and actual shifts were complementary, saccades did not project as far as perceptual report of the extent of displacement. Finally, when a frame shift induced a large illusory displacement in one direction, and a smaller veridical shift in the target stimulus was made in the opposite direction, the saccade again centred in the true direction of shift.

These results illustrated a much clearer dissociation between the perception of displacement induced by the frame and the saccade to the actual stimulus post-frame-shift position.

In a second experiment the perceptual and visuo-ocular systems appeared to be further teased apart by introducing a second, delayed response whereby the observer produced a second saccade to the perceived original stimulus position. The results showed that although, as in the first experiment, the first shift was centred at the veridical position of the stimulus (although in this case the stimulus was not extinguished, and so in this 'closed-loop' design this was not an indicator of a perceptual/visuo-ocular dissociation) – the second saccade (to the 'remembered' original location) was heavily influenced by the perceptual experience of displacement. This second saccade, therefore appeared to be driven by the memory of the frame-shift-induced illusory displacement.

The authors suggested that the apparent illusory effects for delayed saccades was a result of the decay of the retinotopic coding of target due to the imposed delay. This claim is strongly supported by the correlation between the recorded perception of illusory target shift, and the displacement of the second (assumed perception dominated) saccade ($r^2 = .89$). As such it appears that this second experiment engineered a condition whereby perception and oculomotor responses were both dominated by the same (illusory) mechanisms, based on the long-term persistence of perception of displacement against the quickly decaying retinotopic coding of the target's actual position. This pair of studies, therefore, addressed three of the potential criticisms of Bridgeman *et al*'s (1981) experiment. First by using a saccadic response (which according to the Milner and Goodale model is more directly driven 'action' mechanisms). Secondly by not having to rely on a titrated illusion magnitude in order to control for the individual differences in illusory displacement. Finally by explicitly examining the differential decay rate of the perceptual and oculomotor coding of position.

Bridgeman, Perry and Anand (1997) extended this work on the potential difference between "cognitive and sensorimotor" processing of visual space (after the terms adopted by Paillard, 1987). The suggested theoretical determinants of their experiment were expressed in terms of 'motor and cognitive' mapping of visual space. A similar design to previous studies was employed, utilising a frame offset from centre, and involved a judgement condition (button presses to indicate position) and a pointing response (hand unseen) using a mechanical pointer as the two contrasted measures. Stimuli were presented in one of five horizontal positions: with a frame that was either centred, or with small or large offset to left of centre or the same magnitude of offset to the right of body centreline. In responses made immediately following stimulus offset, or after a delay of 4 seconds the results showed a curious distribution of effects amongst the 10 subjects. In 5 subjects there was a significant illusory effect in both the button press (perceptual) and the pointing condition, but in the other 5 subjects there was a significant and "robust" effect on the button press, but no reliable effect on the pointing measure. The authors report that this was not due to a normally distributed effect across the group, but seemed to be genuinely bimodal.

Nine subjects of the group were involved in a follow up study which applied the same tasks but which imposed a 4 second delay before response. Eight subjects showed a significant effect of the illusion in the button press measure, and 7 now also showed a significant effect in the pointing measure. Of the two subjects not displaying an illusory effect in pointing measure, one was found to be sensitive to the Roelofs effect if the delay was increased to 8 seconds. It appears that one subject consistently showed no illusory effect in either measure, with or without the 4 second, or an extended 8 second delay. The authors suggest that the group of subjects who showed resistance to the illusion in the pointing measure did so through access to spatial information qualitatively different from those subjects who succumbed to the illusory effect, but that this 'privileged' information degraded over time, hence the emergence of the illusory effect in pointer adjustment following imposed delays. A follow-up study using a continuous but metric perceptual measure for target position (an estimate in centimetres of the target's displacement from the edge of the display) resulted in a "similar" magnitude of illusory effect overall in the 'judging' measure. However there appeared to be some reduction in effect as 2 of the 5 subjects tested showed trends, but not significant effects, in the predicted direction of illusion (cf. Vishton, Rae, Cutting and Nunez, 1999 below).

These results are a strengthening of the suggestion for differential persistence and salience in the coding of position between the two conditions, with the 'motor representation' showing sensitivity to the effects of delay. The authors also noted that in the motor task there appeared to be larger variance in response data, although the mean bias towards the illusory effect was consistently smaller than in the cognitive measure. This raises the issue of the 'noisier but more accurate' data associated with the motor tasks, an effect which, if present in visuo-motor measures generally, has implications for the statistical analyses that are performed in comparing perceptual and action measures (a point that will be returned to later).

Illusions of size perception: Aglioti *et al* and related studies

The most heavily cited study in the use of illusions in the context of the perception vs. action model is that of Aglioti, De Souza and Goodale (1995) which drew from the earlier work of the Bridgeman group ,to suggest that differential processing of the same visual information was required for perception and visuo-motor systems. The authors proposed that illusions based on size-constancy (an assumed mechanism of perceptual processing) would have differing effects on perception and visuo-motor responses. The suggestion here was that the perceptual distortions of the Titchener circles (aka Ebbinghaus illusion – see appendix A, figure a3) were the result of size comparisons between target and annulus. This would result in underestimation of the size of the target circle surrounded by an annulus of larger circles, and over-estimation of the target size when surrounded by an annulus of smaller circles.

However only brief speculation as to the actual causal mechanisms of the illusions was reported.

The study predicted that the visuo-motor system would not be as influenced by the perceptual distortions induced by the annulus, but would be driven by the veridical dimensions of the target stimulus. The theoretical basis of the study was couched in terms of the dominance of relative coding of size in the perception system, whereas the visuo-motor system was coding targets within absolute egocentrically coded space. The dependent variable was maximum grip aperture, a measure taken relatively early in the response, which has been shown to correlate strongly with object size in a prehensive act (Jeannerod, 1980). The study's prediction was that maximum grip aperture would remain dominated by veridical rather than illusory size of the target circle. As in the Bridgeman *et al* (1991) study, the experiment used a titration method to determine each individual observer's magnitude of illusion. The experimenters derived, independently for each subject, disk sizes which, when placed within the small and large circle annuli were perceptually matched in size (but physically different). Perceptual responses were determined by instructing observers to grasp a specific target (in either the left or right array of stimuli) on the basis of whether they believed the target circles in the two arrays to be equal in size or not. This method has the advantage of ensuring that if there are any changes in the magnitude of the illusion over trials, that this would become apparent from the observer's report of perceptual equivalence of physically different targets. However the comparison of the illusory effect on maximum grip aperture and on perceptually matching targets was not a comparison of contemporaneous measures nor counterbalanced across the group (matching always preceded grasping). The concern that illusory effects may be changing over time is allayed through the authors explicitly stating that there is no evidence for the reduction in the illusion magnitude over the course of trials.

The statistical comparison of effects on perception and grip scaling did not indicate whether there was a statistically significant effect of the illusion on grasping (although the figure presented suggests that there was an effect of some kind). Although there was a statistically larger effect of the illusion on the perception measure in comparison with grip scaling, it may be the case that there is a *quantitative* difference in magnitude of effect from which *qualitative* inferences about the perceptual and visuo-motor systems were made. Although grip aperture was reported as clearly being influenced by actual rather than perceived size, there are indications that both measures were influenced by the illusion to some, though statistically differing, extents. The study concluded that "…the calibration of grip aperture is quite refractory to the compelling size-contrast illusion induced by the display." (Aglioti *et al*, 1995, p.684). It may be more judicious, however, to suggest that the results are more in line with the Bridgeman *et al* (1981) conclusion: that they are better described as indicating a partial, rather than a complete dissociation of effect between the two measures. The critical determination is not reported: a comparison of grip aperture to a control target (a single stimulus without annulus) versus the same dimension target with an illusion inducing annulus. Further potential methodological criticisms of the study are that reaching was performed in full vision (closed-loop), so that on-line corrective grasping could have been employed by subjects to influence prehension (although it is normally assumed that maximum aperture occurs before visual comparison between target and hand can be made). Additionally there was constant haptic/tactile feedback during the reaching trials which could have informed grasp, or, depending on the randomisation of trials, may have resulted in perseverative motor responses in grasping.

Haffenden and Goodale's later (1998) study addressed a number of these issues using a very similar design to the Aglioti *et al* (1995) study and again using the Ebbinghaus illusion. Observers performed open-loop grasping, and maximum grip aperture was compared with a 'mimed' manual estimation of the target circle as the perception measure as well as the dichotomous choice measure of perception that was used by Aglioti *et al* (1995). Observers were also instructed to grasp the target even in the perception measure to match the haptic feedback across conditions. Finally two additional control conditions were included: a target without a surrounding annulus and a control annulus with circles mid-way between the illusion inducing large and small circles. The results replicated the Aglioti *et al* (1995) study and showed that maximum grip aperture was consistently resistant to the illusory influence of the annulus even in the open-loop condition, whereas both the dichotomous choice condition (indicating relative size perception judgements) and the miming (perception) measure were significantly influenced by the illusion. This study addressed a number of methodological criticisms of the previous study and allowed a strengthened reiteration of the suggested dissociation between perception and visuo-motor control.

One notable point raised by the authors was that there was some evidence to suggest that maximum grip aperture may have been affected by the surrounding annulus in the control condition, and that the annulus may have been regarded as an obstacle requiring avoidance. They suggest that the factor of avoidance in prehensive measures may be a potential confound (a point discussed below). Although the authors report that these effects failed to reach statistical significance in their experiment, they noted that there was both anecdotal evidence for perception influencing action as well as neuroanatomical evidence for cross-connections between the ventral and dorsal visual streams (Jeannerod, Decety and Michel, 1994; Sirigu, Cohen, Duhamel, Pillon, Dubois and Agid, 1995). This speculation again raises the question as to whether, in the intact visual cortex, the presence of two *separable* but potentially not wholly *separate* visual streams could result in a partial, rather than a complete dissociation of effects when the illusion paradigm is used in measures suggested to be dominated by these two neural substrates.

Otto de-Haart, Carey and Milne (1999) followed up a study by Marotta, DeSouza, Haffenden and Goodale (1998) – the earlier study having found evidence that monocular viewing of the Ebbinghaus illusion reduced the differential illusory effect between perception and action in monocular viewing conditions. Otto de-Haart *et al* (1999) suggested that if binocular processing in the posterior parietal cortex was key in the mediation of veridical grip scaling to targets, then presentation of the target 'shaft' within a Mueller-Lyer illusion would result in different effects on monocularly and binocularly-driven prehension. The study reported large effects of the illusion in grip-miming (the perceptual measure) but also found evidence for some illusory effects on grip-scaling in both the monocular and binocular prehension measures (however after correction for error these were rendered non-significant). The results presented again suggest an illusory influence on maximum grip aperture in the predicted direction of illusion (see Otto de-Haart *et al*, 1999, figure 2). This again raises the question as to whether a partial dissociation may give the appearance of a full dissociation as a result of the relatively 'noisy' visuo-motor data (as noted by Bridgeman *et al*, 1997) rendering an illusion unreliable for the action measure when statistically tested. However if the perceptual measures return relatively 'clean' data, then statistical analysis is more likely to find a reliable effect in this measure alone.

Evidence for a lack of a full dissociation between perception and action measures was also suggested by Pavani, Boscagli, Benvenuti, Rabuffetti and Farne (1999) who again used the Ebbinghaus illusion. The study addressed the issue that perceptual measures involved contrasting two stimuli each within counter-acting arrays whereas the visuo-motor condition involved a response to a single target within a single illusory context (the annulus). A single Ebbinghaus array was presented and observers matched the perceived size of the central target circle with a range of disk annuli of differing sizes. Importantly this design included both larger and smaller disk annuli and a control 'neutral' annulus with disks of a size that had been found to induce no perceptual illusion. Maximum grip aperture in a closed-loop grasping condition was used as the visuo motor measure. Illusory effects were found in both conditions, and the magnitude of effect (measured in millimetres) was actually larger in maximum grip aperture than in the perception measure. The authors concluded that this suggested no evidence for a disparity in illusory effect between visuo-motor and perception measures. However, it must be borne in mind that maximum grip apertures are larger than the targets to which the grasping response is made (although they are correlated with target size). As such, the comparison made by Pavani *et al* is between maximum grip aperture and the perceptual measure and not a comparison of the *relative* strengths of the illusion between conditions. The critical comparison would be to determine some comparable 'magnitude of illusion' in both measures and then compare these magnitudes directly, a comparison that is notably absent. Although the results suggest evidence for an illusory affect on both measures (arguing against the action measure being refractory to the illusion) there is some evidence for a partial dissociation (whereby the grasping response was relatively less affected by the annuli than the perceptual measure). If the difference between the mean magnitude of effect in response to the small circle annulus and the mean response to the large circle annulus is expressed as a percentage of the mean response to the control ('neutral') stimulus, and this is calculated for both conditions, this seems to indicate that there may be a greater illusory effect on perception than action (see figure 1.4 below).

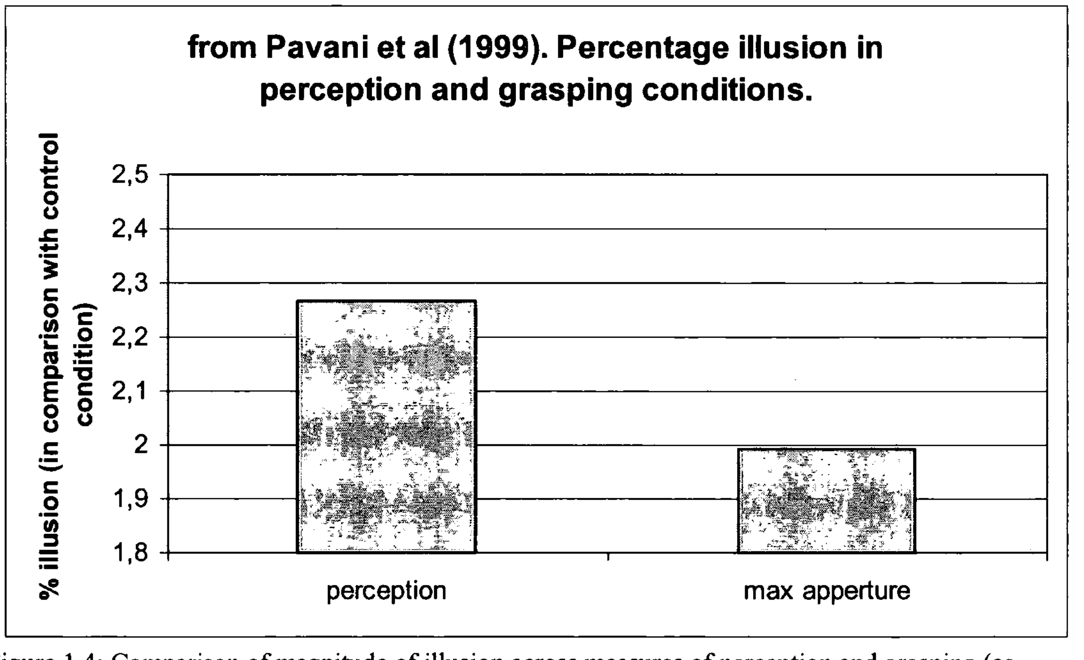

Figure 1.4: Comparison of magnitude of illusion across measures of perception and grasping (as measured through maximum grip aperture) - data extracted from Pavani *et al* (1999, p 99). Percentage illusion calculated as: 100*((a-b)/c) where a = mean response to target with small annulus surround; b = mean response to target with large annulus surround and c = mean response to target with neutral annuls surround (the control stimulus).

This re-analysis suggests that the annuli have a greater magnitude of illusory effect on perception than on maximum grip aperture, again suggesting a partial, but identifiable dissociation between the two measures. Without the raw data from which a statistically viable analysis can be performed, this evidence is best regarded as illustrative, but again it would suggest that when controlled bases of comparison are adopted, a predictable pattern of effects emerges: that of quantitatively larger effects of illusion in perception, but persistent residual effects on visuo-motor responses.

Haffenden and Goodale (2000) performed a re-analysis of their Haffenden and Goodale (1998) study. This aimed to expand upon the subsidiary finding that grip aperture was affected in a way that indicated an opposite effect of the surrounding annulus than was found for the perception measure. They found that grip aperture was reduced for a target surrounded by an annulus of slightly smaller circles in comparison with a control circle with no annulus, whereas the opposite effect was found in the perception measure. Both effects were significantly different from baseline (and in opposite directions) as well as being reliably different from each other.

The proposed explanation for this opposing pattern if effects was that the visuo-motor system regarded the annulus as an obstacle during grasping (in spite of these being 2-dimensional, whereas the target is a 3D solid) Grip aperture was reduced in order to 'place the hand in the hole' between the target disk and the annulus. The study found that there was a non-significant trend towards grasping being influenced by 'flankers' (obstacles placed close to the target stimulus) if these interfered with the intended grasp points on objects. There appeared to be a critical distance between the target object and the flankers, which induced the proposed 'reaching in a hole' effect, however the perceptual measures seemed largely immune to these 'flanker effects'.

Haffenden and Goodale suggested that these effects may have been influential in the findings of Franz, Gegenfurtner, Bulthoff and Fahle (2000, see below) and Pavani *et al* (1999) where illusory effects in the visuo-motor measure of similar magnitude and direction to those found in the perceptual condition are reported.

Additive effects of multiple arrays affecting perception measures

Franz, Gegenfurtner, Bulthoff and Fahle (2000) set about determining what other factors could account for the patterns of results found in the illusion paradigms when perception and action measures are compared. They specifically aimed at controlling for the different attentional factors in the perception and grasping conditions of Aglioti *et al* (1995). Franz *et al* pointed out (as had Pavani *et al*, 1999) that the Aglioti *et al* (1995) perception condition required the comparison of two targets within annuli simultaneously decreasing the apparent size of one target (surrounded by large disks), whilst increasing the size of the other disk (surrounded by the small-disk annulus). However the grasping condition required attention to be fixed on a single target which was, presumably, being influenced by only one annulus. The Franz *et al* (2000) study reported using a complex design which included comparisons between grasping of annulus surrounded targets (illusory arrays) and control targets without illusion inducers. They report illusions in both the maximum grip aperture of reaching and in perceptual measures. Additionally they showed a strong correlation between the illusions in the grasping and the perception measures suggesting a common causal mechanism of illusory effect. However the most critical determinant is lacking: a comparable measure of the magnitude of illusion across both conditions. The study reports that the effect on maximum grip aperture and perception were not statistically different, however this again raises the issues associated with maximum aperture being a correlate of final grip aperture, and not grip aperture itself whereas the perceptual illusion measure is a direct quantification of illusory effect. As such the analysis suffers from the same limitation as outlined in the discussion of the Pavani *et al* (1999) study above. The more direct comparison would need to be applied i.e.. comparing maximum grip aperture to a control stimulus versus one with an illusory annulus and determining from that the magnitude of illusion. If this magnitude was compared with a perceptual measure of magnitude of illusion it would control for the non-linear relationship between maximum aperture and actual final aperture.

Once more the key criticism of making comparisons between non-comparable measures can be applied to a paper which cites this as the basis of its criticism. The study dismisses the results reported by Haffenden and Goodale (1998). Franz et al suggest that the 'mimed' manual response used as the perception measure in the Haffenden and Goodale study produced a greater magnitude of illusion than the 'classical perception measure'. It is assumed that Franz et al are referring to the results from the Franz *et al* (2000) experiment 1. This is in spite of the fact that the Haffenden and Goodale (1998) study found a magnitude of illusion in the perceptual (mimed) measure that seems consistent with the dichotomous choice perceptual measure reported by Aglioti *et al* (1995). Franz *et al* do not acknowledge that the mimed perception measure of Haffenden and Goodale (1998) in effect controls for both the non-additive effect of the illusion and requires similar visual attentional strategies to be adopted across conditions and yet still produces consistent results in terms of the magnitude of illusion found in other perceptual measures. Franz *et al* offer no explanation as to why they would predict that the 'mimed' grasp should give a larger illusion size than other measures of perception. Essentially the paper again highlights the critical issue of the requirement for valid bases of comparison across the two fundamentally different conditions of perception and visuo-motor control.

Large scale illusions and their affect on action and perception measures

A novel approach to the potential dissociation between perception and action was adopted by Wraga, Creem and Proffit (2000) by producing a large scale (175 cm and 325 cm long) 'walkable Mueller-Lyer configuration" using the Delboeuf (1892) 'dumbbell' variant (see appendix A, figure a4) of Mueller-Lyer illusion. They were extending a previous study (Creem and Profitt, 1998) which had found that verbal and haptic estimations of geographical slant had been found to dissociate between what they described as 'action' and 'awareness' measures. In their later study (Wraga *et al*, 2000) the design specifically differentiated exocentric coding of extent from egocentric coding of position by performing two action measures: walking in a direction perpendicular to the stimulus (offset measure); and an 'open loop' (blindfold) measure that involved walking along the stimulus itself (direct measure). Each action measure was independently compared with a perception measure of extent in the observer's choice of measurement units (a verbal report). The reported analyses produced a unitless measure of magnitude of illusion calculated as the percentage difference between the two opposing forms of the illusion : 'circles in and circles out' (analogous to the 'fins in' and 'fins out' of the more traditional Mueller-Lyer stimuli). They reported significant illusions in both the offset walking condition and the perception condition but no reliable illusion in the 'direct' walking measure. Although there was a trend towards the offset walking condition resulting in a smaller magnitude of illusion than verbal report, this difference failed to reach statistical significance and so it might be inferred that both measures were returning undifferentiable illusory effects. However the 'offset' response precluded the use of egocentrically coded cues being directly transformed into an action response, and as such are likely to be influenced by the perceptual system (see below for a discussion of the 'pantomimed pointing' measure as used by Mon Williams and Bull, 2000).

In a second experiment a single hoop (one-ended Delboeuf Mueller-Lyer variant see appendix A, figure a4) was used. Here the comparison between perception and the direct walking measure indicated no reliable illusion in the action measure (although a notable trend was observed) but a significant (3.7%) illusion in the verbal estimation task. In the study's conclusion the authors highlight the need for a consistent and stable egocentric coding of actual end-point as a factor in reducing the illusory magnitude found in the action measure. The results point towards a full dissociation between the visuo-motor and the perceptual measure, but indicate again that there may be some residual illusory affect in the former condition.

Interim summary: magnitudes of illusion .vs. absolute effects across conditions

In summary these studies seem to highlight a number of points. First, the need to determine magnitudes of illusory effect, rather than merely the presence or absence of an illusion in each measure (in order to determine whether a partial dissociation may be present). Second, that if comparisons of illusory effects between measures are made, it must be borne in mind that, for instance, maximum grip aperture is a correlate of target size, not an absolute measure of final grip size and as such cannot validly be compared with an absolute measure of perceptual illusory effect. These issues become critical where illusory influences are found in both conditions: a finding that appears to be present in a number of studies.

Further evidence for illusory effects in visuo-motor measures

van Donkelaar (1999) investigated the influence of the Ebbinghaus illusion on a pointing response by employing Fitts' Law (Fitts, 1957) which states that movement times are inversely related to target size as a result of an assumed speed/accuracy trade-off. Observers performed a task involving moving their finger from one circle to another, the target circle being surrounded by either an annulus of smaller circles, an annulus of larger circles or no annulus. It was found that although accuracy was not statistically different across stimuli, there were significant effects on movement times. When targets were perceptually smaller, there was an increase in movement times in comparison to the condition where targets perceptually larger. Additionally there was no significant difference in movement times between targets that were perceived as being of equal size (but were actually different). The study results suggest that ballistic pointing responses are influenced by the illusory effects of the annulus and as such this is evidence for action measures not being wholly immune to illusory changes in size. If visuo-motor measures are not resistant to illusory effects, then this result obviously challenges previous finding, but once more there is no measure of perception with which the effect in the pointing measure can be compared. As such the potential for partial dissociation between measures remains unexamined.. However, there is another potential explanation for this pattern of results. The large circles in the annulus may act as visual distracters in the response, and this additional attentional load could be the factor accounting for the slowing in movement times. The van Donkelaar results do however, represent evidence for an effect of a relatively distal stimulus on the low-level kinematics of movement.

Fischer (2000) attempted a replication of the results from the van Donkelaar (1999) experiment, suggesting that a number of methodological issues may have affected the earlier study's results. Fischer pointed out that the design employed by van Donkelaar included delays between stimulus offset and response, and did not control for changes in movement amplitude, or examine the effects of reaction time. Fischer failed to substantiate the van Donkelaar results, finding that the visuo-motor task seemed resistant to the illusory effects in the presence of clear and predicted perceptual biases. Furthermore the introduction of delays before the visuo-motor response now introduced illusory biases into the pointing measure (see Hu and Goodale, 2000, below).

In a follow up study Lee and van Donkelaar (2000) provided more direct evidence for the 'cross-talk' between the proposed ventral and dorsal streams assumed to be mediating perception and visuo-motor control. Using a similar paradigm to the van Donkelaar (1999) study, the authors administered a transcranial magnetic stimulus pulse across the ventral stream coinciding with the response cue. The increase in movement time that was noted in the earlier study was eliminated for perceptually smaller (veridically equal) target sizes. A similar effect was reported for pulses directed at the dorsal stream, but no change in effect was reported where the pulse was administered to control sites. The authors noted that this would seem to indicate that both ventral and dorsal streams were involved in the observed illusory effects. The direct manipulation of the underlying neurological substrates thought to mediate responses indicates again that perception may be influencing even the lower level kinematics of movement and would suggest that there is some inter-play between perception and action processes.

Illusions of size and inferences of object mass

Brenner and Smeets (1996) investigated the effects of a variant of the Ponzo illusion (see appendix A, figure a5) on cylinders of a uniform density, but differing sizes. Subjects grasped targets presented within the illusory array and then lifted them from the supporting platform. The study found a pattern of effects similar to previous studies: that grip aperture was not affected by perceived size with any statistical significance, whereas a perceptual measure (a matching task comparing the change in perceived disk size at opponent ends of the Ponzo illusion) was influenced by the illusion. However an indirect measure of the lift-force applied to the objects (drawn from the initial velocity of the hand when lifting the target) *was* reported as being influenced by the illusion (although the absence of error bars on the result histograms presented prevents any even rudimentary verification of the magnitude of differences). The study argued that the motor act of lifting the target appeared to be influenced by the illusion and the visuo-motor system showed a lack of immunity to the illusion in (a conclusion similar to that of van Donkelaar, 1999). This would seem to indicate that the mechanisms used for inferring mass from size were separable from those influencing grip aperture. They suggested that an explanation of the immunity of grip aperture to the illusion could be that observers selected specific grasp points and this coding dictated maximum grip aperture, rather than processing the size of target *per se*. They argued that the negligible illusory effect on maximum grip aperture could be explained by this effect without any reference to different visual processing for perception and action, and suggested that the presence of an illusory affect in another visuo-motor measure (implied lift force) clearly showed a visuo-motor measure being influenced by the illusion.

A development of the Brenner and Smeets (1996) study was carried out by Jackson and Shaw (2000), where a combination of vertical and horizontal targets and the Ponzo illusion was utilised (see appendix 1, figure a5). This study included a direct measure of lifting force exerted on the target rather than one inferred from movement times of the lift phase of the grasp (as had been the case with Brenner and Smeets, 1996). The study reported no statistically significant illusion on grip aperture although, curiously, a near significant effect of the illusion on grasping ($p = .07$) was reported in the *opposite* direction to that predicted by the illusion. However there was a significant effect of the illusion on lift force, replicating the Brenner and Smeets (1996) finding. McIntosh (2001) noted, however, that if mass is inferred from volume, and it was the illusory increase in cylinder diameter which caused the increase in initial lifting force, then as the relationship between cylinder volume to cylinder diameter is not linear, a very large illusory effect on lift-force might be expected, rather than the relatively small effect reported in the lift-force measure .Additionally a rather convoluted form of statistics was used for this determination. In the study, two pairs of illusions were presented: one pair with a vertically oriented target with a horizontal Ponzo array (one converging left and one converging right), and one pair with a horizontal target and a vertical Ponzo array (one converging distally and one converging proximally). The statistical analysis appears to have conflated the results of both these two pairs of target/illusion arrays for the comparison of differences. It is uncertain why the effects of each pair of target/illusion orientations is not separately analysed, but the histograms presented in the paper's figure 3 (pp. 422) suggests that the difference between a single pair of stimuli may not have returned a statistical significant comparison (i.e. no effective illusory influence on lift force for any single illusion). Even if there is evidence for the perceptual illusion affecting lift force, this presents a serious criticism for the differentiation between perception and visuo-motor control only if the assumption of complete dissociation is made. If only a partial dissociation is present in healthy observers, the question to be addressed is whether both a visuo-motor measure and a perceptual measure of mass are similarly affected by the illusion. However there is no perceptual measure of mass for a comparison to be made. The only visuo-motor and perception comparison that is reported relates to target size and this does suggest a difference across the two measures.

In summary the Brenner and Smeets (1996) and Jackson and Shaw (2000) studies raise the suggestion that all aspects of the prehensive act may not be equally refractive to illusory effects of context, the latter paper proposing that the perceptual system may in fact influence the prehensive act to a larger extent than previous studies had assumed. However in the absence of a perceptual measure of mass, the presence of a partial dissociation between perception and action is not falsified. Another potential explanation of the mixed results of the Jackson and Shaw (2000) study is that the lift force response may depend on learned size-weight relationships, whereas grip-size calibration is based on direct isomorphic visual/motor transformations. Potentially the reference to a 'learned relationship' between size and weight in the lifting measure is more dominated by the ventral stream on the basis of it utilising a long-term perceptual 'rule', rather than the direct transformation of size into action co-ordinates, which is suggested by Milner and Goodale (1995) to be dominant in the grasping measure. Support for this comes from the finding that the visual form agnosic patient 'DF', does *not* show evidence for a scaling between object size and lift-force, but *does* show grip-aperture scaling with object size (Dijkerman, McIntosh and Milner, unpublished data). This would implicate ventral stream involvement in the calculation of force required in lifting, which cannot be performed solely on the basis of the visual characteristics of the target.

Illusions of extent and location: effects of vertex coding

Coren and Girgus (1978) were one of the first groups of experimenters in the field of visual illusions to suggest that there may be a dissociation between the perception of extent and location. They suggest that some of the findings associated with the Mueller-Lyer illusion could be explained by this differentiation. Mack, Heuer, Villardi and Chambers (1985) investigated this issue explicitly by determining the different effect of the illusion on closed and open loop pointing. Their investigation suggested that "...spatial attributes bound together in Euclidean space, are not necessarily bound together in perceptual space". (p. 336). They argued that as extent is determined through exocentric coding of the relative separation of stimulus vertices, that if position was egocentrically coded then a change in relative exocentric position need not be accompanied by an egocentric shift (as evidenced by Bridgeman's work on the Roelofs effect). The authors argue that there is evidence for separate coding of extent and position. This may suggest that there are different processes associated with egocentric vertex position coding being utilised in a pointing paradigm whereas in perceptual measures it is the processing of stimulus extent that dominates. However their study also raises issues associated with the effect on prehension of the point of visual fixation. Their first study they found essentially no illusory effect when subjects marked (open loop) the vertices of the Brentano version of the Mueller-Lyer illusion (see appendix A, figure a6), whereas in a perceptual matching task a strong illusion was found. Mack *et al* suggested, however, that the visual fixation involved in the pointing condition (versus the 'whole perceiving' approach of the perceptual measure) could have accounted for the differential effect.

A second experiment manipulated the point of fixation (at vertex or non-vertex points within the stimulus) with brief exposures to prevent completion of saccades to vertices, the responses being made after stimulus offset. Perceptual judgements of extent (excluding vertex position as a cue) and 'pointing-like' responses (marking of the vertex position) of left and right vertices positions were conducted on Mueller-Lyer figures with inward and outward fins and a control figure with vertical fins. In the perceptual measure of extent, there appeared to be no effect of fixation point on the illusion magnitudes reported, however there was an effect of point of fixation in the pointing measure: greater illusion magnitudes where found where fixations were away from vertices. Even controlling for the larger illusory effect in the perception measure, fixation point had a significantly greater effect on the illusory magnitude in pointing compared with perception. The apparent higher salience of vertex fixation in the visuo-motor measure seems to suggest that 'vertex coding' may be a feature of this pointing task. It may be akin to the grasp-point coding suggested by Brenner and Smeets (1996) as a possible additional cue available to the visuo-motor system that is denied to the perceptual system.

Post and Welch (1996) also adopted an open-loop pointing paradigm (to preclude visually guided on-line corrective adjustments of the hand), by using virtual stimuli. In so doing they also controlled for effects associated with the occlusion of the inducing stimulus elements during prehension, although this was not a stated design aim (see Mon-Williams and Bull, 2000, below). In the first of a series of three experiments they employed the Brentano and Judd variants of the Mueller-Lyer illusion and a ballistic pointing .vs. perceptual measures paradigm. Virtual stimuli were presented using a semi-mirrored apparatus to ensure a clear view of the target stimuli without a view of the hand.

Using the Brentano illusion, perceptual judgements of the extent of the two shaft elements showed a significant illusion in comparison to a control figure, whereas when pointing to the stimulus vertices, there was no difference in response that could be attributed to the same illusory effect, thus indicating a dissociation of effect across conditions (essentially replicating the Mack *et al*, 1985, results). A second experiment examined the effect of the Judd illusion (see appendix A, figure a7) . This illusion has two noted effects. Firstly if a line bisection task is employed on the central bar of the array, this is usually biased in the direction opposite to that indicated by the arrow-head of the figure (i.e. a left pointing arrow head will cause a bisection bias to the right of true centre). If the displacement of the whole figure is examined, there is an illusory displacement of the whole figure in the opposite direction to that indicated by the arrowheads (i.e. to the right for an array with leftward pointing arrows). The study reported a strong illusion of the bisector position on a perceptual measure in the predicted direction but no reliable illusory effect on pointing to the bisection point. There was, however, a significant (although inferred) illusory shift of the entire figure to the right in the pointing condition (on the basis of an analysis of pointing biases to all the vertices of the control figure). However there was no measure of any perceptual shift of the entire figure with which the inferred figure-shift in the pointing condition could be compared. The relative magnitude of the illusory whole-figure shift cannot be compared across conditions and as such no investigation of potential partial dissociations were examined.

In the final experiment an equilateral triangle was used as the illusion-inducing stimulus. This causes a bias in a bisection of the distance between base to apex towards the base of the triangle (see appendix A, figure a8). In this array there was an illusory effect on pointing to the apparent bisector of the figure, as well as a perceptual illusion of the bisector. However once more there was no analysis of any difference in magnitude of illusion between the visuo-motor and the perceptual measure, although (if the figure presented is accurate) the perceptual measure appears larger. Again the study stopped short of discussing any potential partial dissociation in terms of magnitude of illusion on both measures, it merely illustrated that there were illusions present in both.

In summary the paper presents another pattern of results which suggest that visuo-motor responses are influenced by figural illusions, especially where the use of vertex coding as a cue has been minimised, but that there are different patterns of effect overall, as evidenced by the absence of an illusion in the pointing response in the bisection task.

Effects of delay on illusion magnitude

Gentilucci, Chieffi, Daprati, Saetti and Toni (1996) also investigated the effect of open and closed-loop reaching to the Mueller-Lyer with the illusion lines being presented along the sagittal plane with respect to the observer and used a pointing response. This study now controlled for, and manipulated, the latency between stimulus offset and response using 4 response conditions: full vision, no visual feedback (using virtual target in view throughout the reach but no view of hand during response) and two in complete open-loop (no view of either hand or stimulus), one with no delay and one with a 5 second delay. The pattern of results (illustrated in figure 1.5) seem to indicate two separable effects: an increase in illusion magnitude in the absence of visual feed-back (the full vision .vs. no-visual feed-back comparison) and an increase in illusion strength by introducing delays between stimulus offset and response (the open-loop 0 second delay .vs. the open-loop 5 second delay comparison).

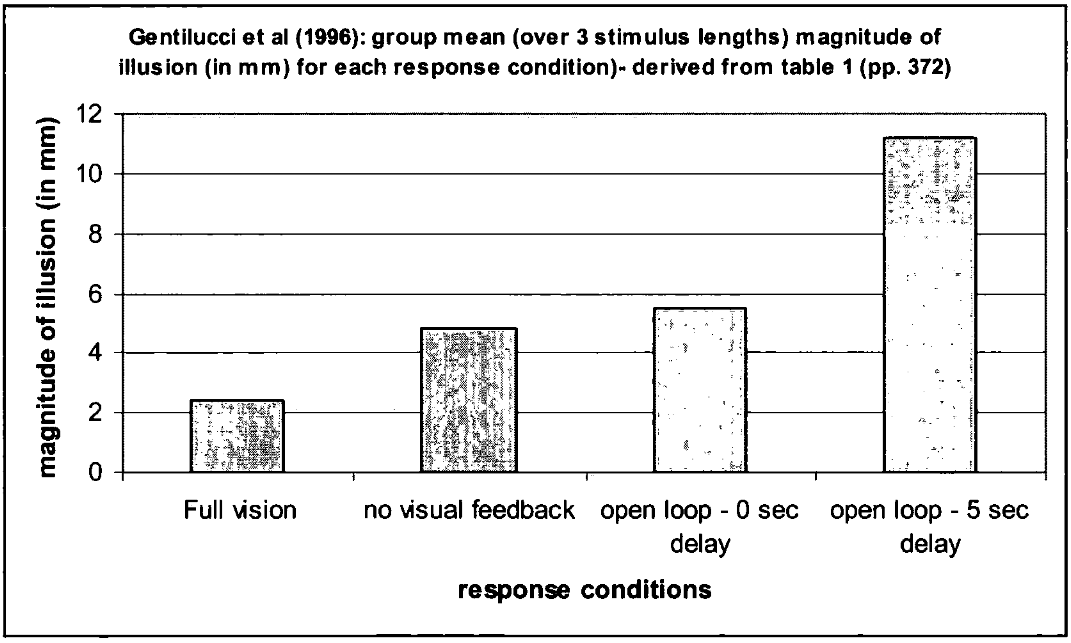

Figure 1.5: Group mean magnitude of illusion across response conditions derived from Gentilucci *et al* (1996).

The authors concluded that "...our data suggest the existence of the gradual cross-talking between 'perceptual' and 'pragmatic' object representation. This occurred when the efficiency of the egocentric frame of reference was correspondingly reduced". (p. 374). They also report that, although small, there was an illusory effect in the full vision condition but suggest that this may be due to "... that component [of the illusion] occurring in the early visual pathway" (p. 376): an issue that will be examined in some detail below.

It is, however, the pattern of change in the magnitude of the illusion across conditions that is notable, rather than the presence or absence of illusion in any one condition. A reliable illusion is found even in the full vision condition, suggesting a clear affect on the visuo-motor response. The study also gives some indication (although, without any explicit statistical analysis, this is conjecture) – that although the magnitude of illusion may be smaller in the full vision condition than in the 5 second delay condition, the difference between the no visual feedback condition and the complete open loop condition may be small – in terms of illusion magnitude at least. The difference between these conditions is that one is to a virtual target (target present, but no visual correction of hand 'in-flight') versus a real target in open loop (no vision of target or hand). The common factor is the absence of the ability to make visually-guided late corrections to the reach as the hand approaches the target. This finding may suggest that the magnitude of illusion in a prehensive response increases if visually guided correction is precluded; a further indication that illusions are acting in the visuo-motor modality, although in attenuated form where on-line correction is available.

In a follow up study Daprati and Gentilucci (1997) used the Mueller-Lyer illusion again, but used a grasping task as the visuo-motor measure, as well as a matching task (grip miming of the stimulus length) and an open-loop line drawing task. Stimuli were again presented along the sagittal plane, with the central bar of the Mueller-Lyer and control figures being a graspable bar of varying lengths. The study reports finding small, but statistically reliable effects of the illusion on the maximum grip aperture but larger effects in both the open-loop line drawing and a matching task. This pattern of results again seems to show that there was a quantitative rather than qualitative difference between tasks assumed to be perception-driven and visuo-motor. Although at first there again appeared to be a step-wise progression in the magnitude of illusion across conditions (grasping < line draw < matching) there was a significant tendency in the open loop drawing condition for all stimuli to be underestimated. If the results are re-examined in terms of the percentage error of the response to the control figure (a measure of the magnitude of illusion), there appears to be a differentiation between the non-prehensive measures in comparison with the grasping response (fig 1.6 below).

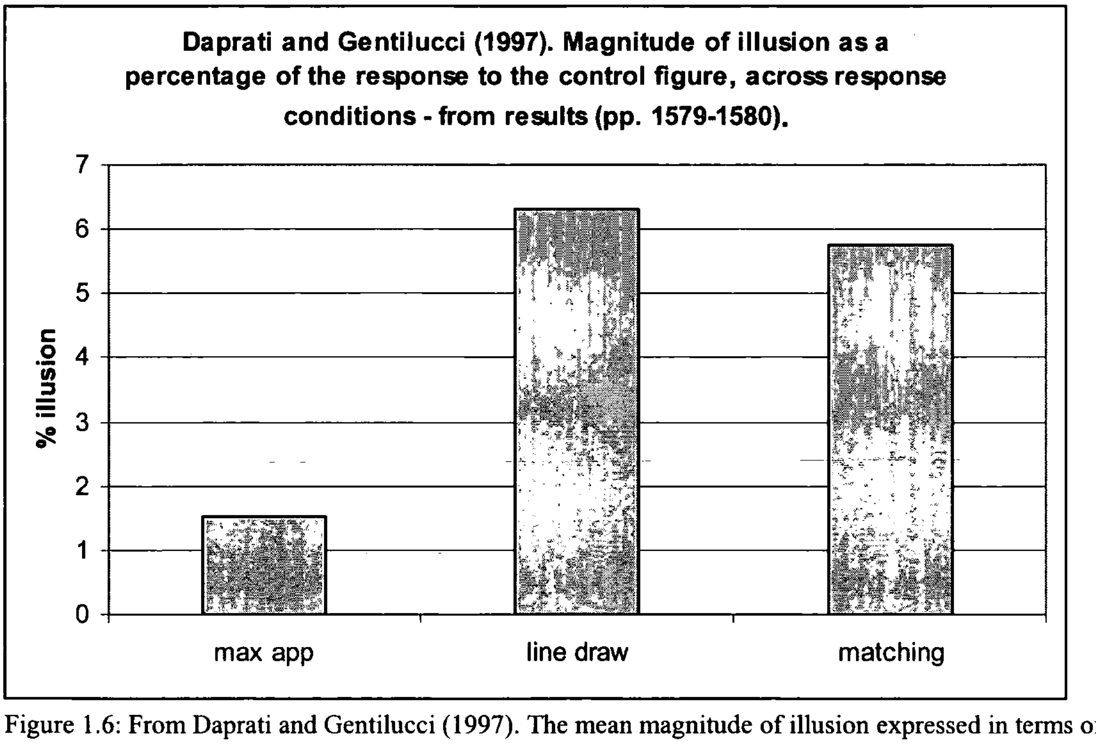

Figure 1.6: From Daprati and Gentilucci (1997). The mean magnitude of illusion expressed in terms of the difference between 'open' and 'closed' fin Mueller-Lyer stimuli as a percentage of the response to the control figure.

In terms of the percentage magnitude of error therefore (which controls for the underestimates in line drawing) maximum aperture in grasping is affected by the illusion, replicating the findings of effects in the action measure from the earlier study. However this effect appears far smaller than the resultant illusion in both line drawing and matching conditions. In the absence of statistical analyses, however, again this must be a guarded conclusion, but it fits the emerging pattern of results: illusory effects in visuo-motor responses, accompanied by larger effects in perception measures, and where delays between stimulus offset and response are imposed on visuo-motor tasks.

Westwood, Heath and Roy (2000) found that the Mueller-Lyer illusion affected maximum grip aperture in both open-loop responses with a brief delay (essentially the elapsed movement time), and with a longer (3 second) delay, but that closed-loop reaching was unaffected by the illusion. This might suggest that the online visual processing of veridical target dimensions can in fact render grip aperture refractory to the illusory effects, even though direct visual comparison between grip and target could not be effected at this early stage in the reach. However the authors also report the presence of a statistically significant illusory effect on even the open-loop, 'no delay' condition. The authors suggested that any reliance on memory of extent, caused an increase in the illusory effect on maximum grip aperture.

Of note was that once more there was an effect of the illusion in the predicted direction on closed-loop grip aperture, but because this failed to reach statistical significance the relative magnitudes of illusory effects between measures were not further analysed. This result suggests that the visual absence of the target during reaching causes a greater effect of the illusion even when minimal delays are imposed (cf. Gentilucci *et al*, 1996, above). It would appear, therefore, that the presence of illusory effects in action measures performed under these conditions may be explicable, at least in part, by a reliance of the motor system on the perception dominated, more persistent memory of target attribute (in line with the findings of Wong and Mack, 1981; Bridgeman *et al*, 1997). However, this and other studies (e.g. Aglioti *et al*, 1995; Gentilucci *et al* 1996, Haffenden and Goodale, 1997) have reported that there is evidence for some effect of the illusion even in closed-loop conditions. It would appear, therefore that even without delays, some illusory effects seem to be acting in visuo-motor measures.

Hu and Goodale (2001) presented subjects with three-dimensional virtual images of target blocks in an immersive 'virtual reality' environment. Each block was paired with an image of another block that was either 10% wider or 10% narrower than the target block. The distracter block was found to induce a strong 'size-contrast effect' in a perception measure (mimed grip): the target block was consistently judged as smaller when it was paired with the large block than when it was paired with the small block. However when subjects reached out to grasp the target object, maximum grip aperture was found to be reliably the same whichever distracter the target block was paired with. This task was, in effect, another replication of previous work (Aglioti *et al*, 1995, Haffenden and Goodale, 1998). However when a delay was imposed before response, it was found that the prehensive measure was now reliably influenced by the paired distracter in the direction predicted by a size-contrast effect. This was proposed to be more evidence to suggest the fast decay of the visual coding of size within the visuo-motor system, with the subsequent reliance on the more persistent perceptual coding of size which is subject to the size-contrast illusion.

In general these studies seem to indicate that the relative refraction of visuo-motor responses to illusory effects may be largely nullified where delays are introduced between stimulus offset and response.

Judgements of centre of gravity

Ellis, Flanagan and Lederman (1999) used the Judd variant of the Mueller-Lyer illusion and the Ponzo illusion (see appendix 1) to examine the difference between perceived centre of gravity of an object and the grip points selected by observers to give a 'balanced' grasp of an object. In one study a graspable bar formed the central element of the Judd figure, and in a separate experiment it was placed within the Ponzo figure so as to give the illusory appearance of a 'wedge' shape, i.e. with one end appearing thicker than the other. The study reports not only illusions in both grasping and perceptual judgements of centre of gravity, but strong correlations between effects across response conditions. In addition the study compared the illusion strengths across conditions and reported a reliably larger illusion in the perception measure than in the grasping measure, with the grasping measures being consistently nearer the veridical centre of the bar than the perception measures in both experiments.

The study also reported a left/right bias in the grasping task, which the authors attributed to the occlusion of the asymmetric Ponzo illusion, during the (right-handed) prehensive response. No evidence of bias is reported in the Judd illusion experiment. This study again points to a partial dissociation of illusory effect between measures, rather than assumptions of either a full or nil dissociation being present. The inclusion of the measures of correlation, in particular, shows evidence for strong shared effects of the illusion across conditions, especially in a visuo-motor task that requires the incorporation of inferences of distribution of mass before the 'calculation' of the point of grasp can be successfully achieved. As discussed above in relation to the Jackson and Shaw (2000) finding of illusory influences on lift-force, the Ellis *et al* results may perhaps be explained in terms of the visuo-motor task requiring reference to a 'rules base' to determine grasp points that bisect the centre of gravity, and that such a 'perceptual database' would be influenced by the illusion resulting in errors in a visuo-motor task. However it has been argued that the visual form agnosic 'DF' *does* accurately code the centre of mass in determining her grasp points to irregular targets (Goodale, Jakobson and Keillor, 1994). It could be argued that the task undertaken by DF could be said to represent a potentially different form of response: not the 'conscious' report of centre of gravity (via an instruction to perform a bisection task) but rather a more 'automatic grasp' of a small object where object shape is processed in determining the position of grasp, but without explicit calculation of the objects centre of mass. Reconciling the Ellis *et al* (1999) results and the neuropsychological evidence would suggest, therefore that such a task may be successfully achieved in the absence of an intact perceptual system, but that in the healthy subjects there is some, albeit reduced, influence of the illusion from the perceptual system spilling into the performance of the visuo-motor task. This again suggests that in the intact visual system we may expect some influence of illusions on visuo-motor acts, a point that bears on the subject of this thesis as a whole.

Ellis *et al* (1999) summarised their findings with the following point:

> "It may be that the action stream can more easily process, integrate, and utilise sensory information acquired by other modalities such as touch. It seems reasonable that, in a reaching and grasping task, visual and haptic information would need to be integrated for efficient object manipulation, but that this integration and upgrading need not affect the recognition system of either modality. In fact, such intersensory information would probably interfere with constancy mechanisms inherent in object recognition systems. *Thus while either a haptic or perceptual illusion would tend to be preserved across repeated presentations of the same stimulus, an inappropriate action would not*" (pp 114, italics added by RTD).

This would suggest that veridical feedback in visuo-motor measures might have the effect of reducing measured illusions in action measures. However if these cues *were* influencing the visuo-motor response then there should be some evidence to show a relatively smaller illusory effect in later trials than in earlier trials: on the basis that the latter trials were successfully incorporating the feedback to effect a more accurate response. Therefore in order to check for such feedback effects, analysis of any change in illusory magnitude over time is necessary (which was not the case in the Ellis *et al* study).

Mon-Williams and Bull (2000) followed up this study by using a large subject group (n = 101) and the Judd illusion in a design very similar to the Ellis *et al* experiment. Three conditions were used in the determination of the bisector of a bar distorted through presentation as the central shaft of the Judd illusion: perceptual judgement, closed-loop reaching and a form of 'open-loop reaching'. The study reported that there was a significant difference in magnitude of illusion between the perception and closed-loop conditions (supporting dissociation between the two measures) but that there was no difference between the perceptual condition and the open-loop condition. The paper argues that this points not to dissociation between perception and visuo-motor measures, but to a difference between the closed-loop response and both other measures. The authors suggest that occlusion of the illusion in the transport phase of the closed-loop reach was the critical factor in the reduction of illusory effect in this condition. However the open-loop response involved factors that may have introduced confounds. The response required was to reach under the supporting platform, hand unseen, to a point that the subject judged to be the mid-point of the stimulus that lay on top of the platform. The point of response is therefore offset from both the target object and the visual fixation point, and so only proprioception and motor efferent copy are available to guide this response, there is no access to egocentrically-coded visual space to inform the reach directly. In effect the response was a kind of 'pantomimed' pointing (a criticism echoed in Carey, 2001).

In a personal correspondence, the paper's first author reports that the correlation in illusion magnitudes between the closed-loop pointing task and the perceptual task (a verbal report) has $r^2 = 0.52$ (indicating some shared causal effect in both measures). This is much in line with results from Ellis *et al* (1999) which reported a coefficient of $r^2 = 0.44$ between the perceptual measure and the grasping condition. However the correlation between open-loop pointing and verbal report was $r^2 = 0.03$ (n.s.) and the correlation between closed-loop pointing and open-loop pointing was $r^2 = 0.07$ (n.s.). The absence of any evidence supporting a correlation between these measures (especially with such a large subject group) seems to indicate that there was little or no causal factor shared between the illusions found in the open-loop condition and either of the other two conditions (which *do* seem to share a common process). As such the lack of any statistical difference between the open-loop and the perception measure is more likely to have been the result of experimental noise (the experiment was conducted as part of a psychology undergraduate practical class rather than being laboratory-based) than an indication of different effects of occlusion of the illusion inducers across conditions. The study would appear to suffer from the very flaw which it suggests may have affected other studies in this area, namely that the response condition that showed the least parity with previous findings (the open loop 'pointing') showed effectively no relationship with either of the other two measures. Accordingly, it could be regarded as behaving in a way that seemed incongruous with both perception measures and other visually guided prehensive responses where egocentric coding of target position *was* available as a cue.

Absolute versus relative judgements

Vishton and Cutting (1995) reported a dissociation between visuo-motor and perception measures for the horizontal-vertical illusion (Avery and Day, 1969 – see appendix A, figure a9) whereby observers often report that a vertical stimulus appears longer than a horizontal stimulus of the same length. However a later study, reported in abstract form only (Vishton, Cutting and Rae, 1997), suggested that there was no illusion in either a visuo-motor or perceptual measure for either the Ebbinghaus or horizontal-vertical illusion where absolute measures were utilised: the perceptual report involved estimates not of comparative size of targets, but their absolute size in mm. However there was a strong (and equal) illusion in both perceptual *and* visuo-motor measures when the Mueller-Lyer illusion was the target stimulus. Vishton, Rae, Cutting and Nunez (1999) subsequently investigated not only the potential dissociation between perception and prehensive measures, but also the effect of adopting specific strategies in the perceptual measures that may be analogous to those dominant in visuo-motor responses. In experiment 1 they found a small but statistically significant illusion on open loop grasping: reaches to vertical elements being on average 3% greater than those to horizontal elements. In a judgement task a much larger illusion was found: one average vertical lines were judged to be 20% larger than horizontal lines. However the authors suggested that the two measures were not comparable in that the grasping response involved visually attending to a single stimulus (the line to be grasped) whereas the perception measure involved observers reporting the relative size of the two lines and expressing the size of one in relation to the other (a theme examined explicitly by Pavani *et al*, 1999; Franz *et al*, 2000, above).

A second experiment involved training observers to use a self-determined metric technique in line length perceptual judgements. Observers estimated line lengths in millimetres (with correctional feedback) for horizontal and vertical stimuli presented singly, then went on to apply the same technique to presentations of the horizontal vertical illusion. The authors report that the magnitude of illusion was now reduced to around 4% in this perceptual measure, which was attributed to the judgement of single stimuli using the trained technique. Effectively, the illusion magnitude had been reduced to the level of that found in the grasping condition through adoption of a technique that might be being applied during prehension – the use of a form of absolute metrics. A third experiment involved subjects marking a horizontal and vertical response line to indicate their perception of the extent of the presented stimulus elements of the horizontal-vertical illusion, but did not involve a training period or any corrective feedback. Under this condition an illusion of 10% was reported. In a final experiment the study presented a control stimulus of a square, and an illusory stimulus of an inverted triangle with base and height of equal length (essentially the horizontal-vertical illusion with vertices of the horizontal line joined to the end vertex of the vertical line).

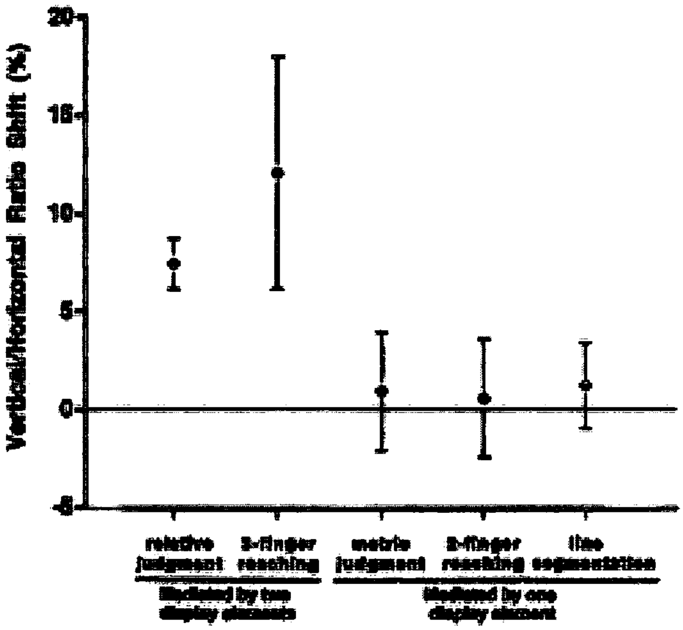

Figure 11. Percentage effect of the illusion on different size-mediated tasks. Both multiple target tasks indicate a large effect of the horizontal-vertical illusion (relative judgment and three-fingered reaching). All tasks that were mediated by a single element of a display were largely immune to the illusion (two-fingered reaching, metric judgment, and line segmentation). The gray line indicates the region of veridical performance; vertical error bars indicate ± 1 *SEM*.

Figure 1.7: From Vishton, Rae, Cutting and Nunez (1999), pp. 1669. The bars represent (from left to right) the group mean illusions in the conditions: relative judgement and 2-finger reaching (mediated by two display elements); metric judgement, 3 finger-reaching and line segmentation (mediated by one display element).

Five response conditions were examined: a relative judgement task (as in experiment 1), a three-fingered grasp with thumb on the bottom of the stimulus and forefinger and middle finger on the two upper vertices, a metric judgement (as in experiment 2), a two-fingered grasp (as in experiment 1) and a line segmentation task (as in experiment 3). The authors report that there is a clear difference between the illusion strength in the first two conditions which are 'mediated by two display elements' and the latter three conditions 'mediated by one display element'. They suggest that relative rather than absolute judgements are a key factor in the strength of illusion.

However there are issues that remain to be resolved before this interpretation of the dissociation can be accepted. Most prominently is that the illusion magnitude in the relative judgement is reported as being 8%, whereas in experiment 1 the same task yielded a 20% illusion. There is no explanation as to the large decrease in effect between these two experiments. One possible explanation may be that even in the relative judgement task observers applied some variation of the metric technique. There is no statement as to whether observers had taken part in earlier experiments, or on the counterbalancing of the 5 conditions. If metric judgement had preceded relative judgement for any subject, then they may have been applying some form of the metric technique in both measures. The second concern is regarding the three-fingered grasp condition. In the two grasping conditions, the magnitude of illusion is determined by the difference in response to the control figure (the square) and the illusion stimulus (the inverted triangle). In fact in neither the three nor the two finger grasp does the difference between horizontal and vertical achieve statistical significance (in the three finger grasp the difference is reported as reaching "$p = .05$" (p. 1670) and this is reported, by the authors, as being 'marginally significant'.)

The authors carried out additional analyses and found that although the vertical distance between the two fingers and the thumb did not significantly increase, the horizontal distance between the two fingers did significantly *decrease* between the control and the illusory condition. From this they reported a "clear effect of the horizontal-vertical illusion on this component of grip scaling" (pp. 1670). The authors had already reported that there was a difference between vertical distance between fingers and thumb and horizontal distance between fingers when the control figure was grasped. The authors reported that this was as a result of what they assumed to be a biomechanical artefact of this grip posture. As inter-finger distances and finger to thumb distances had a tendency to be inconsistent, the results of grasping the illusory figure may too have been influenced by this effect. Whereas there is consistent evidence to suggest the presence of a reliable correlation between maximum finger and thumb aperture and target size, the authors fail to provide any evidence to support their conjecture that the same relationship may exist between 1st and 2nd finger opening and target dimensions. This issue may have been further exacerbated by the fact that the key difference between the illusory stimulus and the control is a reduction in the horizontal dimension of the target (from a square to an inverted triangle) and it is only in this horizontal dimension that any reliable shift was found.

In summary the paper provides some evidence to suggest that an explanation of differential effects of the illusion on perception and grasping may be in terms of the incorporation of absolute and relative dimensions of stimuli in mediating the two responses. However the adoption of this particular grasping posture may have itself introduced factors over and above the potential effects of biomechanical constraints. Visual form agnosic 'DF' has been found to have finding difficulty with such tasks that require novel postures or strategies: she fails the 'T-posting' task (Goodale, Jakobson, Milner, Perrett, Benson and Hietanen, 1994) and 'X-grasping' (Carey, Harvey and Milner, 1996) This suggests that these tasks may again recruit the perceptual system, and they may represent paradigm cases of action requiring ventral stream participation.

At the theoretical level the study raises the issue of what relationship absolute and relative judgements have with visuo-motor control and perception respectively. Haffenden and Goodale (1998) suggest that "...perception typically involves relative not absolute judgements of object size" (pp. 131). As such it would appear that the metric techniques applied to perceptual judgements in the Vishton *et al* (1999) study that reduced the illusory effect may depart from the normally applied perceptual processes. This begs the question as to why such techniques are not more widely applied in perception. Haffenden and Goodale (1998) suggest that "...because perceptual representations, unlike goal-directed movements involve the analysis of the entire visual array, a metrically accurate representation would be computationally expensive" (p. 132). Bridgeman *et al* (1997) echo a similar sentiment "The price the cognitive system pays for gaining this sensitivity [...to small motions or translations of objects...] is that it loses absolute egocentric calibration of visual space" (p. 468)

Servos, Carnahan and Fedwick (2000) conducted a study using a similar design to that applied in the Vishton *et al* (1999) study (experiment one) but found a different result. A titrated 'perceptually equal/veridically different' version of the vertical-horizontal illusion was determined for each subject and maximum grip aperture was reported as being little affected by the perceived size of objects, but seemed dominated by the veridical dimension of the stimulus. Where the horizontal and vertical elements were the 'veridically equal/perceptually different', grip aperture was again guided by the actual, not the perceptual dimensions This failure to replicate the Vishton *et al* results suggests that some of the criticisms raised above may have been potentially confounding the results of the Vishton *et al* study. Servos *et al*, did not, however, report a comparison of grip aperture between a non-illusion control stimulus and an illusory array to determine if there was *any* illusory effect on grip scaling.

Interim summary: the visual illusion paradigm

Using figural illusions to determine their potential for differing effects on perception and action measures has produced a pattern of results that appears initially to be conflicting. However, as is often the case where a novel technique is applied in a number of studies, differences in method, design and the analyses may have been contributing towards the apparent 'mixed-bag' of results.

Some discernible patterns do appear to be emerging, however. There seems to be evidence that action measures are affected by illusions to some degree. There is consistent evidence for small effects on visuo-motor measures, even if in many cases these effects fail to register as 'reliable'. Where direct comparisons are made between measures using appropriate metrics to determine illusion magnitude, the pattern seems to be one of partial dissociation: with action measures being largely, but not completely refractory to illusory effects whereas measures of perception appear much more subject to the illusory effects.

One approach to trying to disentangle the effects that may be acting in these studies is to utilise illusions in a differing stimulus domain, to determine if the same patterns of effects emerge. One such area that has not as yet been examined extensively is that of illusions of visual orientation.

Orientation: A new domain for experimentation

The studies reviewed above have centred on visual illusions affecting the stimulus features of location and size. Two recent studies, however (both published after the experiments reported in this thesis were completed) have addressed the issue of visual orientation, one of the first features of a visual stimulus to be processed in early cortical vision. Van der Willigen, Bradshaw and Hibbard (2000) used two variants of the simultaneous tilt illusion (Gibson and Radner, 1937 – see appendix A, figure a10) to investigate their effect on a 'posting' visuo-motor task and a 'matching' adjustment task. The two variants of the illusion involved a 2-dimensional stimulus array with an annulus grating offset in orientation from a target grating to induce an illusory tilt of the target, and a 3-dimensional version that involved moving the annulus in the depth plane relative to the target grating (using stereoscopic viewing). In the 2-dimensional version they found equal effects of the illusion on both measures (although magnitudes are not reported), whereas in the 3-dimensional array there was a *larger* magnitude of illusion in the 'posting' measure than in the perceptual matching condition. Their results (briefly summarised in abstract form) suggested that there was a quantitative difference between the two measures, but that a qualitative difference between the two was not present. The finding of (presumably) significant and similar magnitudes of illusion in the 2-D version of the stimulus across both measures, is an apparent falsification of the suggestion that visuo-motor responses are refractory to illusory effects.

Another experiment, using the same illusion type, is reported by Glover and Dixon (2001) who compared hand posture with a perceptual measure of the simultaneous tilt illusion (STI). They investigated how an induced shift in the orientation of a 'handle' placed as the target stimulus embedded within a grating annulus of varying relative orientations changed abductive and adductive two-finger closed-loop grasping postures, on the basis of assumptions concerning end-state comfort (Stelmach, Castiello and Jeanerrod, 1994). The study reported that the illusory effects on both grip posture *and* a perceptual measure of illusion that were "quite similar". In a second experiment (examining the kinematics of hand movement) the authors reported that the illusory influence of the background appeared early in the prehensive response and diminished during the movement (presumably being corrected online, as the hand approached the target in full vision).

This and the Van der Willigen *et al* (2000) abstract seem to indicate a significant departure from previous studies – equal or even larger illusory effects on the visuo-motor measure compared with measures of perception. As such, both reports suggest this as evidence for an absence of a dissociation across the two measures. However this conclusion is predicated on the assumption that all illusions will have a similar pattern of differential effects on perception and visuo-motor behaviour and that the results of each illusory distortion are present either completely or not at all in the relevant cortical systems. It may be the case, however, that by examining the likely causal mechanisms of the illusions themselves, and the way that each of these distortions is likely to influence the two contrasted measures, that the perception vs. action model can make specific predictions in terms of both dissociation *and* association of illusory effects across perception and visuo-motor control.

Visual Orientation

The early cortical visual system must first identify then categorise contours, from the complex array of the stimuli presented to it. Contours are defined by patterns of either luminance, colour, or texture (the latter largely defined through micropatterns of luminance). Contour appears to be the basal unit in cortical visual processing and it has been suggested that even so-called 'subjective' contours share much of the post-V1 early visual system processing of 'objective' ones (Coren and Harland 1993, Van der Zwan and Wenderoth, 1995).

Hubel and Wiesel (1959, 1968) initiated the extensive research into the mechanisms for contour processing in the early mammalian visual system and the operation of channels selective to contours of specific orientations. These channels have direct neural correlates in the columnar structures of V1 (1968). Recent evidence suggests, however, that these structures are not as uniformly arranged (in terms of their orientation selectivity) as was initially suggested, but contain "...reversals, sharp jumps (fractures) and point singularities." (Das and Gilbert, 1999, p. 655). However it seems generally accepted that a degree of homogeneity of arrangement, in terms of their orientation sensitivities, is an established characteristic of primary visual cortex.

A notable feature of the mammalian visual system is the absence of strong evidence for significant sub-cortical orientation selectivity, although Daniels *et al* (1977) and

Levick and Thibos (1980) found evidence of some orientation biases in the lateral geniculate nuclei (LGN) of the cat. There is also limited evidence for some extra-striate orientation processing e.g. in the 'Blindsight' syndrome (Weiskrantz *et al*, 1974; Perenin, 1978) perhaps within V4 or parietal visual regions receiving direct thalamic inputs, and the potential effects of feed-back mechanisms (Ferster and Miller, 2000). However it can be argued that the principal processing of orientation is effected in striate cortex, and the results of this processing then radiate through to the higher visual areas via 'feed-forward' mechanisms (Hubel and Wiesel, 1962).

Electrophysiological studies involving selective deprivation during critical stages of development (Blakemore and Cooper, 1970; Blakemore and Mitchell, 1973) strengthened the suggestion that orientation sensitivity is achieved through the action of orientation selective neurones in the primary visual cortex and that the continued activation of cells with specific selectivities is required in order for them to develop or avoid atrophy. This work was conducted alongside studies that examined the proposal that orientation selectivity is enhanced through the action of lateral inhibitory connections between neurones maximally sensitive to similar orientations (Andrews, 1965; Blakemore, Carpenter and Georgeson, 1970, Blakemore and Tobin, 1972; Virsu and Taskinen, 1975; Nelson, 1991; Sengpiel *et al*, 1997). This suggestion is supported by Sillito (1975) who found that the blocking of these inhibitory connections broadened the cell's orientation tuning curve.

Ringach (1998) provided strong complementary evidence for inhibitory connections by showing a similar 'Mexican hat' distribution of orientation sensitivity (decreased sensitivity to non-targets close in orientation to targets) in human subjects who responded by button press to target orientations randomly inter-leaved within non-target orientations presented in rapid succession. The results mirrored the findings of the same rapid-serial visual presentation (RSVP) paradigm applied in electrophysiological recordings of monkey single neurones in primary visual cortex (Ringach *et al* ,1997). However Ringach (1998) reiterates the issue that there is still uncertainty over the extent to which feed-back mechanisms from later visual areas sharpen orientation tuning in primary visual cortex. The nature and function of intrastriate lateral connections has become a subject of some interest recently and it is suggested that longer dendritic projections may contribute to composite feature detection as well as more primitive characteristics such as orientation (Eysel 1999; Yabata and Callaway, 1999).

Howard (1982) concluded that no single, simple model could adequately accommodate the results of studies into orientation selectivity in primary visual cortex, and that adaptation, assimilation to principal meridia, and positional effects may all play a part. Complex iterative processing, involving feed-forward and feed-back mechanisms may be present within early visual systems and potentially beyond (Ferster and Miller, 2000). However, although almost certainly an over-simplification, the model of relatively broadly tuned inhibitory connections interacting with more selectively tuned excitatory responses of orientation specific cells in V1/V2 provides an elegantly simple model of how the observed precision in orientation sensitivity is achieved.

Tilt contrast and the simultaneous tilt illusion (STI)

The vehicle for much of the early research on lateral inhibitory connections was the tilt contrast effect whereby contour pairs forming an acute angle (between 5 degrees and 90 degrees) appear more obtuse, whereas obtuse angles (> 90 degrees) appear more acute (Carpenter and Blakemore, 1973). A variant of this effect is found when gratings of differing tilts are juxtaposed. The apparent orientation of each grating appearing to be mutually distorted away from one another (Gibson and Radner, 1937). This phenomenon (the simultaneous tilt illusion or STI see appendix 1) can also be demonstrated as a tilt after-effect (TAE) following exposure to an inducing grating. Initially it was claimed that the STI and TAE versions of these grating effects stemmed from different causal mechanisms (Campbell and Maffei, 1971; Parker 1972, Georgeson 1973). However these conclusions were challenged, and the differences between the effects of both illusion types reconciled, when gratings were matched for contrast, and sine-wave gratings were employed (Ware and Mitchell, 1975). Tolhurst and Thompson (1975) also suggested that both the STI and the TAE stemmed from the same causal processes, namely inhibitory/excitatory interactions between orientation sensitive neurones in early cortical processing. This view was supported by Magnussen and Kurtenbach (1980) who found linear additive effects between STI and TAE versions of the illusion. A number of successive studies drew similar conclusions about shared causal mechanisms of the two illusion types (e.g. Wenderoth, O'Connor and Johnstone ,1986; Wenderoth and Johnstone, 1988a and 1988b).

The causal mechanisms of these illusions are unlikely to be significantly optical or even subcortical in origin, as tilt contrast effects:

(a) are found to display inter-ocular transfer (Virsu and Taskinen, 1975);

(b) are present when no physical intersection between contours exists – either through omitting the vertex (Weale, 1978) or through the use of subjective contours (Smith and Over, 1976); and

(c) the effect increases with the degree of stereo-acuity of the subject (Mitchell and Ware, 1974; Ware and Mitchell, 1974).

Research into the STI also examined a smaller effect, analogous to the findings of tilt contrasts with obtuse angles – whereby if the difference between the central target grating and the inducing annulus is greater than 50 degrees, that a reversal of the normal 'repulsion' (direct effect) between gratings occurs. An effect is observed in which the grating orientations appear to mutually 'attract' and was named the 'indirect' effect (Gibson and Radner, 1937). This effect is smaller in magnitude than the direct effect and it is suggested to be the result of different causal mechanisms. Wenderoth and Johnstone (1988b) and Poom (2000) concluded that the direct (repulsion) effect was likely to be V1 centred and the result of inhibitory connections, whereas the indirect (attraction) effects "....occur at a higher level, possibly areas concerned with stimulus-specific interactions beyond the classical receptive field" (Wenderoth and Johnstone, 1988b). The suggested difference in magnitude of the two effects was proposed to be the result of additive effects of local and higher order orientation processing in the case of the direct effect, whereas the indirect effect was caused solely by processing in the higher visual cortices (Wenderoth and Johnstone, 1987). This suggestion was supported by the finding that presenting the STI within a frame aligned with vertical and horizontal negated the indirect effect, but had no effect on the direct effect magnitude (Wenderoth and Johnstone, 1988a; Poom, 2000). Furthermore, briefly flashed stimuli nullified indirect effects but not direct ones (Wenderoth and Johnstone, 1988a).

Evidence for dual orientation processing

Differential effects of stimuli placed outside the classic receptive field (CRF) in what has been termed the total receptive field (TRF) were proposed by Desimone, Schein, Moran and Ungerleider (1985) who argued that cells in IT may be concerned with global processing and constancy "...the sensitivity of most IT neurones to shape, appears based on a global property of shape, rather than the size or location of local contours." (Desimone *et al*, 1985 p. 449). Wenderoth and Johnstone (1987) cite this and other evidence to suggest that multiple mechanisms for orientation processing may interact, and that in certain circumstances (e.g. direct and indirect effects in the STI) these mechanisms may be differentially dominant.

The argument for inferotemporal 'reprocessing' of the results of the initial orientation mechanisms in early visual cortex in order to achieve the constancy mechanisms necessary for stable perception, sits well with the suggestion of different processing of position, size and shape proposed within the Milner and Goodale (1995) model. However, a potential criticism of this model is the apparent inefficiency involved in the reprocessing of such a basic characteristic. Milner and Goodale (1995) are suggesting, however that in effect the initial orientation processing is used as raw material for later computations. For visual perception this necessarily incorporates visual context in order to generate a stable and meaningful representation of the visual world (and as such demands the assimilation of higher visual processes to achieve this). Although such re-processing seems at odds with arguments centred on the efficiency of 'neural workload' this could be an indication of the necessary additional processing required to maintain a stable visual percept. Essentially, *constancy* is expensive in terms of processing but the costs are offset by the benefits of establishing a representation of the visual scene that is predictable (ref. Bridgeman *et al* 1997 above). As a consequence, these constancy mechanisms are potentially disruptive to visuo-motor planning and guidance as they are, by definition, a reinterpretation of the veridical stimulus characteristic. Access to both the 'unadjusted' and 'reprocessed' characteristic would be necessary to meet the demands of both visuo-motor and perceptual responses respectively, and as such may not be regarded so much as redundancy of processing, rather a generation of two representations required for two potentially exclusive ends.

The presence of visual orientation constancy mechanisms seems to be supported by our experience that head and body tilts do not result in profound changes in the orientation of our surroundings. However constancy mechanisms fail to adjust completely for body tilts as evidenced by the 'Aubert' and 'Mueller' effects (Howard, 1982). Judgements of vertical are biased towards small head tilts (Mueller effect) and away from the large tilts (Aubert effect). There is also physiological evidence for constancy mechanisms even in early cortical vision. Horn *et al* (1972) and Sauvan and Peterhans (1999) found small populations (c. 5% in the case of the latter study) of V1 neurones that retained selectivity for gravitational vertical even when the subject animals (cat and monkey respectively) were tilted. This would imply that vestibular processing is interacting either directly with striate neurones, or else via feed-back projections from higher visual areas. Sauvan and Peterhans (1999) also found significantly larger proportions of V2 neurones (40%) demonstrating orientation constancy effect. As such it would appear that again the assumption of a unitary mechanism effecting constancy is an over-simplification, but it appears tenable that such constancy mechanisms may be involved in visual illusions of orientation, where the array is suitably configured.

Potentially the direct and indirect effects of the STI would present a vehicle for examining their differential effects on measures of perception and visuo-motor control and the perception vs. action model would make novel predictions on their influence. The early sited direct effect, occurring, it is proposed, in V1/V2, should carry its illusory effects to both visual streams, and so it would be predicted to have an associative effect on perception and visuo-motor control. The indirect effect, proposed to be sited in higher visual cortex, potentially in IT (as may be inferred from the views of Desimone *et al*, 1995) should show the dissociative effect characterised by the number of studies using illusion paradigms (e.g. Aglioti *et al*, 1995 and others). However the magnitude of the indirect effect, although apparently robust, is consistently quite small, usually between 1 and 2 degrees or less (Wenderoth and Johnstone, 1988a; Poom, 2000) and is not reported to be present in all STI arrays. The psychophysical methods employed in previous studies can control for such small effects, but the inherent noise involved in visuo-motor responses may well swamp the indirect effect. However there is an alternative illusion of orientation that it is suggested may be based on a similar, higher visual system processing, which might present an illusory effect large enough to be effectively examined.

The rod-and-frame illusion (RFI)

Howard (1982) described the concept of 'frame of reference': "an attribute of certain objects which does not normally vary, and in terms of which variations of the same attribute in other objects perceived at the same time are judged" (p. 419). Asch and Witkin (1948) investigated the effects of distorting the normally reliable environmental cues to vertical by exposing subjects to a view of a tilted room. After a brief assimilation period, subjects' assessment of gravitational vertical was shifted 15 degrees towards the tilt of the 22 degree tilted room, but allowing a view of the tilted room within the context of a normally oriented environment reduced this effect to around 8 degrees. They also used a simple frame to induce a similar effect, although the effect was considerably smaller, and they noted large individual differences across the subject group.

After a lamentable period during the 1950s when these individual differences in the rod-and-frame test were correlated against personality traits, more controlled examination of the illusion subsequently resumed with theories relating to the causal mechanisms underlying the effect. Beh, Wenderoth and Purcell (1971) and Wenderoth and Beh (1972) suggested that subjects' responses in correcting the rod to vertical tended towards whichever frame axis (diagonal from each vertex or mid-line to opposing mid-line across the frame) was closest to vertical. Ebenholtz (1977) determined that it was the retinal, rather than the actual size of the frame that was the key determinant of the magnitude of effect, suggesting that a more pronounced framing affect was achieved by placing the frame further into peripheral vision.

However these early studies tended to use rods of lengths approaching the frame dimensions, and as such were likely to have confounded frame of reference effects with tilt contrast effects as a result of contour interactions between frame and rod.

Ebenholtz (1985) however examined the effects of both altering the rod lengths, and of removing frame edges and corners. He reported a significant reduction in the RFI magnitude (from 4.72 to 3.28 degrees of effect) between rods of length 95.5 cm (49.7 degrees of retinal arc) and 10.8 cm (6 degrees of retinal arc) when presented in a frame of 103.2 cm (55. 9 degrees of retinal arc). This is in line with the suggestion that large rods produce an additive effect between a frame-of-reference and a contour interaction between rod and frame. Removing either the frame corners or frame edges caused a reduction in magnitude of effect in both cases compared with the effect with a full frame (although only the long rod was used in this condition). This again supports the notion that the juxtaposing of frame and rod may cause a contour interaction, which is significantly reduced if portions of the frame contour are removed. It is notable (although not commented upon, nor statistically analysed by the author) that the magnitude of effect with the short rod (a group mean of 3.28 degrees) seems comparable with the magnitude of effects when frame edges or corners are removed (2.94 degrees and 2.52 degrees respectively). This observation again seems to support the suggestion that frame edge/rod interactions are a contributing factor if not appropriately separated.

More recently Zoccolotti, Antonucci, Goodenough, Pizzamiglio and Spinelli (1992), developing the work of Coren and Hoy (1986), found that the size of the gap between rod and frame for large (peripheral) frames was inversely related to RFI magnitude.

This again supported the suggestion that contour interactions as well as frame of reference effects were in evidence where the rod and frame had small separations. The same pattern of decreasing illusory effects with increased gap sizes was found for small (central) rod and frame arrays, with the absolute magnitude of the illusion being consistently smaller than that found in larger frame arrays.

Further support for the frame-of-reference effect is given by Di Lorenzo and Rock (1982) who used a double frame array. They report that with the inner frame tilted, no consistent illusion occurred, whereas if the outer frame was tilted this induced the predicted illusory effect, a finding replicated by Spinelli, Antonucci, Daini and Zoccolotti (1995). This latter study also found that presenting the rod and frame in a normally lit room abolished the effect for large frames with large separations between frame and rod. This again suggests that the presence of strong peripheral cues for vertical, in this case the walls and furniture, largely nullified the illusion. They also investigated the effects of double frames, finding that for arrays with small gaps between rod and frame, the presence of an outer frame at vertical/horizontal was negligible in terms of nullifying the illusion, whereas for large gap frames a significant nullifying effect was reported. This once more suggests that different causal mechanisms underlie the 'contour interacting' small-gap rod/frame arrays and the 'frame of reference' mechanisms involved in the large-gap rod/frame arrays. They concluded that "Therefore, it appears that the most peripheral stimuli determines contribution [sic] to the illusion of visuo-vestibular processing...this means that the most external frame of reference acts as a world surrogate" (Spinelli *et al*, 1995b, p. 1116).

The suggestion that the most dominant reference is the most peripheral 'frame' is strengthened by Ebenholtz and Utrie (1983) who found that the rod-and-frame effect was significantly reduced by placing a circular stimulus outside the frame. Thus it appears that the most peripheral stimulus has a dominant role in the illusory effect, even if this provides no orientation information. Spinelli *et al* (1995b) report a replication of this finding. It can perhaps be inferred that the outermost visual stimulus forms the most compelling global reference frame for visual orientation. If this outer reference is neutral, as is the case with the 'circular frame', then the perception of orientation returns to reliance on an unbiased, or at least significantly less biased, set of visuo-vestibular processes.

Zoccolotti, Antonucci, Daini, Martelli, Spinelli (1997) specifically aimed to address the potential differential effects of room lighting and frame sizes by again using the double-frame paradigm. They reported results that supported Di Lorenzo and Rock (1982) in that a tilted outer frame presented in the periphery (in 'dark-room' conditions) appeared dominant in influencing the perceived orientation of the rod surrounded by an upright inner frame. In fact the outer frame's effect was so compelling as to induce a perceived tilt of the inner frame as well. However this study also found evidence for the influence of the inner frame being dominant where small frames were presented in fully lit conditions.

It appears that the two key factors in ensuring the frame of reference effect is dominant in the RFI are the use of peripherally presented frames in 'dark room' conditions, and ensuring large 'gap' separations between rod and frame to exclude contour interaction as a factor.

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As with the STI, it is important to exclude, or at least identify, the likely influence of other potential mechanisms in the RFI. One such effect is torsion of the eye (rotation to match the orientation of a tilted scene) which may be a factor in the RFI in that such effects have been found in large visual arrays. However Goodenough, Cox Sigman and Strawderman (1979) suggested that torsional effects are likely to amount to around only 1 degree of effect, which does not account for the magnitudes of illusion associated with the RFI. Wenderoth (1973) argued that it was "...extremely unlikely that torsional effects can explain the present results..." (p. 247). Other factors may also contribute to the RFI effect, however, and Howard (1982, p. 423) concluded "...tilt adaptation, eye torsion and apparent body tilt contribute something to, but do not fully account for, the effect of a tilted visual frame on the apparent tilt of a rod. The other factor is presumably the subject's inability to dissociate non-visual impressions of gravitational vertical from cues provided by the visual framework.".

The 'frame of reference' concept as applied to the domain of orientation, echoes the same mechanisms suggested to be involved within the frame effects used by Bridgeman *et al* (1981) and Wong and Mack (1981) in studies which investigated perceived shifts in position. These studies were based on the same principles of perceptual processing being dominated by visual context, whereas visuo-motor processing use egocentric co-ordinates which are less influenced by 'peripheral' reference cues. Thus when examining the Roeloffs effect, Brosgole (1968) reported that placing a second, stationary frame, outside the shifting-frame surrounding the central stimulus, abolished the illusory displacement of the target stimulus. This appears to be acting much the same way that Di Lorenzo and Rock (1982), Ebenholtz and Utrie (1983), Spinelli *et al* (1995b) and Zoccolotti *et al* (1997) have found that when double-frames are used in the context of orientation, the most peripheral stimulus-element appeared to have the most dominant 'framing' effect on the orientation of the central rod.

The Milner and Goodale (1995) model of perception versus action makes specific predictions of a dissociation of effect between visuo-motor measures and perceptual measures where an illusion arises as a result of processes associated with perceptual 'interpretation' of a stimulus characteristic. It would appear that the 'frame of reference' effect represents a robust illusion caused by the integration of multiple sensory inputs: visual, vestibular, and potentially somatosensory. The key factor appears to be that in order to manipulate the visual context within which orientation is perceived, the influence of the most distal visual stimulus – the frame- is predominant. The perception vs. action model predicts that the visuo-motor system, which can code the orientation of the target within egocentric co-ordinates and can directly map this coding into co-ordinates for action, is less likely to be influenced by the peripheral frame.

Only one previous study has looked at the effects of a tilted frame on visually-guided action. Goodenough *et al* (1979) used a visuo-motor paradigm to measure the RFI, and found in a open loop (hand unseen) response of matching a hand held rod against a rod set within in a tilted frame, that consistent illusions were present. Critically, however, the rod was of such a length that the gap between rod and frame was less than one degree of arc, and as such a contour interaction as well as a frame of reference effect is likely to be involved (which, it is proposed, would have an illusory influence on the visuo-motor systems). Also no comparison of magnitudes of illusion between the visuo-motor measure and a perceptual measure are reported. An array with a frame in the peripheral extreme, and a small central rod, should allow the effects of frame of reference to be examined in isolation.

A note of caution, however, must be raised as there is as yet no direct evidence to support the conjecture that the RFI causal mechanisms are sited within the ventral stream. However, the frame of reference effect does seem a likely candidate to demonstrate dissociation in terms of the perception .vs. action model. Direct support for conjecture as to the siting of the illusion would preferably require either electrophysiological or neuroimaging evidence.

An electrophysiological investigation would involve the suggestion that an orientation sensitive visual cell in, for instance, IT would be influenced by the presence of a tilted frame surrounding a stimulus (outside the classical V1 receptive field, but within the large receptive fields typical of IT neurones). In contrast, an orientation selective cell in V1, or in a dorsal stream visual area, should be largely immune to a peripherally presented tilted frame.

Neuroimaging could potentially examine the same effect to determine the different activation attributable to the influence of the tilted frame on the rod, by partialling out the activation associated with the tilted frame alone, or rod alone (using a factorial design).

In the absence of such direct evidence for the 'siting' of the RFI, the argument for a prediction of a dissociative pattern of effects between perception and action must rely on the inferences drawn from the psychophysical and behavioural research reviewed above. It can be argued that this evidence suggests the RFI to be a likely candidate for a larger effect on perception than action measures.

Application of the STI and RFI to a perception vs. visuo-motor comparison

There seems strong evidence to support the suggestion that the illusory biases involved in the STI 'direct' effect stem from contour interactions sited early in visual cortex. As such, this illusion, according to the perception vs. action model, should show evidence of an association of effect between the two measures. Both perception and action should be subject to the mis-processing of visual orientation in early cortical processing that feeds-forward into both ventral and dorsal visual streams.

The key benefit of examining an illusion that is predicted to affect both visual streams is that it directly tests whether the intrinsic inequalities between measures of perception and visuo-motor control (which must, by definition, involve different response modalities to differentially tap the ventral and dorsal streams) can in themselves have been the determining factor in studies that have found different effects between the measures. Establishing evidence for an association of effect across measures would help allay concerns that previous reported dissociations are simply an artefact of effects associated with the different forms of response (e.g. Mon Williams and Bull, 1999).

In spite of the absence of direct evidence as to the causal mechanisms involved in the RFI, there are grounds to predict that the RFI, in contrast to the STI, would exhibit a pattern of dissociation between the two measures along the lines of previous investigations of different illusory effects on action and perception. However this is dependent on ensuring that the visual 'frame of reference' effect is maximised, and potential optical effects and contour interactions are minimised. The purpose of such an investigation would be to demonstrate a dissociative effect in the orientation domain. Combined with the STI, this would demonstrate that the causal mechanisms underlying visual illusions and their predicted affects on neural substrates, are a critical element in predicting the likely pattern of effects on action and perception.

The comparison of the predicted dissociative effects of the RFI and associative effects of the STI are, of course predicated on the assumption of different, and separately sited causal mechanisms. However, this assumption would not be unreasonable and has been made, explicitly or implicitly, by many other investigators:

"....tilt contrast [e.g. the STI] is an oculocentric shift arising in an early stage in visual processing probably in the primary visual cortex. The visual frame effect [e.g. the RFI] is probably not an oculocentric shift, but most likely depends on a higher level of processing involving the assessment of the orientation of objects relative to internal standards of vertical and horizontal" – (Howard, 1982, p. 156 – text in square parentheses added by RTD).

The visual illusion paradigm: Summary of methodological cautions

There seems to be consistent evidence that visual illusions do affect action measures. Even where these effects fail to reach statistical significance, there seems to be a consistent pattern across experiments that indicates a weight of evidence to support the presence of illusory effects on action. However the presence of an illusion in a visuo-motor response is not a negation of the suggestion for the different processing of visual information for action and perception. Depending on the causal mechanisms underlying the illusion, the perception .vs. action model would predict effects in visuo-motor measures if these mechanisms are likely to provide common inputs to both ventral and dorsal visual streams. Even where the illusory mechanisms are largely perceptual in nature, cross-talk between dorsal and ventral processing may result in some illusory effects in action, although under these circumstances it would be predicted that this should present in an attenuated form in the visuo-motor response. Another potential explanation could be that the downstream influences of illusory processing in inferior temporal cortex could feed back on processing in early visual cortical areas (as may happen with illusory contours), and thereby cause leakage of the illusory effects into the dorsal stream via these back projections.

Anatomical evidence from primates suggests that there are cross-projections between ventral and dorsal streams (Bullier, Schall and Morel, 1996; Distler, Boussauod, Desimone and Ungerleider, 1993; Ungerleider, 1995). Additionally there is evidence to suggest that assumed perceptual processing of illusory effects influences a number of even the low level kinematics of movement and may involve cross-talk between streams (van Donkelaar 1999, Lee and van Donkelaar, 2000). There is also neuropsychological evidence to suggest that object familiarity influences veridical grip scaling (e.g. subject 'AT', Jeannerod, Decety and Michel 1994).

Bridgeman *et al* (1997, p 496) concluded that "...the evidence for two distinct functional representations of visual space in humans is strong, but that the interaction between the systems is not as simple as it once seemed". Therefore, in the healthy observer, it may be more judicious to regard ventral and dorsal streams to be separable (in terms of their relative dominance in perception and action) rather than separate (which they may essentially be in patients with specific neuropsychological syndromes such as optic ataxia and visual form agnosia).

Causal mechanisms

If an illusion results from processing associated with early visual cortex prior to the main bifurcation between the split between ventral and dorsal streams, then illusory effects are expected to be acting on both streams and therefore may be expected to be found in both perception and action measures (a point mentioned in passing by Gentilucci *et al* ,1996). Few studies address the thorny issue of the underlying mechanisms that result in illusory effects. Many illusions may have a number of interacting causal effects, before the net resultant illusion emerges. Coren and Ward (1979) carried out an extensive analysis of a number of illusion types and their study concluded "Notions based on simple addition of illusory effects and on serial linear processing are not supported by these [their study] analyses" (p. 324). Depending on the relationship between these causal mechanisms and the assumed separable processing involved in perception and action, there are likely to be a complex series of effects that may vary by illusion type. Therefore the class and perhaps even instance of illusion may have different patterns of effect on perception and visuo-motor control. The presence of illusory effects in visuo-motor measures may be evidence of optical or early visuo-cortical processing which result in illusory effects, rather than arguing against the separability of the perceptual and visuo-motor systems.

The danger here, of course, is that such an argument could always be proffered in order to explain the presence of illusory effects in action measures. In order to address this issue directly therefore, there must be principled and *a priori* prediction as to the likely presence or absence of effects in both conditions as well as predictions as to the relative magnitude of these effects and the patterns of difference. The case argued above is that the STI should produce equivalent effects between measures, whereas the RFI should show a larger effect in a perceptual than a visuo-motor condition.

Statistical artefacts of experimental noise

If the effect of an illusion on a measure returns data with high variable error (i.e. less precise results), but with low constant error (i.e. more accurate results) this may give an overall pattern of data that suggests that there is no effective illusion in that measure. The consequence of such a spread of data is that it may result in a statistical artefact resulting from a higher noise to effect ratio: there is a reduced likelihood of a statistical test finding a reliable bias (constant error) because it is buried within the noise of variable error. If there are equal effects of experimental noise on two conditions then the measure with the greater magnitude of illusory effect may alone remain statistically reliable when tested. The condition with the lower magnitude of effect, when tested statistically, shows an absence of *any* illusory effect as a result of the higher noise to effect ratio. Therefore the failure of a measure to achieve a statistically significant illusory effect should not be taken as evidence of complete refraction to an illusion. A visuo-motor measure contains, by definition variability associated with the movement itself, as well as variability as a result of the precision of the data capture mechanisms for that measure. Measures of perception may be less prone to such artefacts. Visuo-motor measures are likely to return non-significant effects if the effect is essentially 'buried by the noise', resulting in the report of full rather than partial dissociations between perception and action. Therefore analyses must consider two separate issues: whether a reliable illusion is present in either condition, and whether there is a reliable difference in the illusion *magnitude* between measures. It is essential therefore that even non-significant trends in the direction of the illusion are included in analyses to determine the nature of the pattern of differences across conditions. This will reveal whether there may be consistent evidence for potentially small but consistent illusory effects in the action measures.

Strategies for reducing illusory effects in visuo-motor measures

Visuo-motor measures are likely to employ a cocktail of cues to achieve a successful goal directed act. Included within these may be coding of individual grasp point (as suggested by Brenner and Smeets, 1996), haptic feedback (Vishton *et al* , 1997), visual fixation of a vertex in closed-loop paradigms (Wong and Mack, 1996), online visual correction (Westwood *et al*, 2000). Other potential effects may be due to post hoc corrective adaptation of prehensive responses in the closed-loop condition, use of retinal after-images as a cue after stimulus offset where luminescent stimuli are employed and perseverative motor responses where appropriate counterbalancing is not employed. Where these cues are controlled as potential confounds, such procedures are likely to distil the resultant disparities between perception and action to a relatively small number of possible factors (one of which being potentially the different processing suggested to be dominant in each measure). As well as reducing confounds, this is likely to reduce the differential illusory effect between perception and action. Such controls almost exclusively focus on additional cues available for visuo-motor, rather than perceptual measures. Removing these cues may, therefore, actually increase the reliance of the visuo-motor system on perceptual mechanisms (which is the case where delays are introduced before the action response). The net result of such controls will be to reduce the difference in illusory effects between perception and action conditions, but are necessary in order to ensure a 'level playing field' for comparison.

Threshold for action and perception systems

A possible argument that could be raised is that there may be a higher threshold for stimulus movement in perception, perhaps as a result of active filtering processes associated with visual attention, than in visuo-motor measures which could be said to involve a small attentional focus on a small number of stimulus characteristics (i.e. those most pertinent to the motor act). However Bridgeman and Stark (1979) and Goodale *et al* (1986) found that observers failed to discriminate saccade-locked move/non-move trials when a criterion-free two-alternative forced-choice perceptual measure was used. This would suggest that even where the perception measure is specifically designed to capture awareness of movement at, or even slightly below, 'conscious' threshold, that this measure seems unable to tap the processing of movement that seems, nevertheless, available to the action systems. This would indicate that, in terms of the dissociation found for visuo-motor responses and perception during saccadic suppression, threshold elevation in perception is either unlikely to be a factor in explaining the differences found between measures, or represents an elevation in threshold of such an order that it indicates different processing of movement for perception and visuo-motor control.

An associated concern is that perceptual measures involve a greater shift in visual attention, in comparison with the motor measure (a goal directed act being, by definition, singularly focussed on the target stimulus). Potentially this shift in visual attention may be a confounding factor as in many perceptual conditions a large attentional shift is involved. As such, a perception measure without a shift in visual attention should be included as a controlling factor if at all possible.

Absolute vs. relative judgements

The application of specific metric strategies in perceptual judgements has been shown to reduce illusory effects. This seems to indicate that the perception system is flexible enough to adopt more veridical strategies than those spontaneously applied (Vishton *et al*, 1999). If individual observers adopt differing strategies for judgement tasks, the difference between perception and action measures is likely to be minimised. This is likely to be indicated by attenuation in the magnitude of perceptual measures of illusion. Where there is evidence that such strategies may have been adopted, caution should be exercised in accepting the lack of differentiable effect between perception and action.

Occlusion of inducing elements

Ellis *et al* (1999) and Mon Williams and Bull (2000) have suggested that during a reaching response illusory magnitudes may be affected if illusion inducers are occluded. As such, designs that incorporate either virtual displays (where the whole stimulus array remains in view throughout) or open-loop responses (with no stimulus in view during response) should be adopted. There are general concerns as to whether responses to virtual targets will engage the visuo-motor systems in same way as genuine objects, a point resolved to a certain extent in the Hu and Goodale (2000) study by having actual objects placed in real space at the point where the virtual targets were projected. However the related concern with open-loop reaching has been raised in that even short delays between stimulus offset and completion of the motor task may cause the action response to revert to the proposed more persistent perceptual encoding of the stimulus (e.g. Westwood *et al*, 2000). As such, delays between stimulus offset and response need to be minimised as far as possible.

Obstacle avoidance in prehension

Haffenden and Goodale (2000) have suggested that prehension, in particular grasping, is likely to take into account objects (both real and apparent) which are potential obstacles. As such the form of response and the design of stimuli arrays should ensure that the kinematics of response are not influenced by the presence of 'flankers' that could introduce such artefacts.

Point of visual fixation

Mack *et al* (1981) suggested that there are different illusory effects that might result from responding to a position that was not visually fixated (increasing illusory effects disproportionately in pointing measures). This may be the result of changes in visual acuity between foveal and para-foveal vision, for instance blurring has been proposed to increase the magnitude of the Mueller-Lyer illusion (Ward and Coren, 1976). Another factor may be involved in shifts in visual fixation itself if these are demanded by the response, e.g. where the perceptual measures requires the subject to perform an adjustment or assessment task at a point away from the target. A shift in gaze will introduce both optical effects (differing elements of the array passing across the retinae) and higher level effects ranging from processing associated with the gaze shift itself (e.g. saccadic suppression) to factors associated with shifts in visual attention. As such, in order to match the task demands of the two conditions, comparisons of action and perception measures which do not require a shift in gaze should be included in designs if possible.

Individual differences in the magnitude of illusory effects

A number of studies have noted the wide variation in tested populations in terms of the magnitude of illusion (Coren, Girgus and Erlichman, 1976; Coren and Porac, 1987), the latter study reporting negative correlations between illusion magnitudes and 'spatial abilities'. Bridgeman *et al* (1997) have reported suggestions of bimodal patterns of results in their use of the Roeloffs effect, suggesting that some subjects may have access to 'privileged' spatial information. Although the presence of individual differences introduces the problem of more widely distributed data, it also allows correlational techniques to be introduced when comparing across measures of perception and action where association of affect is predicted (unless the spread of data is as a result of random effects). If the neural processes associated with a specific illusion are suggested to be differentially involved in visual processing for perception and action then there should be little evidence of any form of correlation in illusion magnitudes across conditions. If, however, perceptual and visuo-motor processing share a common neural substrate in which the illusion is suggested to have its origin, then there should evidence of a strong correlation in magnitudes of illusion across measures. As such, individual differences in illusion strengths can act as a probe to determine whether the spread of results found in a subject group is suggestive of common or separate processing for action and perception.

Effects of perseveration in motor response

One artefact of the motor system is its tendency to perseverate if multiple consecutive acts are performed. In order to minimise this it may be advisable to include multiple 'filler' stimuli, preferably pseudo-randomised, to ensure that motor perseveration does not distort the comparison between the perception and the action measure (the latter being less likely to produce perseverative responses).

Titration of illusion magnitude

A factor related to individual differences in illusion strength is also the question of whether repeated consecutive exposures to illusions causes changes in illusory magnitude. Some studies (e.g. Aglioti *et al*, 1995) have determined an individual's illusion magnitude at the outset of an experiment, and then assumed that this illusion strength remains invariant throughout. Although there is no evidence to suggest that the illusion magnitude in the Ebbinghaus illusion changes over time, there is evidence that certain illusions do in fact reduce as a result of continued exposures (Glover and Dixon, 2001). As such, although appropriate counterbalancing should reduce these effects in term of their influence on the comparisons of dependent measures, some verifiable examination of the any changes in illusion strength should be undertaken to determine whether this has any artifactual effects on subsequent comparisons.

Assumption of illusory effect symmetry

Franz *et al* (2000) have found evidence for asymmetry in the Ebbinghaus illusion between annular arrays of small compared with large circles. Where magnitudes of illusion are being compared for a specific illusion type across two measures (e.g. perception and action) the stronger the illusion, the more likely it is that patterns of similarity and differences across measures will be reliably determined. One approach would be to determine, if there are asymmetrical effects, which of them is the larger, and then use this in the design of the stimulus array. Another approach is to compare two opposing illusion arrays not to a control figure individually, but to each other. As it is the magnitude of effect, rather than any underlying asymmetrical effects that are the subject of investigation, this technique would have the benefit of generating large illusion magnitudes, and partialling out asymmetries which, as well as magnitudes themselves, may be subject to individual differences. This may be particularly helpful where correlational analyses are intended, and reduces the likelihood of type II errors being introduced as a result of having to correct for multiple comparisons of effects in each direction. Of course there must be *a priori* predictions of illusion direction of each counter-acting array if the correct comparison is to be performed.

Biomechanical constraints

Servos, Carnahan and Fedwick (2000) when investigating grasping of vertical and horizontal lines suggested that the biomechanical constraints associated with hand posture appeared to make grasping of horizontal lines more difficult than vertical. As such, where grasping paradigms are employed it may be best to orient targets nearer to the vertical meridian rather than the horizontal.

Naivety of subjects

Although it may be the case that visual illusions are generally cognitively impenetrable (i.e. knowledge of the presence of an illusion does not influence the degree to which it is perceived) in general the naivety of subjects should be maintained as far as possible. Naivety can be assisted by using unfamiliar illusions (Otto de-Haart *et al* 1999) and through the inclusion of filler stimuli using differing configurations of targets and illusory inducers to ensure that subjects cannot 'guess' the veridical response.

Conclusion and the experimental questions

Carey (2001) suggests that there may be some publication bias against studies that have found effects in both perception and visuo-motor conditions. Even if this is the case, in the published literature there seems to be evidence that action measures are not wholly refractory to visual illusions. However if an assumption of partial dissociation is taken as the underlying theoretical context and studies specifically address the issue of relative magnitude of illusory influence (and devise comparable measures in order to achieve this) then a formal examination of this suggestion can be better examined.

The aim of the series of experiments reported below is to specifically address three questions:

1) to determine whether, in the novel domain of orientation, there is evidence to suggest differentiable effects of visual illusions on measures of perception and visuo-motor control.

2) to determine whether orientation illusions with differing causal mechanisms will have patterns of effect across perception and action measures that concur with predictions based on separable processing in ventral and dorsal visual streams.

3) to address a number of methodological issues that have been raised concerning the illusion paradigm, in particular to address the difference in task demands of perception and action measures.

Carey (2001) concluded his review of illusion studies by nominating a number of questions that could perhaps be addressed in the 'next phase' of experimentation in this area. The first of these was:

> "Are sensorimotor systems sensitive to certain illusions but not others."

This series of studies aims at determining whether or not this is the case. The underpinning theoretical predicate is that where causal mechanisms differ between illusion types, patterns of both dissociation and association across measures can be predicted through assumptions of differential dominance of ventral and dorsal visual streams in perception and action measures respectively.

Chapter 2: Study 1 - The simultaneous tilt illusion (STI)

Introduction

The illusion studies that have investigated perception and action (e.g. Bridgeman *et al*, 1981; Aglioti *et al*, 1995; Gentilucci *et al*, 1996) have been based on predictions of dissociative patterns of effect between the two conditions. The underlying expectation in these studies has been that the illusions studied will have a greater effect on measures of perception than on visuo-motor control. The Milner and Goodale (1995) model predicts that visuo-motor measures will be refractory to contextual illusory effect as they have access to egocentrically coded metrics that can be used to generate the visuo-motor response, and are therefore not influenced, or not *as* influenced, by the illusory inducing elements: the frame in the Roelofs effect; the annulus of circles in the Ebbinghaus illusion; and the angular vertices of the Mueller-Lyer illusion.

It is proposed, however, that there are classes of visual illusion where the perception .vs. action model would predict a pattern of *association* between measures. If the causal mechanisms of the illusion are sited early in the cortical visual system, before the bifurcation of the visual system into the ventral and dorsal streams, then the measures proposed to be differentially dominated by each stream should be affected an equal degree, or at least in a manner which demonstrates a degree of shared causality in terms of illusion strength. It is proposed that the simultaneous tilt illusion (STI) is an example of such an illusory effect. There seems to be strong and convergent evidence that the action of lateral inhibitory interactions between orientation selective neurones in V1 explains many of the observed characteristics of the illusion (e.g. Tolhurst and Thompson, 1974). This, and the suggestion of largely feed-forward mechanisms from primary visual cortex (Hubel and Wiesel, 1962) to the higher visual areas, would suggest that neither the perceptual nor the visuo-motor systems would have access to unbiased encoding of visual orientation where the STI is presented. Van der Willigen and Bradshaw (2000) and Glover and Dixon (2001) have reported results which support the suggestion that visuo-motor measures are prone to the STI, although there are no reports in these studies of specific analyses of the potential associative effects between measures.

The Milner and Goodale (1995) 'perception .vs. action' model suggests that in order to differentially tap these two systems, the response modality must be designed to maximise the use of the different visual information derived from these two sources. In order to tap the dorsally-mediated action systems, responses must be in real time, based on egocentrically-coded visual information, and directed towards the stimulus within egocentrically coded space. In order to tap the ventrally mediated perceptual systems, responses must be biased towards extraction of information from higher level 'scene based' analyses and preclude the use of egocentrically coded cues. This can be achieved by introducing delays between stimulus offset and response, it being suggested that the encoding in the dorsal stream decays quickly, and so latencies between stimulus presentation and response cause a reliance on the more persistent coding of the perceptual system (Westwood *et al*, 2000). Another method for tapping the ventral mediated systems is by denying contemporaneous use of egocentrically defined space as a response cue in the perception measure through responding without a 'goal directed action' towards the stimulus. A common mechanism for achieving ventral stream dominance is to use a 'pantomimed' response, whereby the response is made in a different location from the presented stimulus. It is suggested by, amongst feed-forward mechanisms from primary visual cortex (Hubel and Wiesel, 1962) to the higher visual areas, would suggest that neither the perceptual nor the visuo-motor systems would have access to unbiased encoding of visual orientation where the STI is presented. Van der Willigen and Bradshaw (2000) and Glover and Dixon (2001) have reported results which support the suggestion that visuo-motor measures are prone to the STI, although there are no reports in these studies of specific analyses of the potential associative effects between measures.

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Neuropsychological studies of optic ataxic (Perenin and Vighetto, 1998) and visual form agnosic subjects (Goodale *et al*, 1991; Milner *et al* 1991), have suggested that the processing of visual orientation may be differently processed for perception and visuo-motor control. The method adopted in these studies was to 'post' either the hand, or a hand-held card, through a slot of varying orientation to determine whether the two syndromes showed different patterns of deficit and preserved abilities. These studies reported evidence for relatively preserved processing of visual orientation in perceptual measures in comparison with visuo-motor measures in the case of the optic ataxic group and evidence for the opposite pattern of deficit and preserved abilities in the visual form agnosic 'DF.

A key issue in adopting a similar paradigm with subjects without visual deficits is to preclude the visuo-motor response from being informed by means of a simple visual comparison between the stimulus and the effector in the closing stages of the response. Jeannerod (1984) suggested that a prehensive response could be regarded as involving two stages: a high velocity transport phase and a slower, more precise 'closure' phase. However a difference indicating a more accurate action measure over perception could always be predicted solely on the basis of on-line correction during the closure phase of the visuo-motor measure if the response is performed in full vision. In order to successfully utilise a 'posting' response with healthy subjects (

similar to that used by Perenin and Vighetto,1988 and Milner *et al*, 1991)) it must be performed without visual feedback, or 'open loop'.

A 'pantomimed' matching of the target orientation should, it is proposed, be dominated by the perceptual systems of the ventral stream. However to ensure equivalence of access to available cues, this would need to be performed in a similar, open-loop, manner: i.e. after stimulus offset.

The Milner and Goodale (1995) model predicts that the STI will show evidence for a strong illusion in both a visuo-motor condition and a perceptual condition, on the basis of the siting of the causal mechanisms involved in the STI being in early visual cortex. Furthermore, in examining the magnitude of illusion between conditions for any one subject within the experimental group, there should be evidenee for an associative effect in the magnitude of the illusion across conditions.

Method

Subjects

The subject group consisted of 10 right-hand dominant subjects (6 females and 4 males) in the age range 23 to 52. All had normal or corrected to normal visual acuity, reported no motor or visuo-motor deficits and all subjects were naïve to the illusion and the nature of the experiment.

Stimuli

All stimuli were circular monochrome grating patterns of 74.6 mm in diameter (the target grating) surrounded by an annulus of a monochrome grating of the same frequency, with outer diameter 115mm (the inducing grating). The grating frequencies were 0.5 cycles per centimetre, which matched the width of each white/black element of the grating with the width of the plastic card used in the response. (see appendix A, figure a10 for an illustration)

In referring to the orientation of targets and responses, all orientations are described with the left-hand horizontal meridian (as viewed by the subject) acting as the meridian. As such a vertical orientation is described as "90°", one which is 4° anti-clockwise from vertical is described as "86°", one 12 degrees clockwise from vertical is described as "102°". A variety of STI arrays were presented, each consisting of a target and annulus grating. Each variation of the array is labelled by specifying the orientation of the annulus grating then the target grating. Thus a stimulus with a 102° annulus and 90° target is labelled "102/90".

In order to preserve the naivety of subjects to the illusion, to minimise effects of motor perseveration, and to produce control data, a number of stimuli were presented.

The stimulus set consisted of 7 stimuli:

Two **goal** stimuli – with a vertical target grating (90°) and an annulus grating of either 78° or 102° ("78/90" and "102/90").

Two **filler** stimuli – "102/86" and "78/94"

Three **control/filler** stimuli – "90/90", "86/86" and "94/94".

All visual stimuli were created using the PC graphics package *Paint Shop Pro* (version 5.01). Gratings were not true square wave gratings because, as a result of the achievable resolution of the monitor and presentation software, the use of anti-aliasing was necessary to smooth the 'jaggies' (the stepped edges on inclined elements that result from the size of the screen's square pixels). Presence of jaggies would have clearly differentiated vertical from inclined elements of the stimuli. Anti-aliasing involves applying a stepped grey-scaling to the edge of inclined figures to produce a 'best-smoothing' of inclined lines and so has the result of producing slightly 'round shouldered' rather than square-wave grating profiles.

Apparatus

Stimuli were presented on a high-resolution Sony Trinitron MultiScan 400PS monitor using the 'Psyscope' (v 3.1) stimulus presentation software running on a Macintosh PowerMac 7100. A visual mask in the shape of a torus was attached to the front of the screen of the monitor to ensure that the monitor and screen edges did not provide vertical or horizontal cues (see figure 2.1). The mask was positioned so as to be centred on the stimuli, with the mask's central circular aperture being 50mm larger in diameter than the stimuli. The screen was 49 cm away from the nearest edge of the chin rest, which was used to control subjects' viewing distance and angle. The target grating centre, mask centre and central point of the chin rest were aligned so as to place the centre of the stimuli along the subject body centre-line.

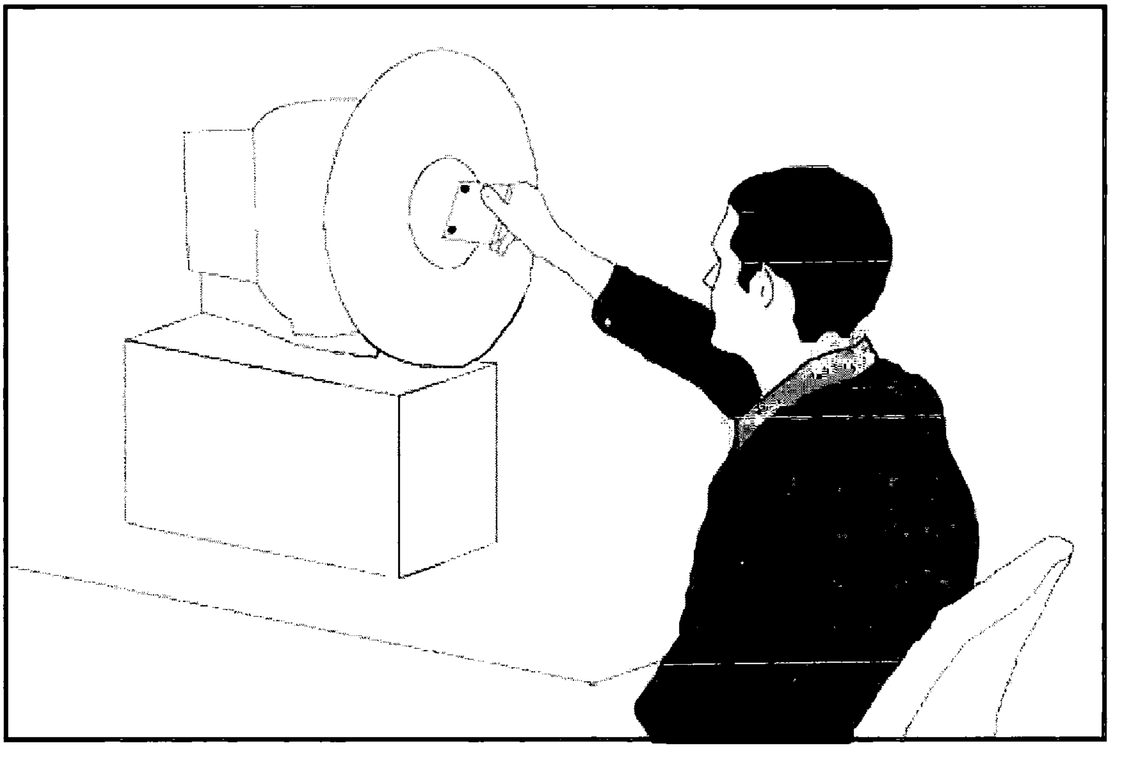

Figure 2.1: Schematic of the visuo-motor 'posting measure'. Note that this illustration does not include the use of a chin-rest, which was used throughout testing.

The visuo-motor response to target orientation was made by reaching out to 'virtually post' a black plastic palette (90 mm by 90mm by 10mm) 'through' the central target grating. Two infrared emitting diodes (IRED markers) were attached to the left hand side of the palette (facing the movement tracking system) towards the front edge. The position in 3D space of these IREDs was recorded throughout each response using a Northern Digital Inc. *Optotrak* system sampling at 100hz. The starting position for the palette for each trial was a marked point on a small raised plinth 3.5 cm above the table height, 10cm to the right of body centre line and 30cm forward of the chin rest.

Design

The dependent variable was the magnitude of illusion in the two conditions: posting and pantomime ('mime'). The dependent variable was calculated by the difference between the mean response to stimuli 102/90 and 78/90 for each subject. This difference, rather than the differences between 102/90 and 90/90, and 78/90 and 90/90 was selected because it both gave a greater magnitude of effect with which to examine the correlations, as well as controlling for any potential motor or visuo-motor biases which may have been affecting subject performance clockwise and anticlockwise from vertical (see chapter 1).

Procedure

Trials were run within 4 blocks with 42 trials in each block. Block order was counterbalanced across subjects (ABBA/BAAB) by response condition (A = post, B = mime). Each block comprised of 6 trials per stimulus completely randomised within the block using the *Psyscope* randomisation facility. Prior to each trial the presentation software (*Psyscope*) displayed the form of response required ("towards" or "mime") in the centre of the visual mask. This acted as both a reminder to the subject of the response type required and as a centralised visual fixation point for the subject. Each trial was initiated by the subject clicking the Macintosh mouse with their non-dominant (left) hand. The stimulus was then presented for 1000 msec, then a visual noise pattern (consisting a random pattern of lines of varying orientations) was presented for 100 msec to reduce the likelihood of the retinal afterimage of the luminescent stimulus acting as a cue. This was followed immediately by a tone that was the subject's cue to respond. Subjects therefore did not initiate their response until after stimulus offset.

Subjects were informed that they should proceed at their own pace throughout the testing session, and that in addition to breaks at the end of each trial block, they could take breaks within blocks if desired (none found this necessary). Subjects were asked to respond as soon as they heard the tone and to ensure that they fixated the screen until the tone sounded, when they were to execute as quickly, accurately and naturally as possible the response required.

In the 'posting' condition subjects were asked to perform a 'virtual-posting' task – to imagine the central target grating as a slot through which the palette should be posted by orienting the palette by rolling the wrist (with as little shift in yaw as was natural). An adhesive gum ('Bluetack") was placed along the front of the palette to allow the subject to maintain the orientation of the palette against the screen until the end of the trial when a tone sounded and the subject returned to the starting position. The experimenter initiated the *Optotrak* sample on the appearance of the target stimuli and observed the subject to ensure that they did not initiate response until the response tone sounded. For each trial the sample data was 300 frames (= 3000 msec in duration) The dependent variable was taken as the mean of the final 50 frames (500 msec) of the *Optotrak* sample, i.e. the final orientation of the palette as it rested against the (blank) computer screen.

In the pantomime condition the presentation of stimuli and visual mask and response cues were identical to the posting condition. Subjects were informed that on hearing the tone that they should 'mime' the orientation of the target grating by inclining the palette either left or right with the base of the palette remaining on the plinth. Subjects informed the experimenter when they were satisfied that they had the orientation correct, then a 1000 msec (100 frame) sample was taken of this orientation whilst the subject held the palette steady. The angle of response was taken as the mean of the 100 frame (1000 msec) sample. A larger sample for the pantomime condition was taken to ensure that any slight movement of the palette during the recording phase did not distort results.

Prior to the bona fide testing session subjects performed two training blocks (counterbalanced across subjects by response mode AB/BA) for each response type in which they were presented with each stimulus twice (presented in randomised order) i.e. 14 trials per practice block. At the end of each testing session subjects were invited to repeat the practice if required (none found this necessary).

Following each trial session subjects were asked if they had adopted any specific strategy to achieve the task. In particular whether there were any visual cues such as retinal after-image of the stimuli themselves that might have created uncontrolled effects.

The Optotrak data were passed through a 10 Hz Butterworth second order filter, then through the *DAP* utility from *Northern Digital Inc.* to extract the angle subtended by the line joining the two IREDs and horizontal (i.e. the orientation of the palette with respect to horizontal).

Results

The study hypothesis was that there would be significant and related magnitudes of illusion in both the posting and pantomime conditions. First it must be established that there are reliable and predicted illusory effects of the illusion itself. The predicted illusory effect is the 'direct' or 'repulsion' effect of the STI, so it would be predicted that responses to the vertical central target grating would be biased away from the orientation of the inducing annulus.

In the posting condition, using a paired-sample t-test, the comparison of mean responses to stimuli 102/90 and 78/90 was found to be reliable and in the direction predicted: $t(9) = 6.33$; $p < .001$ (one-tailed). For miming the same also returned a reliable difference: $t(9) = 4.36$; $p < .001$ (one-tailed). It appeared, therefore that the STI was strongly influencing responses in both measures.

Following this the magnitude of illusion was calculated by subtracting, for each subject, the mean response to stimulus 78/90 from that to 102/90. Table (2.1) illustrates the illusion sizes for the group, figure 2.2 illustrates the group summary of the results.

Subject	Condition miming	posting
1	2.79	3.79
2	5.98	5.35
3	3.67	5.02
4	3.32	7.48
5	7.73	5.69
6	0.57	2.25
7	11.64	11.55
8	3.19	4.16
9	1.13	11.43
10	8.38	5.25
mean	4.84	6.20
s.e.	1.11	0.98

Table 2.1: Individual magnitudes of illusion in degrees (calculated by response to stimulus 78/90 minus response to stimulus 102/90) for the STI in the miming and posting conditions, group mean and standard error of the mean.

The data seem to indicate that there are two subjects who demonstrate particularly high magnitudes of illusion in the posting measure (subjects 7 and 9) and that in addition subject 7 also shows a particularly strong illusory response in the miming condition. Also of note is that taking the mean of the group, the effect on the visuo-motor measure appears to be stronger than the perception measure. However a statistical analysis of the group means for illusion magnitudes shows that there is not a reliable difference between the two conditions: $t(9) = 1.15$; n.s. two-tailed, pair-wise comparison.

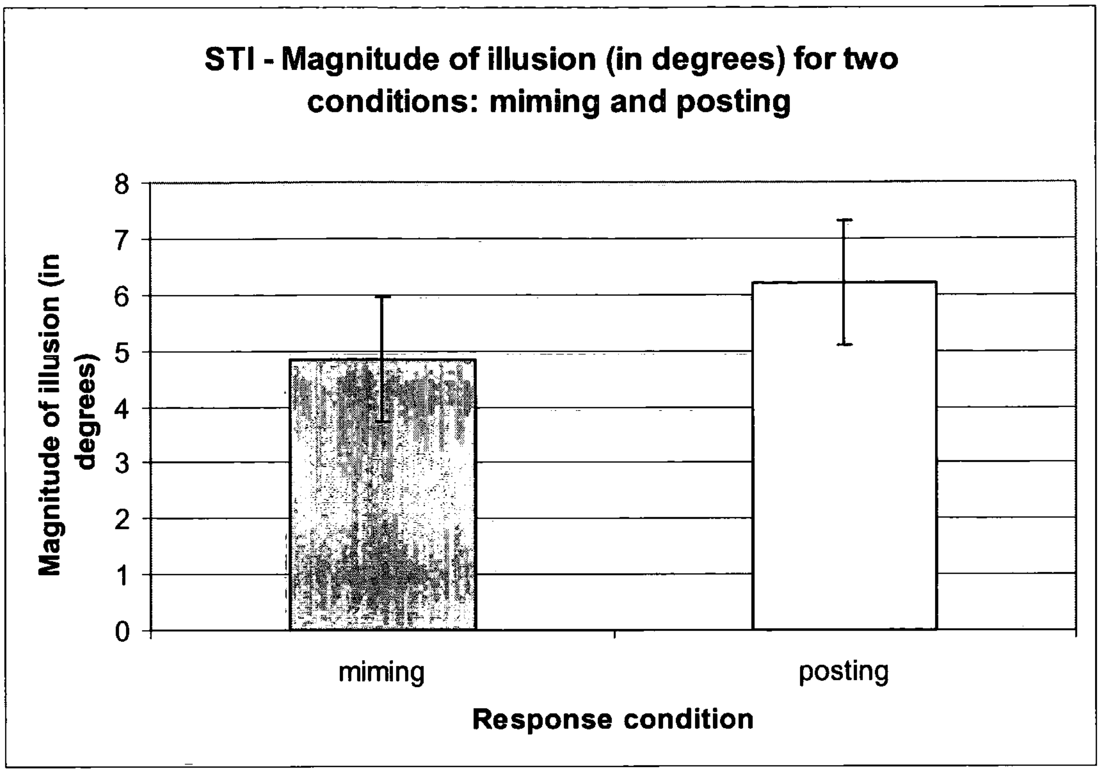

Figure 2.2: Mean magnitude of illusion calculated by response to stimulus 78/90 minus response to stimulus 102/90. Error bars represent one standard error of the mean.

The comparison of group mean magnitudes of illusion across conditions seems to indicate that both the visuo-motor and the perceptual measure are influenced strongly by the illusion. The spread of magnitudes amongst the group suggests that there may be some individual differences in terms of illusion strength and so a correlation of the illusion magnitudes across conditions was performed. However this indicated a weak and non-significant positive correlation: Pearsons $r(9) = .365$; n.s, one-tailed. The results therefore indicate that although both measures are influenced by the STI, that there was not a sound basis for inferring a common causal mechanism underlying the spread of illusion magnitudes within the group.

Discussion

This study had proposed that the STI would influence both visuo-motor and perceptual measures equally. This hypothesis seems to have been supported, with evidence for strong illusions in both conditions. This finding is in line with the reports from Glover and Dixon (2001) who found strong effects of the STI on visuo-motor measures. It also is in line with the findings of Van der Willigen and Bradshaw (2000) their examination of the 2-dimensional version of the STI.

However the weak and non-significant correlation between magnitudes of illusion across conditions does not provide reliable support for the suggestion of an association of effects between measures. However the presence of some positive relationship between posting and miming responses suggested that this might be worthy of further examination.

A number of methodological issues were raised by the study. Most significant was the miming response, which subjects reported as being particularly awkward. Subjects reported that they found it difficult to view the orientation of the palette from their position in the chin-rest, and the shift in gaze from the computer monitor to the plinth where the palette rested was reported as making the response difficult to perform. Also there was a disparity between conditions in the latency between stimulus offset and the sampling taken as the response. The miming condition required the subjects to adjust the palette, then indicate that it had reached the intended orientation, whereas the posting response was initiated as soon as the response cue sounded. As such the latency between stimulus offset and response in the miming condition was likely to have consistently greater than in the posting condition.

Two subjects, and the experimenter, noted that although the presentation of the visual noise pattern initially cleared any retinal after-image, that after a short delay the after-image re-appeared. The significance of the after-image as a cue is uncertain although it did not seem to act as a particularly strong veridical cue as illusory effects appeared consistently in both conditions. Of more concern is whether it may have had a different affect on the two conditions, with the latency difference between the two conditions coming into play. Potentially the returning retinal after-image may have acted as a stronger cue to the miming condition than the posting condition.

A further issue is that of the degree of proprioceptive feedback available in the mime response. Subjects had their hand placed on the raised plinth, and tilted the palette with thumb and forefinger. Essentially they had a constant proprioceptive cue for horizontal throughout the mime condition that was not available in the posting condition. The decision to perform the miming condition without lifting the palette was made after a short pilot study where it was found that holding the palette at the required angle for the sampling period produced particularly noisy data. However there was a concern that the imbalance of potential cues across conditions again favoured the miming over the posting condition.

It had been assumed that having the palette rest on its 10 mm edge on the plinth at the start of every trial would ensure that the starting orientation of the tablet would be controlled. However there was a considerable variance in the starting orientation because subjects were actively holding the tablet which inevitably meant that they would incline it slightly from its flat edge. This meant that the starting orientation could vary: in one case (subject 2) initial orientation of the palette varied between 74° to 104° . Although this would have little effect on the mime response, it could affect the early part of the posting response.

A final point is the latency between the visual target offset and initiation (and completion) of response. It is known from previous studies (Goodale *et al*, 1994; Rosettti, 1998, Gentilucci, 1986, Westwood *et al*, 2000) that introducing delays in responding to visual stimuli may result in the relative dominance of the perceptual systems over the visuo-motor systems. In our study's design, the latency between the removal of the stimulus and initiation of the response was up to 300 msec in some cases (100 msec for presentation of noise, 100-200 msec reaction time). Minimisation of the delays between stimulus offset and response would be a further methodological improvement.

The identification of a number of methodological improvements suggested that the study could be best regarded as a pilot study aimed at determining the best method to examine the effect of this visual illusion on motor acts using this paradigm. It was therefore decided to re-run the study using a similar design but incorporating the identified methodological improvements.

Chapter 3: Study 2- The simultaneous tilt illusion (STI) - revision

Introduction

This study incorporated the methodological revisions identified as being necessary in study 1, but was conducted within the same theoretical framework. This framework predicted that the STI will have strong illusory effects in both visuo-motor and perceptual measures, and that there will be evidence for an association of effect across conditions.

The methodological changes from study 1 were:

(a) The perception mediated response was changed from the 'mime' (study 1) to a 'matching' response. Instead of miming the target orientation, the response required the palette to be placed against a point directly below the position where the stimulus was presented, so as to be parallel to the orientation of the target grating. This method is similar to 'setting lines parallel' method that has been adopted in psychophysical studies of visual orientation. The adoption of this method over the miming response reduced the difference in latencies between conditions, as well as making the availability of proprioceptive cues more balanced (excluding the presence of the hand resting on the plinth which had been the case in the miming condition of the earlier study). It also provided a better view of palette in the perceptual measure as it was now placed at the same distance from the subject as was the case in the visuo-motor measure. This response method also reduced the cross-conditional difference in the degree of 'shift in gaze' from the stimulus to the effector's final response position. Finally it allowed the same sampling method to be applied for calculating the response orientation in both conditions (see method section below).

(b) The initial orientation of the palette prior to each response was controlled so as to approach 90° from the horizontal.

(c) The stimulus set was changed slightly so that the orientation difference between target and annulus grating was either nil or 12 degrees in all cases for goal and filler stimuli.

(d) A more effective combination of visual noise masks was introduced to reduce the likelihood of a retinal after-image providing a visual cue to target orientation.

(e) The latency between stimulus offset and cue for response was reduced to limit the influence of delayed response.

(f) A larger subject group was tested in order to allow for a more powerful statistical analysis.

Method

Subjects

Sixteen right hand dominant subjects, undergraduate students in the Psychology department were tested, 8 females, 8 males in the age range 19 to 53. All had normal or corrected to normal visual acuity, all were naïve to the illusion and had not taken part in study 1. Due to problems assumed to be associated with calibration of the *Optotrak* system, data from 3 subjects (subjects 2, 12 and 16) were found to be unusable and are excluded from analyses.

Stimuli

Stimuli were all of the form used in study 1. Two stimuli were changed however – stimuli "102/84" and "78/94" from study one (which had a 16° difference between target and annulus grating orientation) were replaced by stimuli of the form "98/86" and "82/94" respectively. This meant that all stimuli either had a nil difference in orientation between target and annulus grating, or a consistent 12° difference. The stimulus set was therefore:

Two **goal** stimuli – 78/90 and 102/90

Two **filler** stimuli – 98/86 and 82/94

Three **control/filler** stimuli – 90/90, 86/86 and 94/94

Apparatus

Stimuli were presented on a high-resolution Sony Trinitron MultiScan 400PS monitor using the 'Psyscope' (v 3.1) stimulus presentation software running on a Macintosh PowerMac 7100.

In order to balance the two response conditions, two identical visual masks were in the shape of torus were used. One (the upper mask) was attached to the front of the screen of the monitor to ensure that the monitor and screen edges did not provide vertical or horizontal cues (see figure 3.1). This upper mask was positioned as to be centred on the stimuli position with the mask's central circular aperture being 50mm larger in diameter than the stimuli.

A lower mask (an identical torus) was placed 155mm below the upper mask and vertically aligned with it. A sheet of white card was affixed behind the mask so as to make the background of the central aperture white (matching the aperture of the upper aperture), but with the circular aperture being clearly visible. The aperture of this lower mask acted as the position in which the 'matching' response was made.

The screen and both masks were 49 cm away from the nearest edge of the chin rest that was used to control subjects' viewing distance and angle. The target grating centre, mask centres and central point of the chin rest were aligned so as to place the centre of the stimuli along the subject body mid-line.

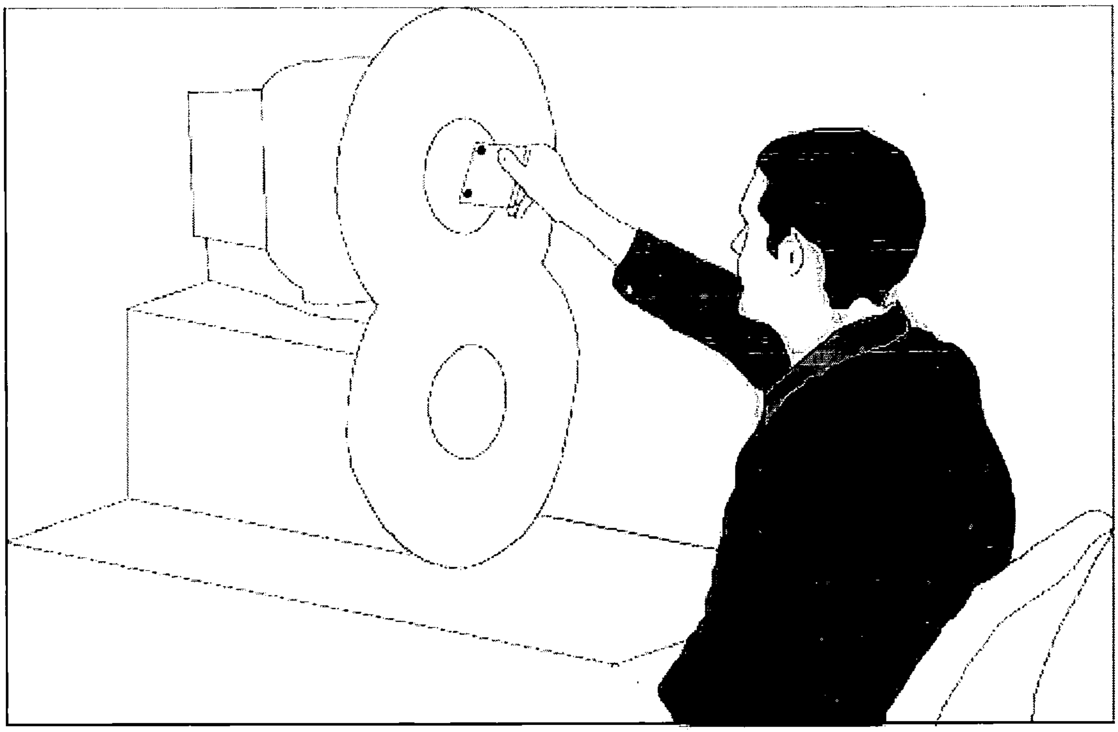

Figure 3.1: Schematic showing the 'two-torus' mask for the posting (upper) and matching (lower) response positions. Note that this illustration does not show the chin rest, which was used throughout testing.

Design

The dependent variable was the magnitude of illusion in the two conditions: posting and matching. The dependent variable was calculated by the difference between the mean response to stimulus 102/90 and 78/90 for each subject.

Procedure

The 7 stimuli were presented in 4 blocks of 40 trials, counterbalanced across subjects (ABBA/BAAB) by response condition (A = posting; B = matching). Each block comprised of 5 trials per stimulus completely randomised within the block using the

Psyscope randomisation facility. The '90/90' control stimulus was weighted so that it was presented twice as often as other stimuli (10 times in per block) to ensure that this benchmark control was as reliable as possible. Prior to each trial the *Psyscope* software presented the form of response trial required - "towards"(posting) or "away" (matching) in the centre of the upper mask. Each trial was initiated by the subject clicking the Macintosh mouse with their non-dominant (left) hand, the stimulus was then presented for 1000 msec. Then a visual noise pattern (a uniformly black pattern) was presented for 30 msec, followed by a tone which acted as the response cue. This was followed by a presentation of a second visual noise (a uniformly white pattern) for 30 msec and a third pattern (as used in study 1) for 30 msec. Reaction time to the tone ensured that the subjects were exposed to the visual noise (to reduce the retinal afterimage) without introducing an unacceptable delay before response.

Subjects were informed that they should proceed at their own pace throughout the testing session, and that in addition to breaks at the end of each trial block, that they could take breaks within blocks if desired (none found this necessary). They were asked to respond as soon as they heard the tone and to ensure that they fixated the screen until the tone sounded, when they were to execute the required response as quickly, accurately and naturally as possible.

The starting position for the palette for each trial was a marked point on a small raised plinth 3.5 cm above the table height, 10cm to the right of body centre line and 30cm forward of the chin rest (as in study 1). Prior to each trial subjects allowed the palette to rest on its narrow edge (vertically oriented) with finger and thumb lightly placed either side. Only on hearing the response cue were they to grasp the palette and perform the response. This ensured that the initial orientation of the palette was more controlled across repeated trials.

The posting condition was performed as in study 1.

In the matching response the subject was informed to place the palette on the central aperture of the lower torus so as to be parallel to the orientation of the target grating and, as in the posting condition, hold this position until the tone indicated the end of the trial.

In both conditions the experimenter initiated the *Optotrak* sample (300 frame, 3000 ms duration) on the appearance of the target stimuli and observed the subject to ensure that they did not initiate response until the response tone sounded. An adhesive gum ('Bluetack") was placed along the front plane of the palette to allow the subject to maintain the orientation of the palette against the screen/torus until the end of the 3 second sample when a tone sounded and the subject returned to the starting position. The dependent variable was taken as the mean of the final 50 frames (500 msec duration) of the *Optotrak* sample data in both conditions i.e. the orientation of the palette as it rested against the torus aperture.

Prior to the bona fide testing session subjects performed two training blocks counterbalanced across subjects by response mode (AB/BA: A = post; B = match) for each response type in which they were presented with each stimulus twice (presented in randomised order) i.e. 14 trials per practice. At the end of each testing session subjects were invited to repeat the practice if required (none found this necessary).

Following each trial session subjects were asked if they had adopted any specific strategy to achieve the task. In particular whether there were any visual cues such as retinal after-image of the stimuli themselves that might have created uncontrolled effects.

The *Optotrak* data were passed through a 10 Hz Butterworth second order filter, then through the *DAP* utility from *Northern Digital Inc* to extract the angle subtended by the line joining the two IREDs and horizontal.

Results

The key study comparison is between responses to stimuli 78/90 and 102/90. Table 3.1 details these results, and figure 3.2 illustrates the group summaries

	Condition	
subject	matching	posting
1	7.33	7.40
2	3.84	4.49
3	9.00	6.11
4	5.47	5.29
5	10.77	8.12
6	8.74	5.66
7	1.72	4.24
8	10.74	16.67
9	15.44	12.62
10	13.38	10.30
11	10.40	6.94
12	7.13	7.17
13	1.84	2.66
mean	8.14	7.51
s.e.	1.16	1.05

Table 3.1: Individual magnitudes of illusion in degrees (calculated by response to stimulus 78/90 minus response to stimulus 102/90) for the STI in the matching and posting conditions.

The data seems to indicate a wide range of individual differences in terms of the magnitude of illusion across conditions, although the comparison on group means indicates that there are equally strong illusions in both measures.

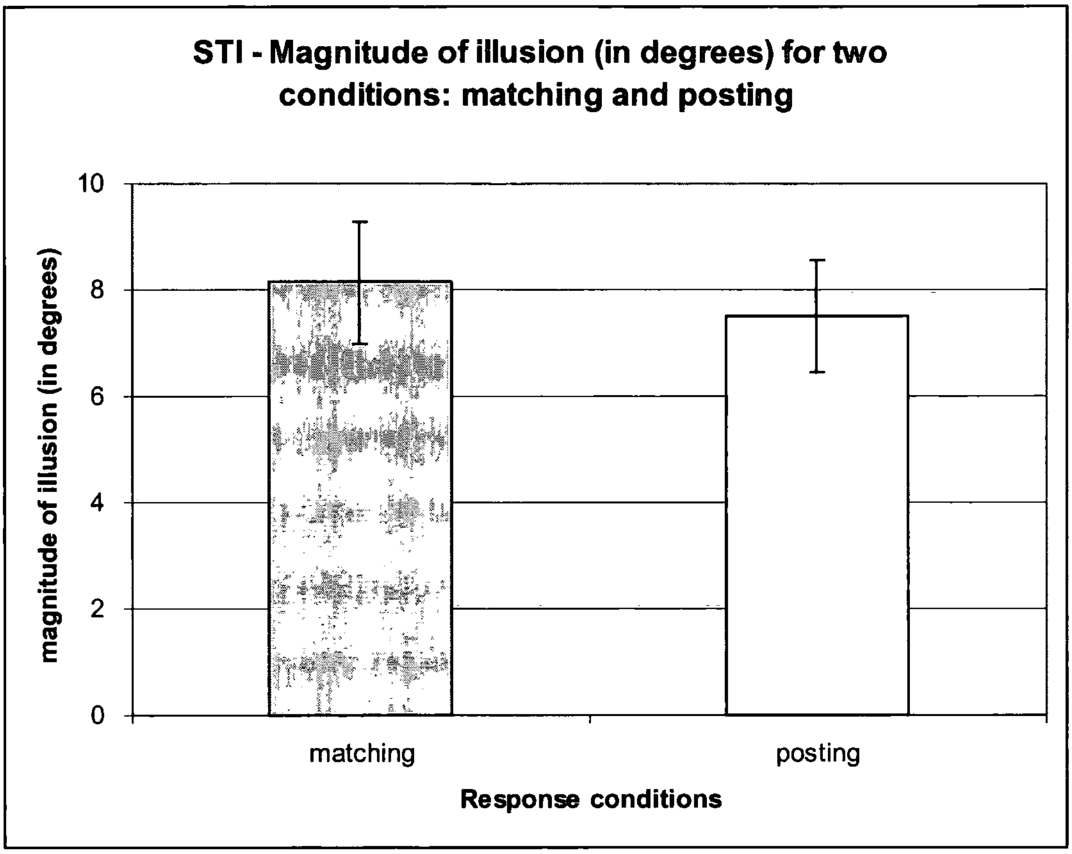

Figure 3.2: Histogram showing the mean magnitude of illusion (mean of the individual magnitude, calculated by response to stimulus 78/90 minus response to stimulus 102/90). Error bars represent one standard error of the mean.

A pair-wise analysis of magnitudes of effect across condition confirmed that there did not appear to be any statistically significant difference between matching and posting conditions : $t(12) = .81$; n.s. A correlational analysis of the magnitudes of illusion per subject indicates an association of effect. Figure 3.3 illustrates the relationship between the magnitude of illusion in matching and posting per subject. There appears to be an indication of a strong positive relationship between the magnitude of illusion across measures. An analysis of this relationship showed that it was statistically reliable: Pearsons $r(12) = .76$; $p < .01$.

However there appears to be one subject whose results do not show this same relationship (subject 8). This subject showed an unusually large effect in the posting measure – in fact their result in the posting measure was 2.4 standard deviations from the mean (the only subject to show a result more than 2 standard deviations from the mean). This may be regarded as a basis for classifying the result as an outlier, however as no *a priori* criteria for exclusion had been made this could be regarded as selectively excluding data. In order to investigate further, the performance of all subjects to the control figure (90/90) in both conditions was examined. The vertical control should provide the best indication of the accuracy with which subjects could perform the two conditions in the absence of any illusory annulus: in effect the motor and visuo-motor aptitude of subjects could, to a certain extent, be determined. The variance over the 20 responses in the control condition was calculated and it was found that subject 8 had a noticeably high spread of responses (with the variance of their responses to the control figure being 3.07 and 4.54 in matching and posting respectively, in comparison to a group variances of 1.46 and 1.81). Calculating the discrepancy between the variance of response for all subjects, it was found that only subject 8's level of variance was more than 2 standard deviations from the group's mean variance (subject 8's results being 2.23 above the mean in the matching measure and 2.50 above the mean in the posting measure). There would appear to be some justification in regarding this subject's results as an outlier and not representative of the target population. In all subsequent analysis, data from this subject has been excluded.

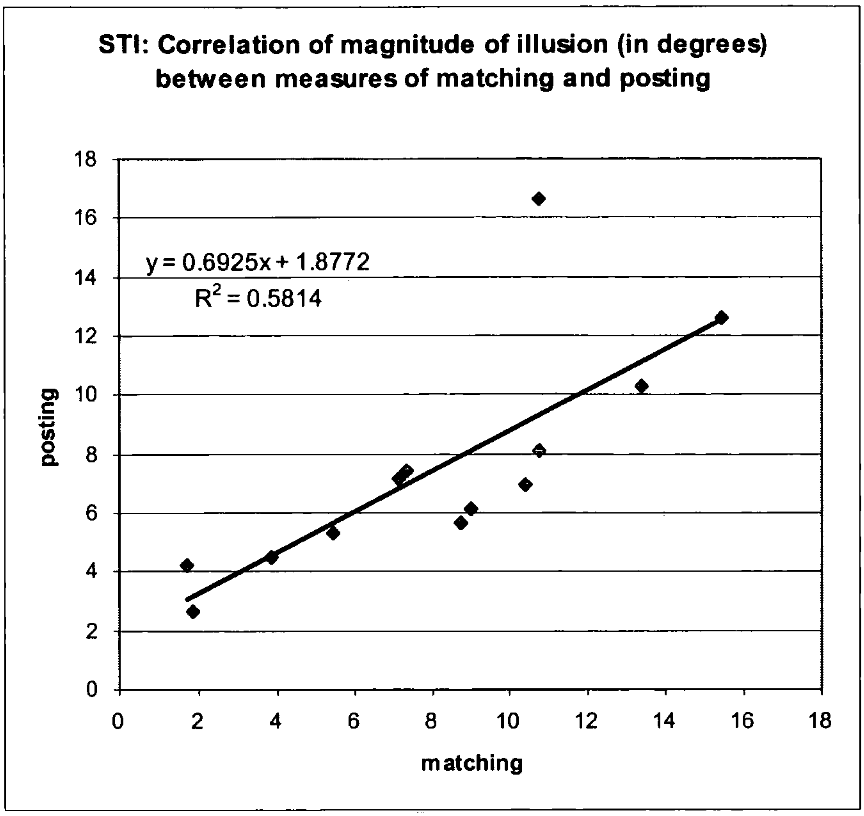

Figure 3.3: The correlation between magnitude of illusion (in degrees) between the matching and posting conditions ; n = 13.

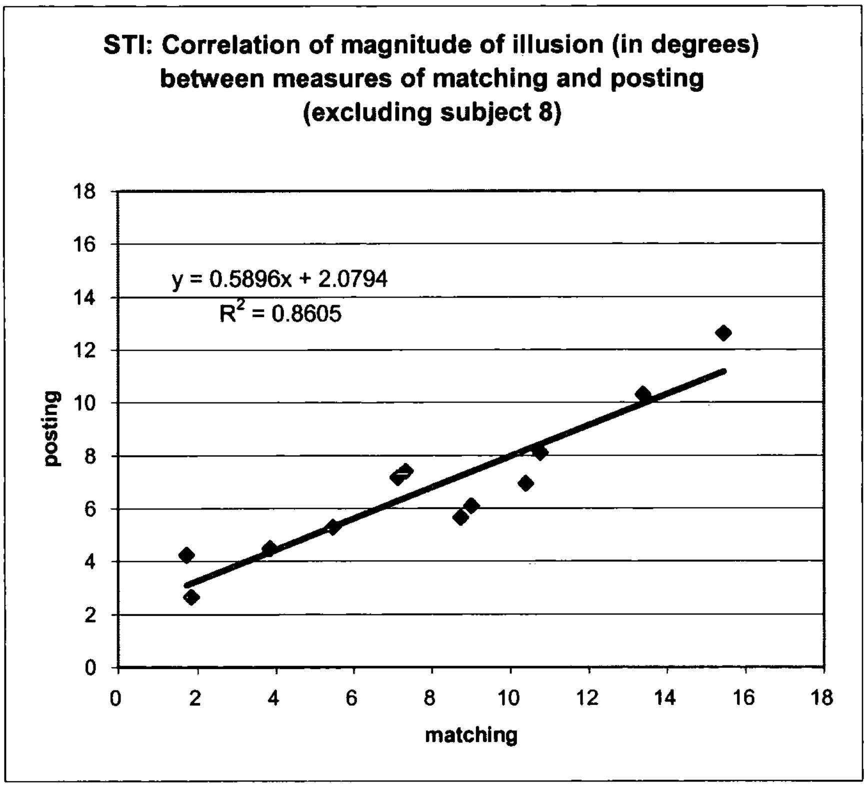

Figure 3.4: The correlation between magnitude of illusion (in degrees) between the matching and posting conditions, having excluded subject '8'; n = 12.

Figure 3.4 shows the correlation for the magnitude of illusion across conditions having excluded the potential outlier (subject 8). The correlation is now highly significant: Pearsons $r(11) = .928$; $p < .001$. The effect of excluding this data results in a change in the difference between mean magnitudes of illusion across conditions, although a two-tailed pair-wise t-test reveals that there is still no statistically reliably difference between the two conditions: $t(11) = 2.00$; n.s (two-tailed).

These results indicate that there is a reliable relationship between the magnitude of illusion found in both measures, and it may be argued that this indicates a degree of shared causality in the illusory effect evident in the perceptual and visuo-motor responses. As such the study prediction of association between measures, in terms of the STI magnitude of effect, seems to be supported.

<u>Comparison of results between study 1 and study 2</u>

Figure 3.5 shows the comparison of mean magnitudes of effect in both studies per condition. Most notable is the apparent difference in mean illusion magnitude between the miming response in study 1 and the matching response of study 2. An analysis of this difference failed to show any reliable statistical difference: Kolmogorov-Smirnov $Z = 1.01$; n.s.

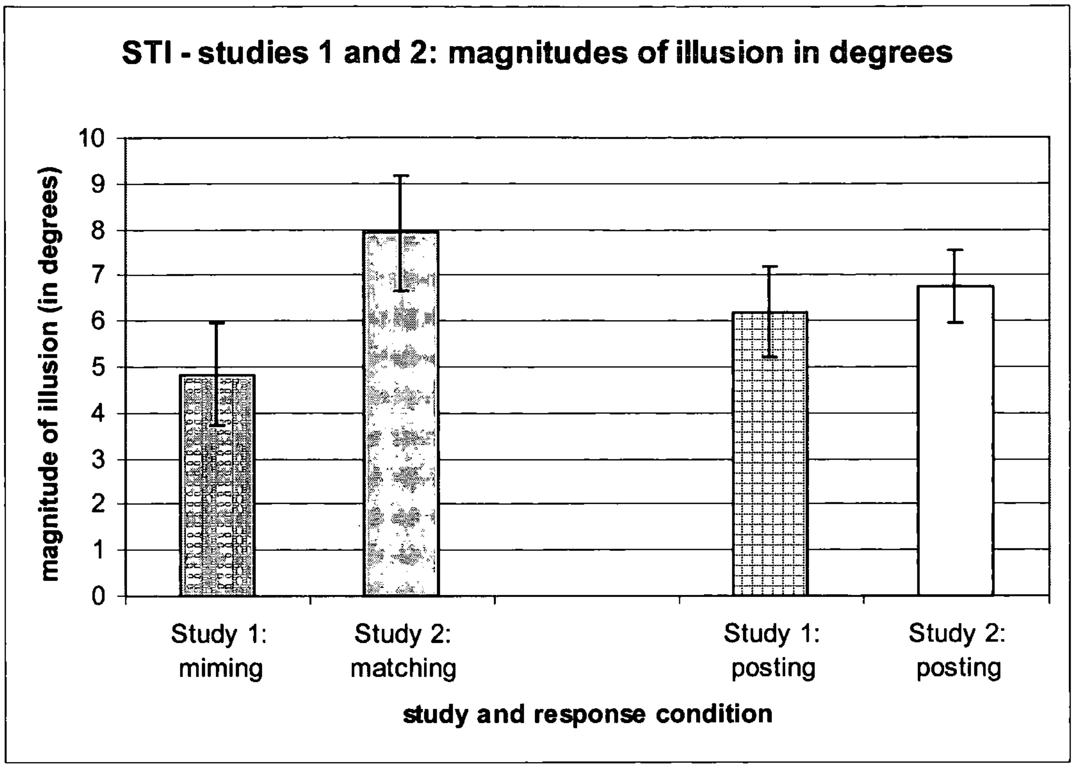

Figure 3.5: Mean magnitude of illusion for perception and visuo-motor measures in studies 1 and 2. Error bars indicate one standard error of the mean.

However this non-parametric test may not have the statistical power to determine whether these samples are from different populations, so the absence of a reliable difference should be treated with some caution. The comparison between mean magnitudes of illusion between the two (identical) posting measures of studies 1 and 2 shows no evidence of a difference, and as such suggests that this measure has a relatively high test-retest reliability.

A further analysis was conducted by collapsing the results of study 1 and study 2. It can be argued that the miming response and the matching both represent a measure of perception. As such, if the study hypothesis of association of illusory effect is to be supported, there should be some correlational evidence in comparisons between both measures of perception and the posting measure. Figure 3.6 illustrates the correlation of magnitude of illusion for each individual within the populations of both study 1 and study 2. The interpretation of this correlation should be made with some caution in that there is some indication that the miming and matching measures of studies 1 and 2 may not tapping a unitary process. The presence of a strong and statistically sound correlation Pearsons $r(21) = +.66$; $p < .01$, indicates that, within the collapsed data of both studies, the perception measures and the visuo-motor measures show a reliable positive relationship, again in line with our hypothesis.

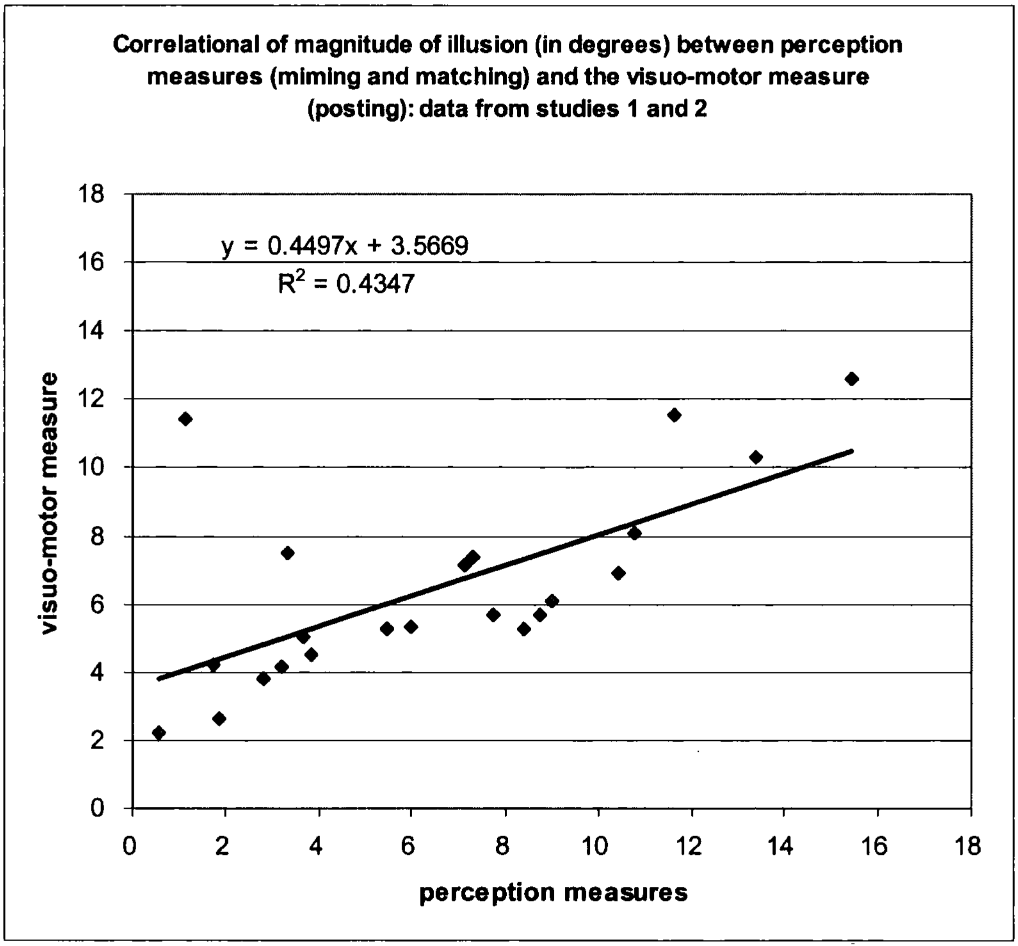

Figure 3.6: The correlation between magnitude of illusion (in degrees) between the perception and visuo-motor conditions, data collapsed over studies 1 and 2; n = 22.

In the interests of a systematic examination of the collapsed data across the two studies, a comparison of the pattern of differences was also conducted. Figure 3.7 illustrates the mean illusion magnitudes in the perception and visuo-motor conditions averaged across both studies which indicates no difference in mean illusion magnitudes across conditions. A statistical analysis confirmed the lack of any evidence a reliable difference: $t(21) = .03$; n.s.

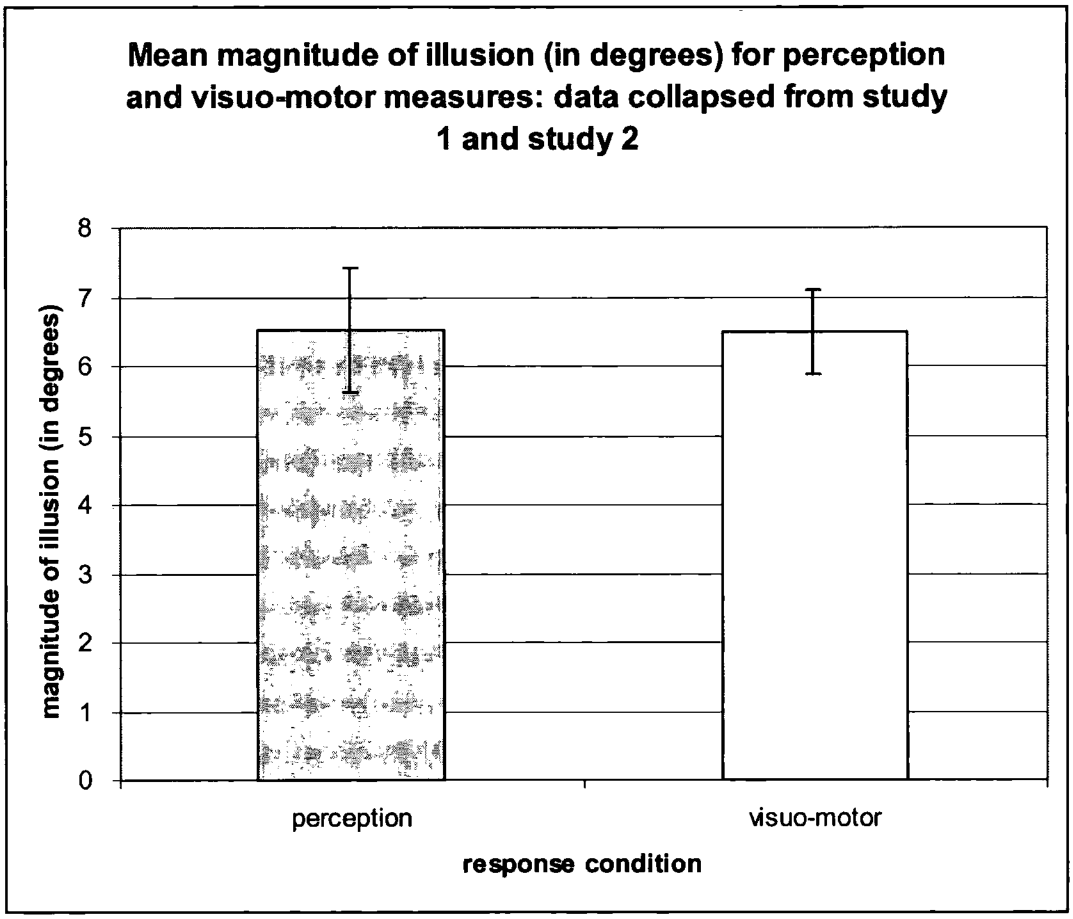

Figure 3.7: Mean magnitude of illusion, data collapsed over studies 1 and 2 by response type: perception (miming and matching) and visuo-motor (posting). Error bars represent one standard error of the mean.

In summary, the results of the collapsed data from both studies clearly support the results of study 2 alone. There is evidence for association of effect both in terms of the absence of clear difference in the magnitude of illusion between conditions, combined with a statistically robust positive correlation between conditions.

Discussion

The results from study 2 seem unequivocal. There is strong evidence for a pattern of effects between the visuo-motor and the perception measure suggesting an association of effect using this illusion type. The combination of the results from study 1 and study 2 seem to further strengthen the supposition that the illusion is having no different affect on perception and action measures. There seems convergent evidence from both studies in isolation, and the combination of studies, to infer that the illusory effect observed in both conditions arose from a common source. This associative pattern of results is predicted by the perception .vs. action model on the basis of the assumed siting of the illusion in primary visual cortex.

The study results are also a clear refutation of the suggestion that visuo-motor measures will be refractory to illusory effects solely as a result of differences in the task demands between the two conditions rather than as a result of differentially dominant underlying visual processes.

Chapter 4: Study 3 - The rod-and-frame illusion (RFI): pilot study.

Introduction

The causal mechanisms of the rod-and-frame illusion (RFI) are less well defined than those of the simultaneous tilt illusion (STI). Howard (1982) suggests that the effects of tilt adaptation, eye torsion and apparent body tilt may be involved in the observed effects on the perceived orientation of a rod placed within a tilted frame. However it is also proposed that these factors alone cannot account for the magnitude of effects observed: "The other factor is presumably the subject's inability to dissociate non-visual impressions of gravitational vertical from cues provided by the visual framework" – Howard (1982, p. 423). This 'frame of reference' effect appears strongly analogous to the contrast effects of size found in the Ebbinghaus illusion, and the illusory displacement of the Roelofs effect. As such, if the RFI effect results from the scene-based coding associated with higher visual processing in the ventral stream, the perception .vs. action model would make the prediction that a visuo-motor measure would be largely refractory to the illusion, in the presence of a perceptual illusion of tilt.

Much of the early research into the RFI involved the potential confound concerned with the effects of contour interactions between the rod and frame by virtue of stimuli having small separations between the target rod and surrounding frame (Beh *et al*, 1971; Wenderoth and Beh, 1972; Ebenholtz, 1977). Coren and Hoy (1986) suggested that increasing the separation between rod and frame essentially nullified the effect, however the stimuli in their experiment consisted of printed variants of the RFI viewed whilst placed on a horizontal surface and within a fully lit room, rather than the more traditional arrangement whereby stimuli are presented in the frontal plane in darkened room conditions. The 'framing' effect of the larger scale stimuli may have been largely negated in the Coren and Hoy study because of the presence of strong peripheral cues to vertical in the visual scene (e.g. walls and furniture) – in line with the suggestions of Di Lorenzo and Rock (1982), Ebenholtz and Utrie (1983), and Spinelli, Antonucci, Daini, Fanzon, and Zoccolotti (1995).

If the surrounding frame causes a reliable and predictable illusion on a vertical rod that can be attributable to the 'frame of reference' effect, it should be the case the more peripheral the frame, and more predominant it is as a reference cue for orientation, the *larger* the illusory effect. If the dominant causal mechanism in the illusion is a contour interaction between rod and frame, then exactly opposite effect would be predicted: the larger the separation between rod and frame the *smaller* the resultant illusory tilt.

In order to test this, a pilot study was undertaken to determine what effect an increase in frame size and rod separation would have in the magnitude of illusion on a small group of observers. Tolhurst and Thompson (1975) and Poom (2000) have presented results that indicate that separations between target and inducing contours in the STI causes substantial reductions in illusory tilt, even where these separations are relatively small (separations of 0.4 and 1.0 degrees of arc respectively). If two forms of the RFI are selected so as to be increasingly less likely to be the result of a contour interaction effect (by increasing the rod/frame 'gap') this should test the extent to which other factors (such as the frame of reference effect) are likely to be dominant.

The purpose of this pilot study was to confirm that contour interaction was not the dominant contributor to the observed illusion, and to determine the strength and reliability of an RFI array with a large rod/frame 'gap' and the frame placed in the far visual periphery.

Method

Subjects

The subject group consisted of 5 right-hand dominant subjects (4 females and 1 male) in the age range 23 to 31. All had normal or corrected to normal visual acuity, reported no motor or visuo-motor deficits and all subjects were naïve to the illusion and the nature of the experiment.

Stimuli/Apparatus

As in all studies reported here, in referring to the orientation of targets and responses, all orientations are described in relation to the left-hand horizontal meridian as viewed by the subject. As such a vertical orientation is described as "90", one which is 2° anti-clockwise from vertical is described as "88", one 15° clockwise from vertical is described as "105". Stimuli are described in terms of the orientation of the outer element (the frame) followed by the orientation of the target (the rod): e.g. 75/90 is a stimulus with a frame 75° from the left hand horizontal enclosing a vertical rod.

Two forms of stimulus array were used: these are designated as the 'small' and 'large' scale rod and frame arrays.

For 'small' RFIs the stimuli were printed on A4 sheets oriented in landscape. The frame was formed by four lines, 4mm wide and 13.8 cm long forming a square. The rod was 3 mm wide and 2.8 cm long positioned centrally within the frame. At the distance of presentation (approximately 57 cm) the frame subtended 13.8 degrees of arc, the rod 2.8 degrees of arc and the separation between rod and frame was approximately 6 degrees of arc (depending on the stimulus: the smallest separation between frame and rod across all stimuli was 5.2 degrees of arc).

Seven stimuli were presented:

2 **goal** stimuli : 75/90 and 105/90 (see Appendix A, figure a11)

2 **filler** stimuli: 75/92 and 105/92

3 **control/filler** stimuli: 90/88, 90/90 and 90/92.

Stimuli were presented at a viewing distance of 57 cm with the stimulus fixed in the frontal plane by being placed on a small pedestal slightly below viewing height and aligned with the subject's body centre line. Viewing conditions were in a normally lit, furnished room.

For the 'large' RFIs the stimuli were formed using a large adjustable frame (70 cm by 70 cm) made from translucent white plastic sheeting. All but the outer 2 cm of the sheet was painted in opaque matt black, leaving a white frame at the outer edges. The frame was mounted on a pivot that allowed its orientation in the frontal plane to be adjusted. Fixed to this common pivot and in front of the frame was a rod 100 mm long, 15mm wide and 5 mm deep, which could also be independently adjusted in orientation. The minimum distance between rod and frame was approximately 37 degrees of retinal arc. A scale on the reverse of the apparatus allowed the rod and frame to be set to given orientations within ±0.5 degrees. The study was conducted in a darkened room with the apparatus backlit, making the frame dimly luminescent, and with enough residual light to make the rod clearly visible. The stimulus set for large RFI array was, in terms of rod and frame orientations, the same as for the small RFI array (above).

Design

The dependent variable was the magnitude of illusion in the two conditions: small and large RFI. The dependent variable was calculated by the difference between the mean response to stimulus 90/105 and 90/75 for each subject.

Procedure

Trials were run within 2 blocks of 35 trials each block. Subjects were tested on each block on separate, consecutive days. Block order was partly counter-balanced across the subject group (AB/BA) by condition (A = small RFI, B = large RFI). Each block comprised of 5 trials per stimulus, pseudo-randomised within each block (no stimulus was presented consecutively on any 2 trials). Prior to each trial the subject closed their eyes whilst the stimulus was adjusted (for the large array) of stimulus sheet replaced (for the small array) and to allow the response sheet to be replaced. On a verbal signal from the experimenter the subject fixated the stimulus and recorded their perception of the target rod orientation by drawing a line with ruler and pen on the 'cross-hairs' bar of the response sheet (Appendix A, figure a12) to match the orientation of the rod. Subjects were informed to perform the task as quickly and accurately as possible. If the subject judged the target to be vertical, an indicating stroke was placed horizontally across the vertical bar of the response sheet (slightly increasing the chance of a response of 'vertical'). As soon as the response was completed the subject closed their eyes in preparation for the next trial.

Following each trial session subjects were asked if they had adopted any specific strategy to achieve the task. The orientation of the response lines was measured manually as a displacement in degrees from the vertical bar on the response sheet.

Results

For the small RFI array a Student's paired t-test returned a reliable illusion in the predicted direction when the mean responses to stimuli 75/90 and 105/90 stimuli were compared: $t(4) = 2.18$; $p < .05$; one-tailed. For the large RFI array the same test again returned a significant result $t(4) = 2.59$; $p < .01$, one-tailed. Therefore it appears that both small and large arrays produced reliable illusory effects in the predicted direction.

Next the magnitudes of illusion for each subject were calculated by subtracting the mean response to stimulus 75/90 from the mean response to 105/90. Table 4.1 details these results and figure 4.1 shows the group summary. The results show a greater illusion magnitude in the large RFI array than the small array for all of the subjects. This difference was shown to be statistically reliable by use of a paired Students t-test: $t(4) = 2.58$; $p < .05$, one-tailed. The direction of effect was as predicted – with the larger effect found in the large scale RFI array.

	RFI array type	
	Small	Large
Subject		
1	0.60	0.80
2	2.80	6.10
3	4.90	12.00
4	0.20	4.50
5	1.00	2.00
mean	1.9	5.08
s.d.	1.95	4.39
s.e.	0.87	1.96

Table 4.1: Individual magnitudes of illusion in degrees (calculated by mean response to stimulus 75/90 minus response to stimulus 105/90) for the small and large-scale RFI arrays.

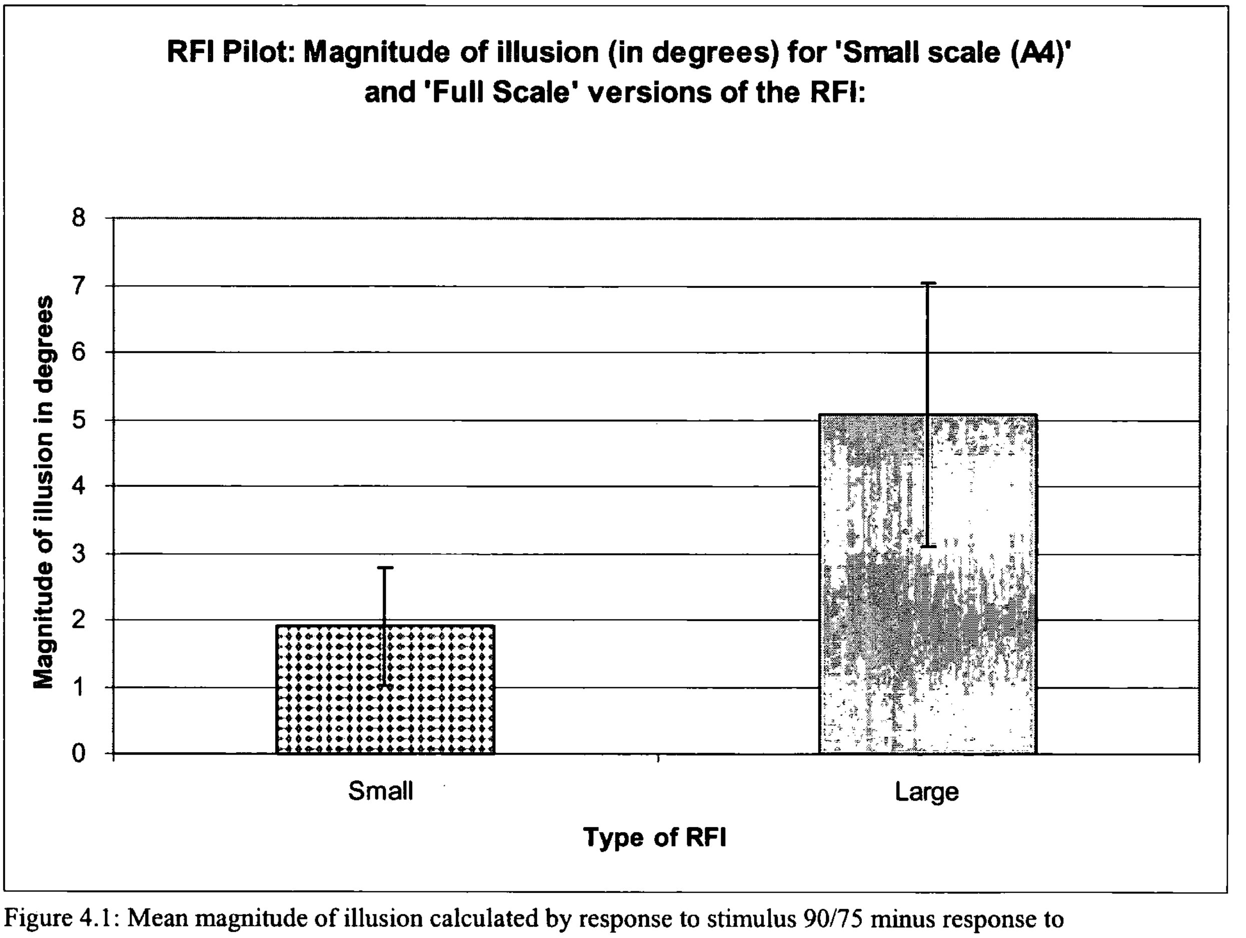

Figure 4.1: Mean magnitude of illusion calculated by response to stimulus 90/75 minus response to stimulus 90/105). Error bars represent one standard error of the mean.

Our conjecture that the pattern of effects between the two arrays was accountable by an increase in the effect of a shared causal mechanism is strengthened by an analysis of the correlations between magnitudes of effects across conditions. Figure 4.2 illustrates this correlation.

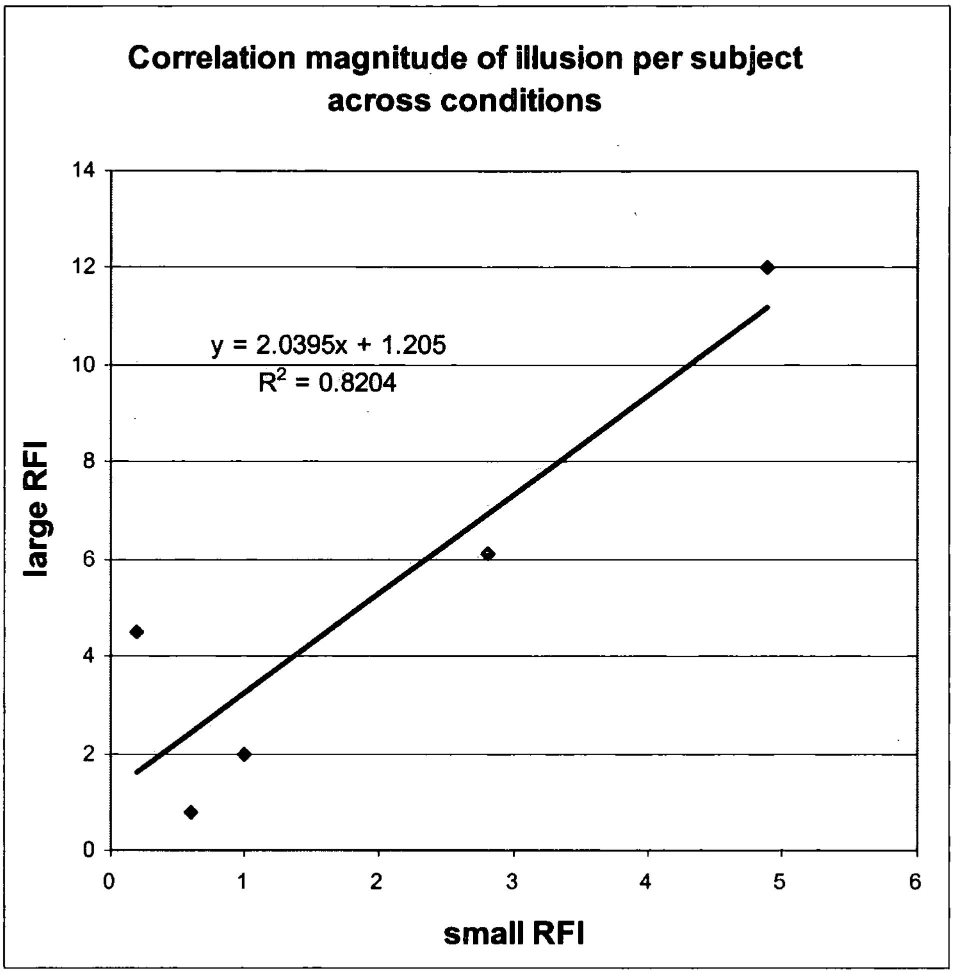

Figure 4.2. Correlation of magnitude of illusion (in degrees) per subject in the small RFI array and the large RFI array.

In spite of the small number of data points, this correlation still shows a statistically reliable effect: Pearsons $r(4) = +.91$; $p < .05$ (one-tailed). This analysis supports the suggestion for shared causality between the effects observed in each condition.

Discussion

We had proposed that the causal mechanisms responsible for the illusory effects of the RFI would be enhanced through presentation of a large tilted frame presented peripherally and acting as the most prominent cue to orientation within the visual scene. The finding of the predicted effect of an increase in effect between the small and the large RFI array supports the conjecture that contour interactions are not a dominant factor in the mechanisms of the two RFI types. Had contour interaction been the dominant factor this would have resulted in a decrease in illusion strength in the larger array. While the results do not exclude the possibility that contour interaction effects might make a contribution to both of the observed illusions, these contributions are likely to be small, especially in the case of the large test array with the greatest rod and frame separation. There also seems to be some evidence to suggest some shared causality between the two RFI types through the presence of a positive correlation in illusion strength across arrays.

The suggestion that cyclotorsion and induced body tilt are dominant factors to the observed effects for both these arrays seems to be unlikely, as these factors are associated with large and predominant tilted arrays (Kertsez and Sullivan, 1978, Goodenough *et al*, 1979), and yet a reliable illusory effect is found even for the small RFI in a normally lit room. It seems reasonable to suggest that one of the dominant factors is the frame of reference effect, which in the case of the small RFI is ameliorated by the presence of cues to true orientation through visual references in the fully lit scene.

This pilot study did not determine in any comprehensive manner the extent to which factors other than the visual frame of reference for orientation are acting. However the pattern of change in illusion strength between small and large arrays suggests that the illusion is not primarily based on contour interactions between frame and rod. It seems to suggest that this effect involves computations of orientation that incorporate distal information from the wider visual context. This effect seems strongly analogues to the contextual effects present in the Roelofs and Ebbinghaus arrays. Therefore the perception .vs. action model would predict a pattern of dissociation of illusory effect in the large-scale variant of the RFI: with a strong perceptual illusion being present in the absence of a strong effect in a visuo-motor measure.

Chapter 5: Study 4: The rod-and-frame illusion (RFI).

Introduction

The results from study 3 suggested that the processing associated with higher visual scene analysis might be a dominant factor in the illusory tilt of a small rod centred within a large tilted frame. This result is in line with other studies that have found illusory effects of frame orientation that stemmed from the original work of Asch and Witkin (1948) and Witkin and Asch (1948).

The large scale RFI array used in study 3 minimised the potential effects of contour interactions between rod and frame. The results from studies 1 and 2 would suggest that effects resulting from low level cellular interactions in primary visual cortex would be present in both perception and visuo-motor control. In the case of the RFI, the perception .vs. action model would predict that the absolute coding of orientation and its direct transformation into action co-ordinates for a motor effector would result in a visuo-motor act being largely refractory to the frame of reference effect which is evident in measures of perception. This pattern of dissociation is in line with the findings of Bridgeman *et al* (1981) for the Roelofs effect, Aglioti *et al* (1995) for the contrast effects assumed to be underlying the Ebbinghaus illusion, and the more recent Hu and Goodale (2000) study into the effects of pairing targets with larger and smaller flanker stimuli in an immersive environment ('virtual reality').

A number of studies (e.g. Pavani *et al*, 1999; Vishton *et al* ,1999; Franz *et al*, 2000) have suggested that any observed difference between visuo-motor and perception measures could result from differences in the task demands and stimulus arrays involved in the two conditions used to separate perception and visuo-motor measures rather than differential underlying visual processing. One criticism is that on-line correction may be used in the visuo-motor measure to minimise illusory effects on the action measure. In the domain of size manipulations this has not been regarded as a problem as the index of preparatory maximum grip aperture has been used. Because the point at which the dependent measure is sampled is relatively early in the reaching/grasping response, it has been suggested that this measure is not likely to be influenced by a direct comparison of the target as the fingers approach the target. However it has been suggested (Westwood *et al*, 2000) that visual feedback may be potentially affecting on-line control even in the initial phases of prehension and it can be inferred that this could, to a degree, explain the resistance of prehension to illusory effects. The performance of the visuo-motor response in a 'complete open-loop' manner (without any visual input at any point after response onset) would be an necessary precaution in ensuring that on-line correction was excluded as a cue available exclusively to the visuo-motor condition. Adopting an open-loop visuo-motor task also controls for effects of occlusion of stimulus elements during the visuo-motor response (Mon Williams and Bull, 2000).

Franz *et al* (2000) also point out that the illusion array should be balanced for each condition to prevent the 'doubling' effect of comparing two oppositionally acting inducing arrays in the perceptual measure, with only a single inducing array acting on the action measure.

The rod of the RFI lends itself strongly to a grasping visuo-motor response, a very natural visuo-motor measure in comparison with the 'pseudo-posting' response employed in studies 1 and 2. However this measure potentially allows for haptic feedback being available exclusively in the action response, even if performed in open loop. As such the dependent measure of hand orientation must be taken before contact with the target rod.

We proposed that the RFI would show the same consistent illusory effect on subjects' perception of the rod orientation that had been found in study 3. However an open-loop grasp of the rod should show that the visuo-motor processing of rod orientation is largely unaffected by the tilted visual framework.

Method

Subjects

The 12 subjects (8 female, 4 male age range 19 through 34 years) were undergraduate psychology students. All were right-hand dominant with normal or corrected-to-normal vision, and were naïve to the illusion. None had taken part in the previous 3 studies.

Stimuli/Apparatus

The apparatus and room conditions were identical to those used for the large RFI array of study 3. The centre point of the rod and frame was 54 cm above desk height. The rod was placed approximately 43 cm in front of the subject. Viewing distances were not strictly controlled as in a short piloting exercise subjects found difficulty in performing the perception measure from the chin rest and so responses in all conditions were undertaken without the head restrained in any way. The centre of the frame and the rod were positioned so as to be along the subject body mid-line.

In the visuo-motor responses, subjects grasped the rod with the thumb and forefinger. Two infrared emitting diodes (IRED) were attached to inside of the metacarpal/proximal phalange joint of the thumb and forefinger of the right hand. The position in 3D space of these IREDs was recorded throughout each response using a Northern Digital Inc. *Optotrak* system sampling at 100 Hz. A third IRED was attached to the wrist of the right hand and its movement was tracked in order to determine movement end time. The initiation of the *Optotrak* system was automatically triggered by Northern Digital Inc software that also generated tones as response cues for subjects. The starting position for each trial was with the thumb and forefinger of the right hand resting together on a raised point 6 cm above the table height along the body mid-line. For all trials the weight of the hand rested on a release switch which was positioned 4cm to the right of the marked starting point at approximately the same height. This switch extinguished the display illumination when released in the open loop reaching condition, while in the other response conditions the switch had no effect. Figure 5.1 shows a schematic of the reaching condition.

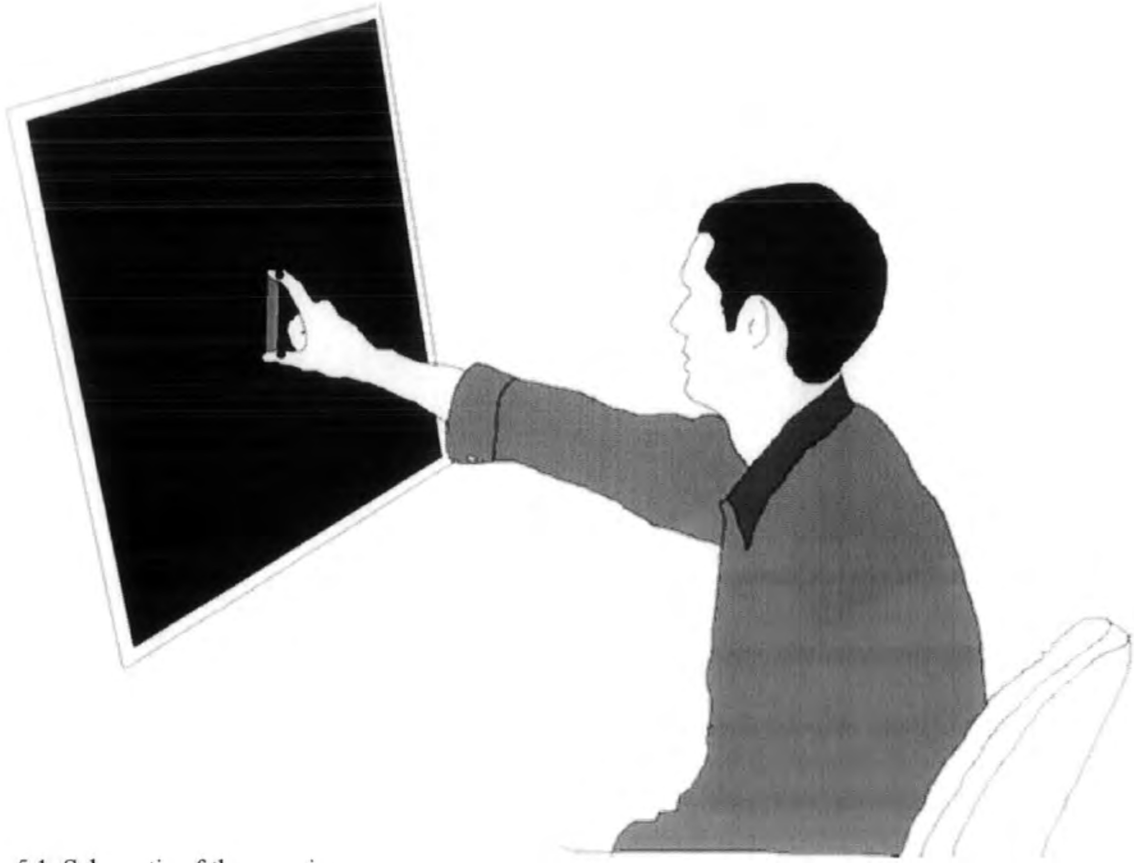

Figure 5.1: Schematic of the grasping response

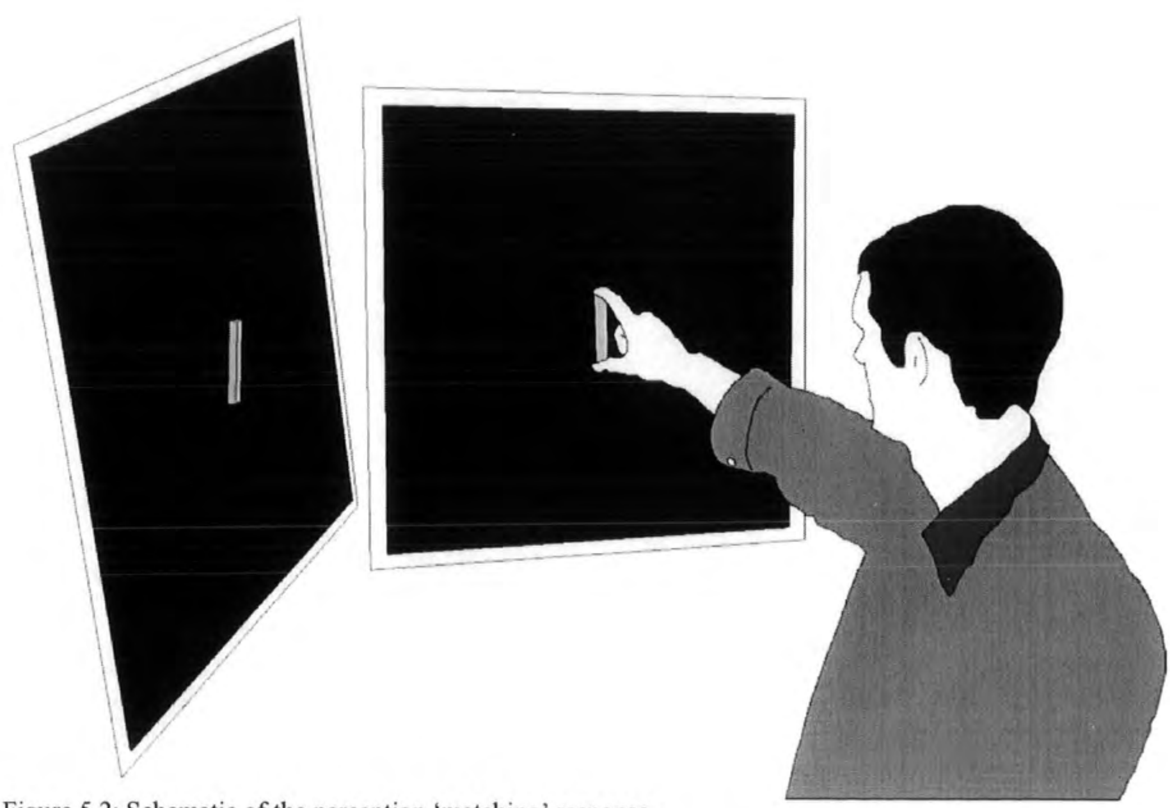

Figure 5.2: Schematic of the perception 'matching' response.

For the perception measure, an identical rod and frame (the matching apparatus) was placed to the right of the stimulus frame. The matching frame was fixed at gravitational vertical with a rod that could be adjusted by the subjects to express their perceived orientation of the target rod (see figure 5.2.)

Nine stimuli were presented:

> 2 **test** stimuli: 75/90 and 105/90 (see appendix A, figure a11)
>
> 4 **filler** stimuli: 75/88, 75/102, 105/88 and105/92
>
> 3 **control/filler** stimuli: 90/88, 90/90 and 90/92.

<u>Design</u>

The dependent variable was the magnitude of illusion in three conditions: 'open-loop' grasping, perception and a full vision 'closed-loop' grasp. The dependent variable was calculated as the difference between the mean response to stimulus 90/105 and 90/75 for each subject. The closed-loop condition was included largely to generate control data.

<u>Procedure</u>

Trials were run within 3 blocks of either 48 trials (closed-loop grasping) or 32 trials (matching and open loop grasping) per block. Block order was counterbalanced across the subject group (ABC/ACB/BAC/BCA/CAB/CBA) by condition (A = open-loop grasp; B = perceptual match; C = closed-loop grasp). Each block comprised 8 trials per test stimulus plus 2 trials per filler stimulus plus 8 trials for each of the 3 control/filler stimuli in the closed-loop reaching condition and 8 trials for the 90/90 control/filler stimulus in the matching and open-loop grasping condition. Presentation order was pseudo-randomised within each block so that no stimulus was presented consecutively on any two trials. Prior to each trial the subject closed their eyes whilst the stimulus was adjusted. At the beginning of each trial the experimenter initiated the control software and instructed the subject to open their eyes and fixate the target rod. After 2000 ms a tone sounded which acted as the response cue.

For the grasping measures the subject then immediately reached and grasped the rod. In the open loop condition releasing the button underneath the subject's hand tripped a switch that turned-off the only light source. Subjects were specifically instructed to report any persistence of the stimulus after tripping the switch. None was ever reported. On conclusion of the *Optotrak* sample, a tone sounded which acted as the cue for the subject to return their hand to the starting position and close their eyes.

In the closed-loop grasp the procedure was identical, except the button release did not extinguish the light.

The *Optotrak* data were passed through a 10 Hz Butterworth second order filter, then through the *DAP* utility from Northern Digital Inc. to extract the angle subtended by the line joining the finger and thumb-mounted IREDs and the horizontal. The dependent measure was taken as the orientation of the markers 50ms prior to movement end. A standard movement end time criterion was used: 5 consecutive frames with a displacement of the 3rd (wrist mounted) IRED at less than 5 cm/s.

In the perceptual matching condition, on hearing the instruction to open their eyes the subjects fixated the stimulus for 2000 ms after which a tone sounded. On this cue the subject adjusted the rod in the matching apparatus to match the orientation of the target rod as accurately as possible. A tone sounded 5 sec later by which point subjects were instructed to have completed the task, signalling them to return their hand to the start position and close their eyes. They were instructed to report if they had failed to complete the task satisfactorily within the time frame. None ever reported this. The starting orientation of the matching rod was set randomly at either 7 degrees clockwise or anti-clockwise from vertical prior to each trial. The dependent measure of the matching rod orientation was recorded manually from the scale at the rear of the matching apparatus.

During the grasping tasks the matching apparatus was masked to prevent it acting as a potential cue.

Results

Reliability of measures used

The use of IREDs attached to relatively proximal positions on the fingers to determine hand orientation is a relatively novel technique. The positioning had been determined in order to avoid occlusion of the markers during the reach. In order to verify that hand orientation was being legitimately measured through tracking these markers, the control data for open-loop grasping were examined.

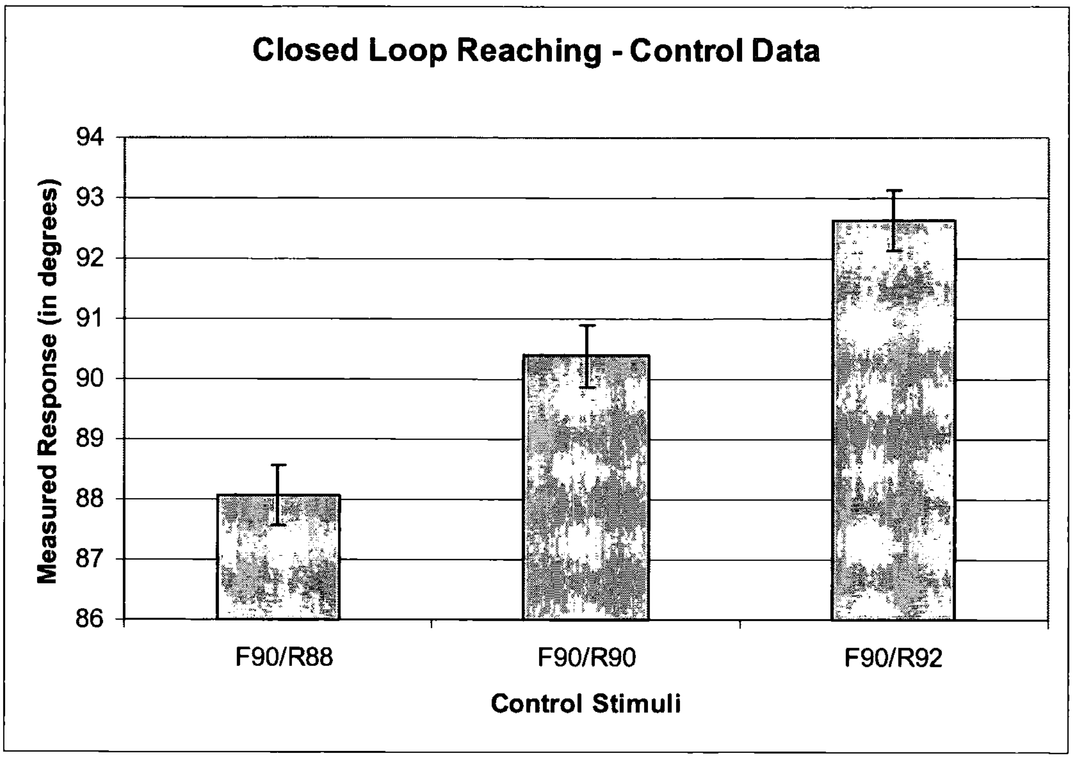

Figure 5.3. The mean group recorded orientation of IRED markers to control stimuli in the closed-loop (full vision) measure. Error bars indicate one standard error of the mean.

As can be seen in figure 5.3 the recorded orientation of markers appears to be an accurate reflection of the target rod's true orientation in this full vision response to control stimuli. A statistical analysis of recorded responses against actual orientation of targets showed that there was no reliable difference between the recorded response and the control target orientation.

In case there could have been some different effect of head or body tilt on the matching measure (which was offset to one side) in comparison with the open loop reaching conditions (which was along body centre line) e.g. as result of the Aubert and Mueller effects (see chapter 1), the mean responses to the control stimulus 90/90 were compared between these conditions. They showed no reliable difference in measured response to this control stimulus: $t(11) = .56$, n.s. Also this indicated that although grasping measures used *Optotrak* derived data, and matching measures used the manual record of the rod orientation taken from the scale at the rear of the matching apparatus, it seems the case that both techniques were returning closely comparable results. For completeness a similar comparison was made for the responses to this control stimulus between open-loop and closed-loop grasping and a comparison between closed-loop grasping and matching. No reliable differences were found and as such it seems reasonable to directly compare these measures.

Measurement of illusion magnitudes

First we need to establish the conditions in which there is a reliable difference between mean responses to the 75/90 and 105/90 stimuli. A series of Student paired t-tests were conducted and showed that only the matching condition showed a statistically reliable difference: $t(11) = 2.91$; $p < .01$, one-tailed. In both the open-loop grasping and closed-loop grasping conditions the difference was not reliable: closed-loop $t(11) = 1.52$; n.s. ; open loop $t(11) = 0.50$; n.s. A Bonferroni correction was applied for multiple comparisons and showed that the significant effect in the matching condition was robust and remained above the 5% criterion. It should be noted, however, that the closed-loop condition did show a tendency towards an illusory effect in the predicted direction (approaching significance in the uncorrected comparison). This might, therefore indicate (even in this closed-loop measure) some influence of the tilted frame.

The magnitude of illusion was calculated for each subject by subtracting the mean response to stimulus 75/90 from that to 105/90. Table 5.1 below summarises the results.

Subject	Condition		
	Closed-loop grasp	Matching	Open loop grasp
1	0.55	5.00	-0.42
2	-0.30	2.13	-0.39
3	1.40	1.52	-0.54
4	-0.82	2.38	-1.60
5	-0.44	3.68	0.24
6	-0.67	8.13	-1.26
7	1.63	22.00	1.60
8	1.22	4.38	2.70
9	-0.57	1.63	-0.28
10	1.06	0.75	0.14
11	0.42	6.32	3.01
12	1.40	1.00	-0.63
mean	0.41	4.91	0.21
s.e.	0.27	1.69	0.42

Table 5.1. Magnitude of illusion (in degrees) for each of the three response conditions. Negative results indicate that the difference in the responses to the stimuli 75/90 and 105/90 are in the opposite direction to that predicted.

Of note from table 5.1 is the large number of 'negative' illusions. These only occur in the two grasping conditions. These negative results indicate an effect in the opposite direction to that predicted (i.e. the frame had an effect of attracting rather repelling the rod orientation). However these data are likely to be the result of random noise in the movement data indicating an arbitrary effect of sampling. This conjecture is supported by the very small magnitudes of these effects. Only one of the 12 negative effects exceeds 1 degree. This is in contrast with the consistency of the positive (i.e. predicted) effect in the matching condition where only one subject has an effect *less* than 1 degree.

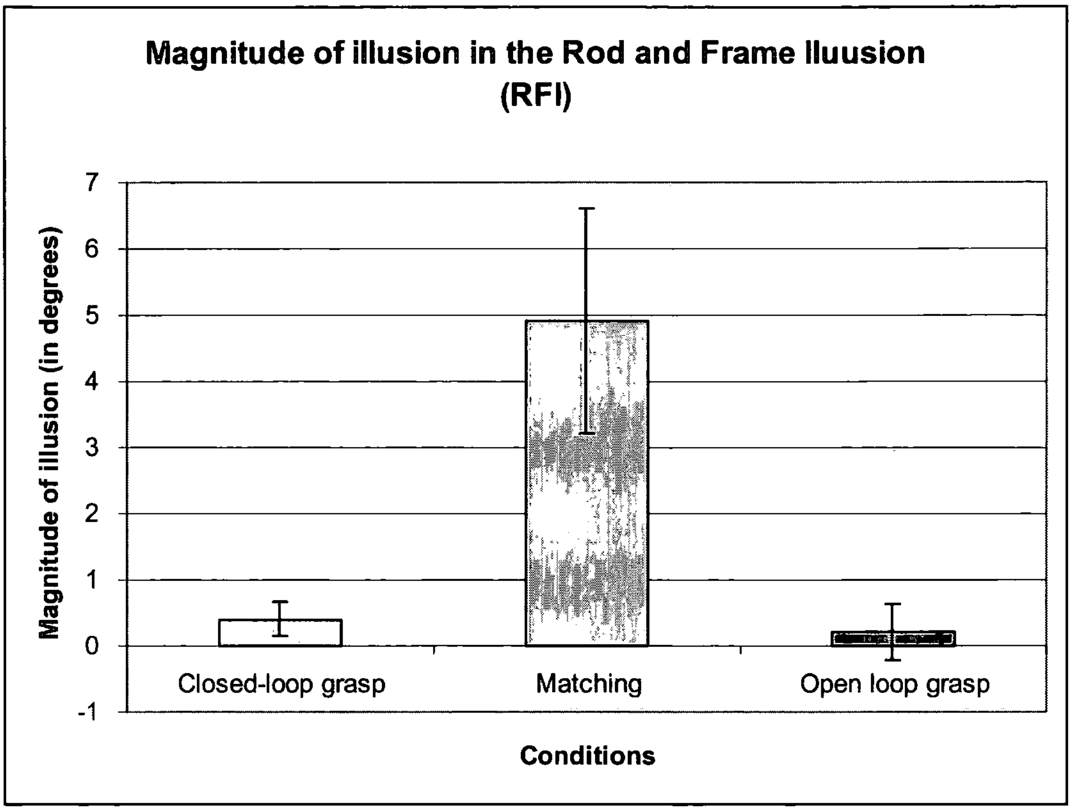

Figure 5.4: The group magnitude of illusion (n=12) measured in degrees for each condition. Error bars indicate one standard error of the mean.

Figure 5.4 illustrates the difference in the group mean magnitude of effect in each condition. The critical comparison is between the matching and the open-loop grasping condition. A pair-wise Student's t-test showed this difference in illusory magnitudes to be reliable: $t(11) = 2.98$, $p < .01$. It would appear therefore that the predicted pattern of dissociation has been demonstrated.

Closer examination of the results shows a single subject (subject 7) who exhibits an unusually strong effect in the matching measure (22 degrees of effect). The RFI has a history of wide individual differences in terms of its strength of effect (the 'frame dependence/independence' classification) but it was necessary to establish whether this one subject alone was contributing disproportionately to the observed pattern of differences. The analyses were therefore re-run excluding subject 7. The results showed a substantial *increase* in the significance of the previous pattern of differences: $t(10) = 4.47$; $p < .001$. It would appear therefore that the subject's net contribution was greater in terms of experimental noise than effect. This would indicate that the difference in illusion magnitude between matching and open-loop grasping is a robust effect, and one that matches the study predictions. It would also indicate, however, that the general population median magnitude of effect may be smaller than the mean of nearly 5 degrees found in this group.

For the sake of consistency with studies 1 and 2, a correlation between the magnitude of illusion for matching and open-loop grasping conditions was completed: this indicated no reliable correlation between measures ($r^2 = 0.14$; n.s.). There is no reliable evidence, therefore, for any shared causality for the small (and in fact non-significant) effect found in the open-loop grasping measure and the perception response

Discussion

It had been our prediction that the RFI would have a robust and reliable effect on a measure of perception of rod orientation, but that the orientation of the hand whilst grasping the rod would be largely unaffected by the tilted frame. The results from the study support this hypothesis, with a strong effect being observed in the perception measure and neither the closed-loop nor the open-loop grasping measure showing a reliable effect of the tilted frame. Furthermore when examining the magnitude of illusion in the open-loop grasping and perception measures, there was a significantly larger effect on the perception of rod orientation.

This can therefore be described as a complete dissociation between the two key measures of open-loop grasping and perception. The method applied addressed criticisms suggesting that on-line correction and occlusion of inducing elements during a prehensive act could account for visuo-motor invulnerability to the illusory effect. The perceptual measure involved a matching task within a veridically vertical/horizontal frame, which discounts the 'doubling' effect of comparisons between opposing illusions (Franz *et al*, 2000).

However it should be noted that there is some indication that the frame may have been having some effect on visuo-motor measures. The closed-loop grasp does show a consistent tendency towards an illusory effect, although it failed to meet with a 5% level of significance. This may indicate that the visuo-motor measure may be partially influenced by the frame. Additionally two methodological issues remain outstanding however.

First, although the dependent measure was sampled before contact with the rod, in both action measures the rod was grasped. Potentially subsequent grasping trials within a trial block may have used tactile feedback as a corrective mechanism. In order to examine this, further analysis was conducted on the open-loop grasping condition. Eight trials were performed for each of the stimuli 105/90 and 75/90, so the mean response to the first 4 trials in each trial block per subject was compared with the last 4 trials. Using a conservative criterion (i.e. NOT correcting for multiple comparisons) a paired t-test analysis showed that there was no reliable order effect between first 4 and last 4 trials. The mean angle of response in the first and second halves of each testing session per subject was compared for the two target stimuli 75/90 and 105 90. There were no reliable differences in either case: $t(11) = .40$; n.s. and $t(11) = .99$; n.s. respectively and the small difference that is present in fact shows a small *increase* in illusory effect over time. This would indicate that there was no evidence for a reduction in effect between first and last halves of the trial block. In case a difference could have been masked by a change in the dispersion of responses, the unsigned difference between response and the veridical target orientation (90) was performed to determine whether the dispersion of responses had changed over time. Again this indicated no difference between the two halves of the test block: $t(11) = 1.00$; n.s.(for the 75/90 stimulus) and $t(11) = 1.11$; n.s.(for the 105/90 stimulus).

Finally the magnitude of illusion was calculated for both the early and late trials by subtracting the mean responses to stimulus 75/90 from the means for 105/90 for 1st half and 2nd half trials. The results again showed no reliable difference: $t(11) = .73$; n.s. In fact again there was a trend towards a small *increase* in magnitude of illusion over time: the mean magnitude in the 1st half of trials was -.05 degrees (s.e. 0.45) i.e. there was, overall, a small effect in the opposite direction to that predicted; the mean magnitude in the 2nd half of trials was 0.43 degrees (s.e. 0.56) i.e. a small effect in the predicted direction.

As none of these small effects were reliable, it would seem justified to suggest that there was no discernible change in the effect of the illusion as a result of repeated trials. There seems no evidence to suggest that haptic feedback caused any reduction in effect in the open-loop grasping measure, and as such this can be largely discounted as a mechanism contributing towards the small (and in fact, unreliable) illusion in this measure.

For completeness the same set of analyses were performed for the matching measure. Again no evidence was found for a discernible change in response between early and late trials.

The second methodological criticism cannot however be so readily addressed. Brenner and Smeets (1996, 2000) suggested that it may be the case that in grasping responses, the specific 'grasp points' of an object may be independently coded as positions in space with which finger and thumb are aligned. If this is the case, then for both size illusions (where Brenner and Smeets' criticisms were originally made) and, by inference, orientation illusions, if grasp points rather than rod orientation were being coded, then the illusion-resistance of a prehensive act could be explained without any reference to a specialised processing of target characteristics for visuo-motor control. It would simply be the case that the visuo-motor response has available a cue that is denied to the perceptual measure. Such a criticism can be made of the grasping of the rod in both open and closed-loop conditions. The presence of two singular and prominent grasp points at each end of the rod could mean the coding of these vertices, rather than the orientation of the rod *per se*, could be dominant in mediating the grasp orientation. In order to address this potential criticism the use of grasp point coding would have to be minimised as a visuo-motor cue. A methodologically revised study was therefore undertaken to take account of this issue and also to determine whether there may be a reliable effect of frame tilt on the visuo-motor measure.

Chapter 6: Study 5- Embedding the STI within a distal frame

Introduction

The results from study 2 suggest a pattern of *association* between visuo-motor and perceptual measures where the simultaneous tilt illusion (STI) was the target stimulus. This had been predicted on the basis of both measures being largely dependent on equally distorting effects from a shared illusory mechanism involved in the STI sited in early cortical vision.

The study 4 results showed a pattern of *dissociation* between measures when the rod-and-frame illusion (RFI) is employed. This had been predicted based on the assumption of the dominant causal mechanism in this illusion type being the 'frame of reference effect' – to which the visuo-motor measure should be largely immune.

From this basis a further prediction may be inferred. If the entire STI is embedded within a tilted frame, then perceptual report should be influenced by both illusory inducers, the tilted annulus of the STI and the more distal tilted frame of the RFI. However the visuo-motor measure should be largely impervious to the frame's influence and as such any residual effects would be dominated by the tilted annulus alone.

Poom (2000) reported that a composite array similar to the proposed one (embedding the STI within a frame oriented at gravitational vertical/horizontal) had a negligible effect on illusion strength for perceptual measures, although it could be argued that the horizontal/vertical frame used was essentially a 'neutral' reference, without a counter-acting affect (which would have been the case had the frame been tilted in opposition to the annulus). Also Poom's results involved collapsing the data from a number of different arrays (where contours were defined by either motion, disparity or luminance) and the results for the luminance defined contours alone are not available. In a personal correspondence with the author he noted that although previous studies (e.g. Wenderoth and Johnston, 1988a) have not found a reliable effect of a vertical/horizontal frame on the STI magnitude, in his research he found that there was a trend towards a small decrease in illusion magnitude to the 'squared' (upright) frame (which was not referred to in his published results). He suggests that because of the unusually large frame used in the research reported in this thesis, which other mechanisms (e.g. the integration of visuo-vestibular processing) may be having a more prominent effect than is the case for smaller scaled frames. The Wenderoth and Johnstone (1988a) study found that composite arrays (framed-STI stimuli) showed little reduction in illusion strength as a result of the framing effect providing a veridical cue to vertical. However, as noted by Poom (personal correspondence) and in the review in chapter 1 of this thesis, these studies, and the original study by Kohler and Wallach, 1944 (where the first observation concerning framing effects on the STI was made) all used relatively small frames (c. 8 degrees of arc). From study 3 we can suggest that an increase in frame sizes may increase the magnitude of the RFI effect, and thereby effects of framing may emerge in the composite arrays. In the Poom (2000) paper it is also notable that this study found that there *were* significant effects on the 'attraction' (or indirect) affect (see chapter 1) - where the difference between target grating and annulus was > 50 degrees. In fact the conclusion of the paper was that these two effects – repulsion and attraction – may result from processing in differing neural substrates (echoing suggestions made in chapter 1).

The present study aimed at investigating the differing effects of frame orientation on the two measures of perception and visuo-motor control using composite stimulus arrays. It applies a hybrid of the methods from previous studies in this thesis, and utilises a virtual posting task to a target grating as the visuo-motor measure in an attempt to minimise the potential effects of grasp point coding on this response.

We predict that in general there should be a significantly greater effect of a distal frame on measures of perception than on the visuo-motor control measure. We also predict that there should be similar effects of a proximally positioned annulus on both measures. From these two predictions a final hypothesis is suggested: that if the tilted frame and annulus have opposing tilts, that the net illusion in visuo-motor measure should now be greater than that in the measure of perception.

Method

Subjects

Ten subjects (7 female, 3 male age range 19 through 23 years) were tested. All were undergraduate psychology students. All were right-hand dominant with normal or corrected-to-normal vision, and were naïve to the two illusions. None had taken part in any related studies.

Stimuli/Apparatus

The frame apparatus and room conditions were identical to those used for the large RFI array of studies 3 and 4.

A new STI stimulus was produced by printing two monochrome 0.5 cycles per centimetre gratings: one circular (forming the target grating 93 mm in diameter) and one torus-shaped (forming the annulus 166 mm in diameter). Both target and annulus gratings were separately affixed to two concentric portions of an adjustable ring array. The inner ring held the central target grating and the outer ring held the annulus. These two rings were joined, but could be rotated in respect to each other, therefore allowing the relative orientation of the target and annular grating to be adjusted as required. This sub-apparatus had a central axle that allowed the STI sub-array to be fixed centrally within the frame in the same way as had the central rod used in studies 3 and 4.

The offset between the target grating and the annular grating was changed from 12 degrees (as had been the case in studies 1 and 2) to 15 degrees. Previous research (e.g. Gibson and Radner, 1937; Campbell and Maffei, 1971; Parker 1972) indicates that the greatest illusory effect of the STI occurs with annulus/target differences of between 10 and 20 degrees. In order to ensure that subjects were presented with the minimum number of differently oriented contours the target/annulus offset was changed so as to be the same orientation as the RFI frame offsets from vertical and horizontal (i.e. 15 degrees)

In the visuo-motor condition, subjects ‘posted’ a plastic card (identical to that used in studies 1 and 2) against the central target grating. Two infrared emitting diodes (IRED) were attached to the card to allow its orientation to be monitored. The initiation of the *Optotrak* system was automatically triggered by *Northern Digital Inc* software which also generated tones as response cues for subjects whilst also synchronising this with the initiation of the *Optotrak* sampling of IRED positions. The starting position for each trial was with the card resting on its edge at a fixed starting point 24 cm from the frame along the subject’s body centre line. Figure 6.1 shows a schematic of the visuo-motor conditions.

The perceptual ‘matching’ measure was similar to that adopted in study 4 (see figure 6.2). A grating, identical to the central target grating of the test stimulus, was placed on an adjustable axle within a frame that was fixed at gravitational vertical and horizontal (the ‘matching apparatus’). The distance from the subject to both the matching grating and the test grating was approximately 60 cm.

In referring to the stimuli used there are 3 elements: the orientation of the surrounding frame, the orientation of the grating annulus, and the orientation of the target grating. Stimuli are labelled in terms of these 3 orientations “from out to in”. Thus an array with a frame of 105 degrees, an annulus of 75 degrees and a target grating of 90 degrees (all as measured from the left hand horizontal as presented to the subject) is be labelled “105/75/90”.

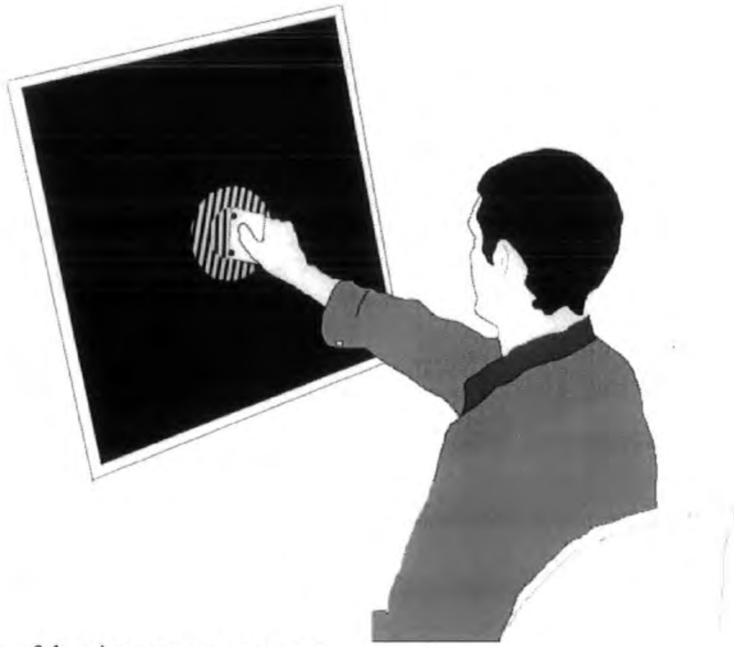

Figure 6.1: Schematic of the visuo-motor responses.

Figure 6.2: Schematic of the perception 'matching' response.

Ten stimuli were presented:

105/75/90 and 75/105/90 - where the 2 illusions were opposing
(the '**opposing pair**' - see appendix A, figure a13)

105/105/90 and 75/75/90 - where the 2 illusions were complementary
(the '**complementary pair**' – see appendix A, figure a13)

90/75/90 and 90/105/90 - where the frame acted as a cue to vertical
(the '**framed-STI pair**'- see appendix A, figure a13).

4 filler stimuli: 90/105/94, 90/105/86, 90/75/94, 90/75/86

Design

The dependent variable was the magnitude of illusion in three conditions: 'open loop' posting, perception (matching) and a full vision 'closed-loop' posting. The dependent variable was calculated by the difference between the mean response to each stimulus of the stimulus pairs (opposing, complementary and the framed-STI).

Procedure

Trials were run within 3 blocks of 60 trials. Block order was partly counterbalanced by response condition across the subject group (ABC/ACB/BAC/BCA/CAB/CBA) (A = closed-loop posting; B = perceptual matching; C = open-loop posting). Each block comprised 6 trials per test and filler stimuli. Presentation order was pseudo-randomised within each block so that no stimulus was presented consecutively on any two trials.

Prior to each trial the subject closed their eyes whilst the stimulus was adjusted. At the beginning of each trial the experimenter initiated the control software and instructed the subject to open their eyes and fixate the target rod. After 2000 ms a tone sounded which acted as the response cue.

For the two posting measures the subject immediately grasped the palette (which rested on its narrow side on the table ensuring a fixed starting orientation) and posted it up against the target grating, as if to 'post through' the target grating (the 'virtual-posting' task as performed in studies 1 and 2). In the open-loop condition the lights were extinguished on the response cue. Subjects were specifically instructed to report any persistence of the stimulus after the lights were extinguished. None was reported. In the closed-loop grasp the procedure was identical, except the light remained on. On conclusion of the *Optotrak* sample, a tone sounded which acted as the cue for the subject to return the palette to the starting position and close their eyes.

The *Optotrak* data were passed through a 10 Hz Butterworth second order filter, then through the *DAP* utility from *Northern Digital Inc.* to extract the angle subtended by the line joining the two IREDs and horizontal. The dependent measure was taken as the orientation of the markers 10 ms prior to movement end. A standard movement end time criterion was used: 5 consecutive frames with a displacement of the upper IRED on the card at less than 5 cm/s. This later sample (cf. Study 4 where the dependent measure was taken 50 ms before movement end time) was applicable as there was no need to preclude haptic feedback as a corrective cue in these visuo-motor measures.

In the perceptual matching condition, on hearing the instruction to open their eyes the subject fixated the stimulus for 2000 ms after which a tone sounded. On this cue the subject adjusted the grating in the matching apparatus to match the orientation of the target grating as accurately as possible. A tone sounded 2 secs later by which point subjects were instructed to have completed the task, return their hand to the start position and close their eyes. This smaller response window (cf. Study 4 where a 5 sec window was allowed) was adopted to ensure that the immediate percept of orientation was being tapped, and as a result of observing subjects in study 4 all of whom completed the matching task well within the 5 sec window which was allowed in that study. Subjects were instructed to report if they had failed to complete the task satisfactorily within the time frame. None reported this. The starting orientation of the matching grating was set randomly either 7 degrees clockwise or anti-clockwise from vertical prior to each trial. The dependent measure of the matching rod orientation was recorded manually from the scale at the rear of the matching apparatus. During the grasping tasks the matching apparatus was masked to prevent it acting as a potential peripheral cue to horizontal and vertical.

Results

Framed-STI array results and comparison with study 2

In examining the framed-STI pair (stimuli 90/75/90 and 90/105/90) we were, in effect, performing a part replication of study 2. However the presence of the upright frame was a strong cue to vertical. We would therefore expect that this distal cue might affect the matching response (which can take the now correcting influence of this distal stimulus into account) but not the visuo-motor response (which should be immune to the frame's influence). The results are summarised in figure 6.3.

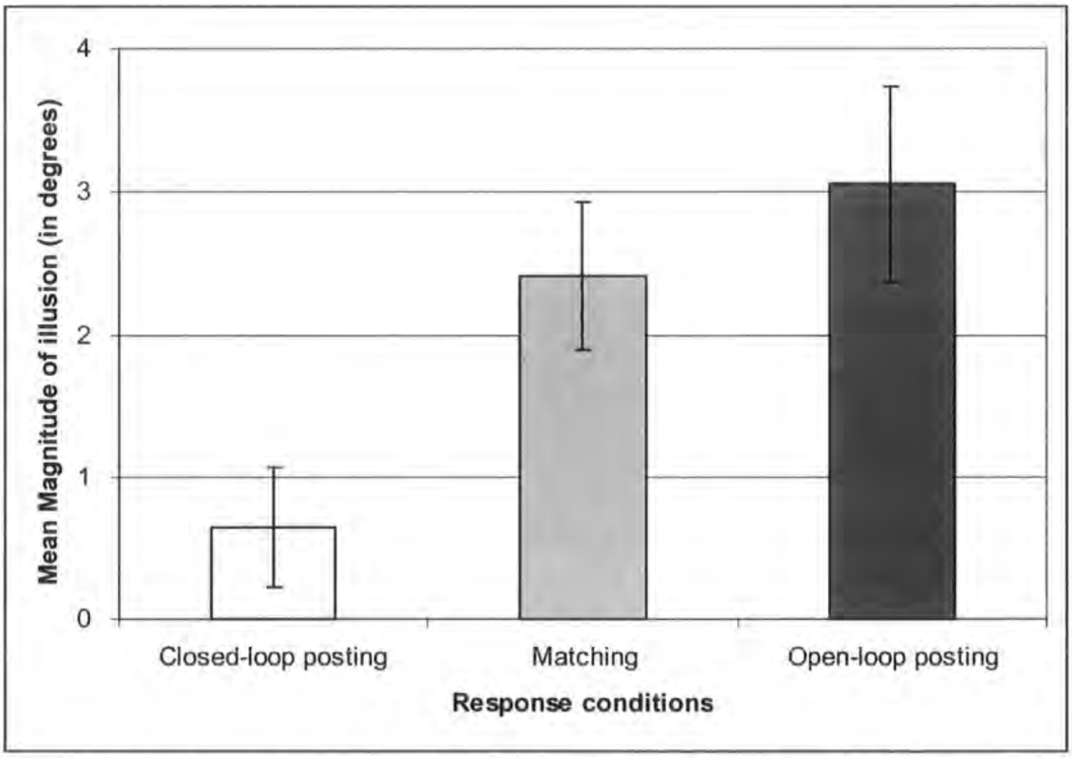

Figure 6.3. Group mean (n = 10) magnitude of illusion for the 'Framed-STI' calculated as the difference in mean response to stimulus '90/75/90' minus mean response to stimulus '90/105/90' (i.e. predicting an illusion in direction found in previous studies). Error bars show one standard error of the mean.

Analyses were conducted to determine there was a reliable illusion in each of the 3 conditions (i.e. a comparison of responses to stimuli 90/75/90 and 90/105/90). A series of paired Students t-tests revealed reliable effects in the matching condition- $t(9) = 4.67$; $p < .001$, (one-tailed); and in the and open-loop posting- $t(9) = 4.48$; $p < .001$ (one-tailed).

However, although approaching significance, the difference between the two arrays for the closed-loop posting response failed to meet criterion: $t(9) = 1.52$ $p = .082$, (one-tailed). A Bonferroni correction left both previously reliable effects above criterion, but further indicated that the effect in the closed-loop posting condition may not be reliable. A possible explanation for the absence of a reliable illusion in the closed-loop posting task is that online correction in this full-vision condition allowed a direct visual comparison between the posting palette and the target grating as the two converged, whereas in the other two conditions such a strategy was precluded.

A comparison of the magnitude of illusion between the matching and the open-loop posting task was then conducted. It showed no reliable difference between conditions: $t(9) = 1.50$; n.s. This indicated, as was found in Study 2, that both measures were being equally affected by this version of the STI array. In fact there is, if anything, some indication that the illusion strength in the matching condition may be *smaller* than in the posting condition. A correlational analysis of the magnitude of illusion across these two conditions was again completed (see figure 6.4).

A statistical analysis showed that the correlation was statistically reliable: Pearsons r = .78; $p < .01$) a result in line with the findings of study 2 indicating a strong shared causality underlying the illusory effects in both conditions.

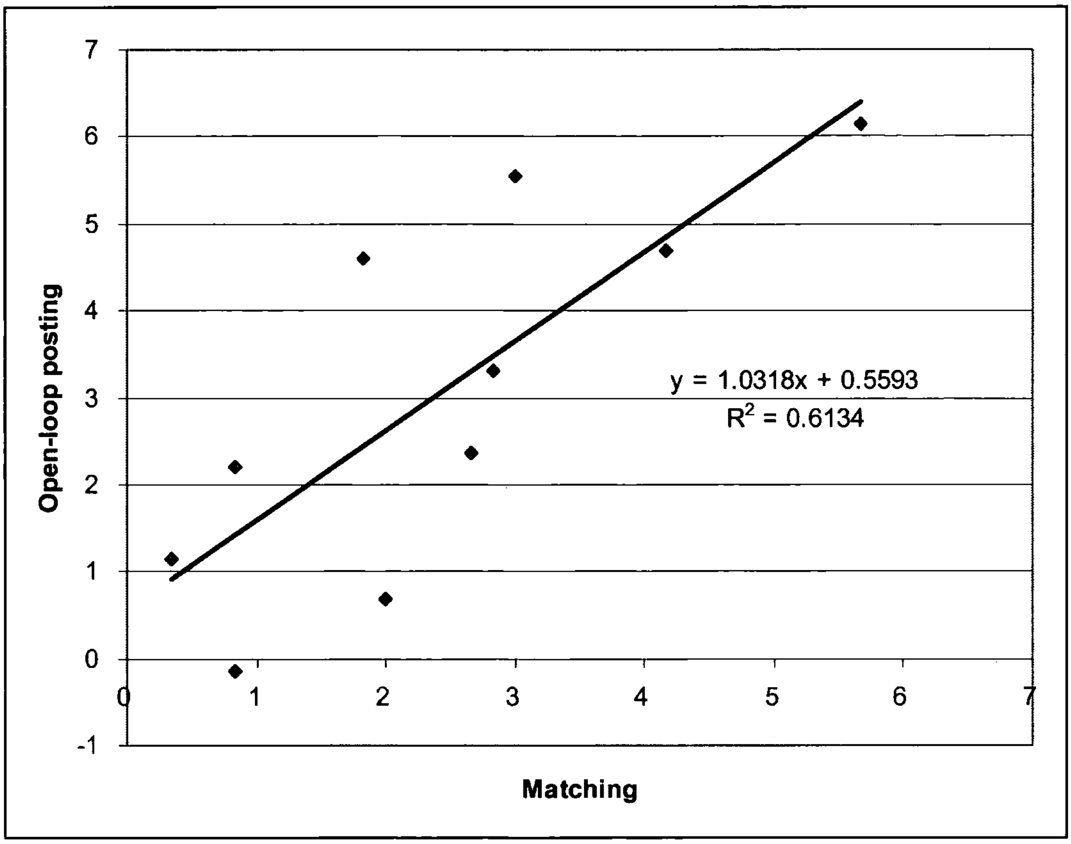

Figure 6.4: Correlation between magnitude of illusion (in degrees) between matching and open-loop posting for the 'framed-STI' array.

One point to note, however, is that when comparing the net magnitudes found in this study and those from Study 2 a clear drop in illusion strength seems to be found in this new array (see figure 6.5).

A 2x2 mixed ANOVA was performed with the factors of 'study' (Studies 2 and 5, group comparison) and condition (matching and mailing, within subject comparison). The main effect of 'study' was found to be significant: $F(1, 20) = 14.52$; $p < .001$ indicating that the reduction in illusion strength between Study 2 and Study 5 was reliable. The main effect of condition was not significant: $F(1,20) = .783$; n.s.; which was, in effect, a re-iteration of the two sets of planned comparison t-tests that have already indicated that both measures are equally influenced by the illusion.

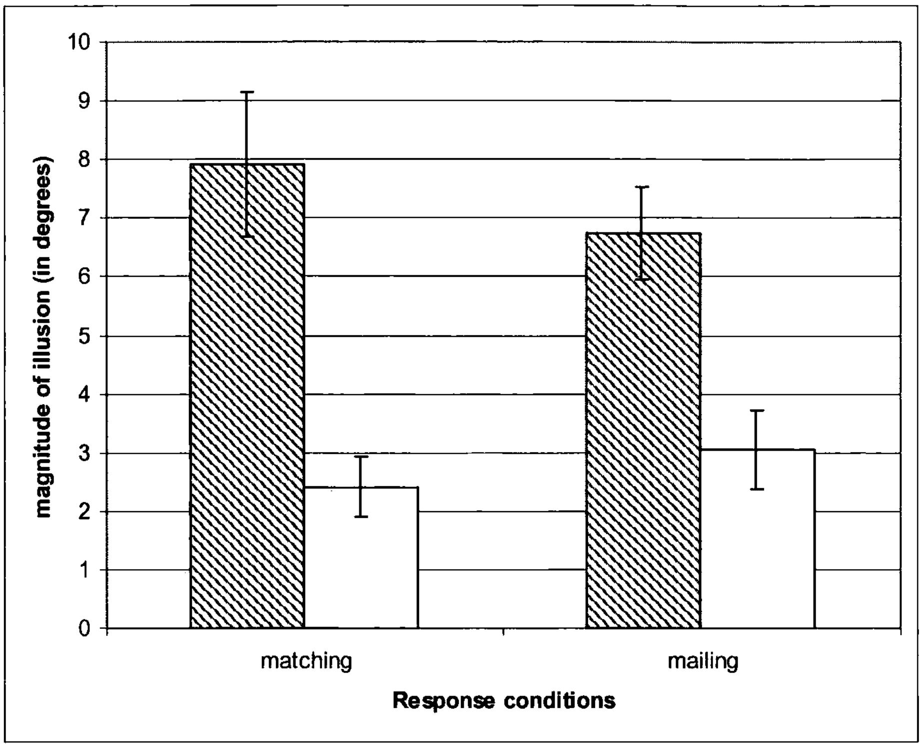

Figure 6.5. Comparison of mean magnitude of illusion between Study 2 (n = 12, filled bars) and Study 6 (n= 10, clear bars) across conditions. – matching (the perceptual measure) and open loop posting ('mailing' – the visuo-motor measure).

The interaction between 'study' and 'condition' was also significant: $F(1,20) = 8.91$; $p = .026$. This indicated that the factors causing a reduction in the illusion magnitude was having a different effect on the matching and posting conditions. A post-hoc comparison of the magnitude of illusion shows that there was a reliable change in illusion strength for the matching measure between studies: Kolmogorov-Smirnov Z = 1.56; $p =.016$. However the change in illusion strength in the visuo-motor measure, although indicating a strong trend, was not statistically reliable: Kolmogorov-Smirnov $Z = 1.32$ $p = .060$.

The presence of the interaction between study and response type would indicate that the framed-STI of the current study had a proportionally larger influence on the matching measure than on the visuo-motor measure. This would support the conjecture that the presence of a distal upright frame would provide a strong cue in the perception response. However there seems to be some indication that the visuo-motor measure may also be influenced by the frame.

<u>Complementary RFI/STI array results</u>

The complementary pair (stimuli 75/75/90 and 105/105/90) represent arrays where illusory effects of annulus and frame are acting in potentially additive ways. In this comparison we would expect to find a larger net illusion in the matching measure than in the visuo-motor measure, replicating the results of study 4. The summarised results for this array are presented in figure 6.6.

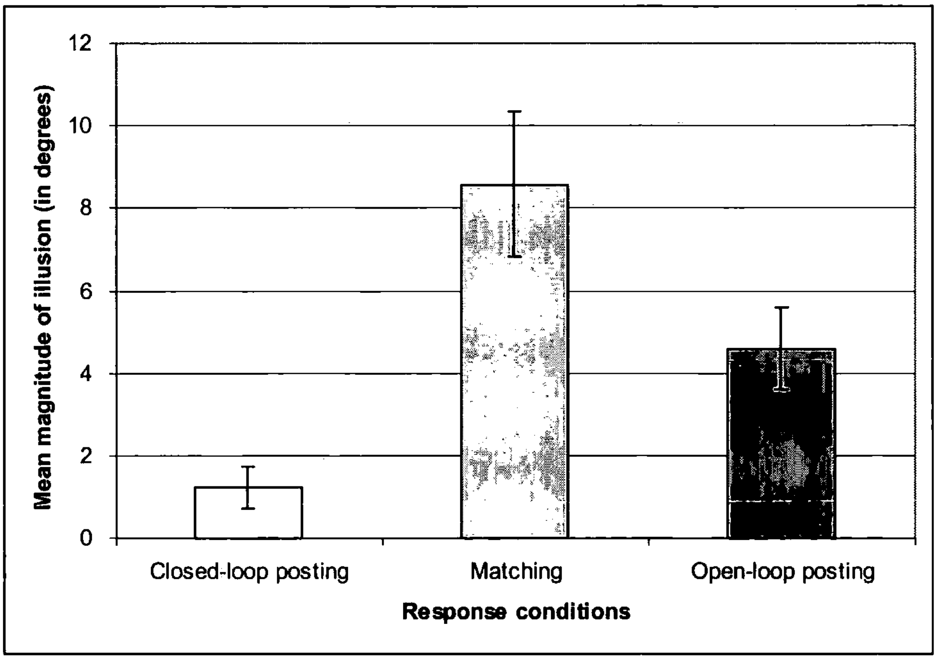

Figure 6.6: Group mean (n = 10) magnitude of illusion in the STI-RFI complementary pair - calculated as the difference in mean response to stimulus '75/75/90' minus mean response to stimulus '105/105/90' (i.e. predicting an illusion in direction found in previous studies). Error bars indicate one standard error of the mean.

Statistical analyses of the magnitude of illusion (paired Student t-tests comparing responses to stimuli 75/75/90 and 105/105/90) indicated that there were illusory effects in all conditions: for closed-loop posting $t(9) = 2.37$; $p = .021$(one tailed); for matching $t(9) = 4.84$; $p = .00046$ (one-tailed); open-loop posting $t(9) = 4.61$; $p = .00064$ (one-tailed). Correction for multiple comparisons demands alpha at $< .0167$ which suggests that the illusion in the closed-loop posting condition may not be reliable, but the illusions in matching and open-loop posting remain above criterion. This seems to indicate a similar pattern to the results of the framed-STI, whereby in the closed-loop posting condition, visually guided matching of the card to the target grating on completion of the response largely negates the illusion in this condition.

We had generally predicted that the frame would have a smaller effect on posting response than on matching. Therefore for this complementary array we predicted that the illusion strength should be higher in the matching than in the posting condition. In order to test this, a comparison of illusion magnitudes between these two conditions was conducted. This test indicated, as predicted, a reliably larger illusion magnitude in the matching condition in comparison with the open-loop posting condition: $t(9) = 2.75$; $p = .011$ (one-tailed). There was also evidence for an association of effects in the complementary array between the magnitude of illusion found in the matching and the open-loop posting measures. A correlation of these two data results in a reliable positive correlation: Pearsons $r(9) = 0.56$; $p < .01$ (one-tailed). This might be expected bearing in mind that the STI had shown an association of effects across conditions in study 2, but the persistence of this associative relationship even where both illusion types are acting, suggests again that there may be shared causality in terms of the illusory effect in not only the STI, but also where is it combined with the RFI in a complementary way. In effect the presence of a reliable difference in illusion strength (matching > open-loop posting) and evidence for association across measures, indicates that the two illusions may be acting in an essentially additive way (when complementary) and that perhaps even in the visuo-motor measure some effects of frame tilt may be present.

Comparing the framed-STI and the Complementary RFI/STI arrays.

If the matching response is influenced by both STI and RFI, whereas open-loop posting is relatively refractory to the frame (but still subject to the STI influence) then when the results of the framed-STI and complementary arrays are compared across conditions there should be an indication of a different effect of the tilted frame on illusion magnitude across measures.

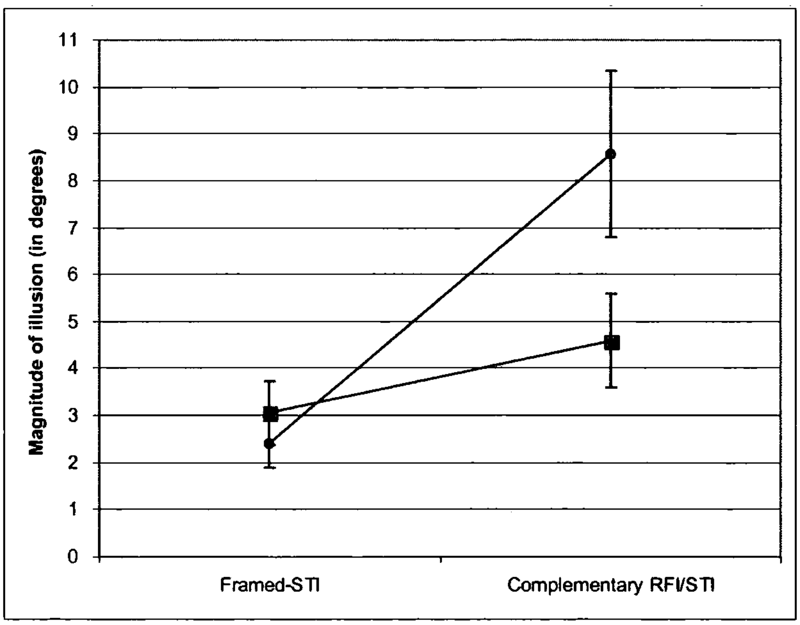

Figure 6.7. Group mean (n = 10) illusion magnitudes for open loop posting (square) and matching (circle) measures in the framed-STI and the complementary STI/RFI arrays. Error bars indicate one standard deviation of the mean.

Figure 6.7 illustrates the mean illusion strengths for the two response conditions across the 2 array types. A 2 x2 repeated measures ANOVA shows that the main affect of array type (framed-RFI vs. complementary RFI/STI) shows a statistically reliable effect: the overall illusion strength increases when both illusions are acting together $F(1,9) = 14.10$; $p = .005$. The main effect of response type (matching vs. open-loop posting) just fails to meet the 5% significance level – $F(1,9) = 4.50$; $p = .063$ indicating that there may be a trend towards the matching measure returning a larger illusion, and from figure 6.7 this appears to be as a result of the predicted large illusory effect on matching due to the tilted frame in the complementary array.

The interaction of array type and response condition is also significant $F(1,9) = 10.39$; $p = .010$. This interaction provides strong evidence for a different effect of the change in array type on response condition – the matching condition being proportionally more affected by the addition of tilt to the frame (in the complementary array) than the visuo-motor condition. Our *a priori* prediction was that the frame should have little influence on the open-loop posting condition. This should have resulted in little change in illusion magnitude where the effect in the framed-STI array and the complementary RFI/STI are compared. A planned comparison of the change in magnitude between the framed-STI and complementary array in open loop-posting measure was carried out. Although this analysis indicated a trend towards a larger magnitude of effect in the complementary over the framed-STI array in the open-loop posting measure, this failed to meet criterion: $t(9) = 1.85$; $p = 0.049$ (one-tailed, predicting a difference in favour of the complementary array); $p = .097$ (two-tailed). As no prediction of difference had been made the two-tailed criterion should be applied, however this relatively strong trend may indicate that the frame may be having some influence on this visuo-motor measure (counter to the predictions of complete dissociation which were indicated from study 4).

A comparison of illusion magnitude between the framed-STI and complementary RFI/STI arrays for the matching condition should have presented a much stronger difference if the results from study 4 are to be replicated. In this comparison we expected to find a reliability larger illusory effect for the complementary array than in the framed-STI array. This prediction was made on the basis that both the frame and the annulus should have additive effects in the complementary array, whereas in the framed-STI array was only one acting illusion. The upright frame may have in fact actively depress the illusion strength in this perceptual measure as was potentially indicated by the trend towards a smaller illusory magnitude in the framed-STI array when compared to the results of the unframed STI of study 2 (as referenced above). This result echoed the finding of a similar (although unreliable trend) by Poom (personal correspondence, reference above). A paired Students t-test showed that the illusion magnitude in the matching measure for the complementary array was clearly larger than that for the framed STI array : $t(9) = 3.91$; $p= .0017$(one-tailed). After correcting for multiple comparisons this analysis still returns a statistically reliable difference.

In summary it appeared that the presence of a tilted frame was having a strong influence on the perceptual measure, but there were some indications once more that the visuo-motor measure was not entirely impervious to the presence of a tilted frame.

Opposing RFI/STI array results

The opposing STI/RFI pair (stimuli 105/75/90 and 75/105/90) was designed to induce a larger illusion in the visuo-motor measure than the perceptual measure. This prediction stems from the findings of study 2 and study 4 that indicate that when in opposition the two illusions should largely counter-act in the perception measure, but should not counter-act in the visuo-motor response. Figure 6.8 shows the summarised result for the opposing pair and does show the predicted effect of a larger net illusion in the open loop-posting task than in the matching response. However, as is implied by the error bars in figure 6.8, the matching response seems to have an unusually high variance across the group.

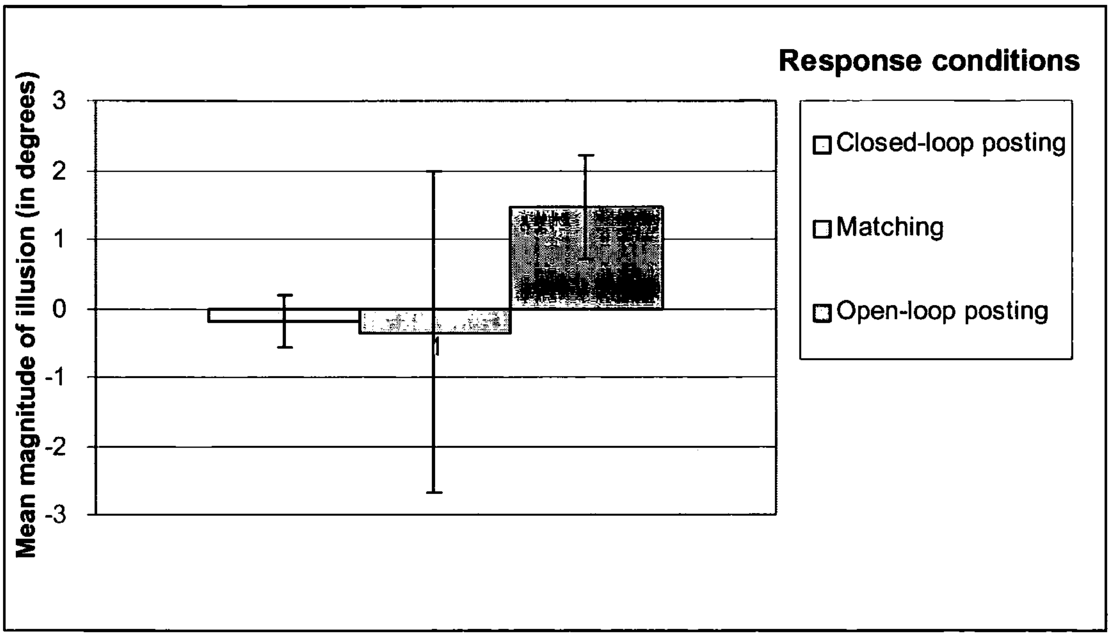

Figure 6.8 . The group mean (n= 10) magnitude of illusion for the opposing array calculated as the mean response to stimulus 105/75/90 minus the mean response to stimulus 75/105/90. Error bars indicate one standard error of the mean.

Table 6.1 details the breakdown of results for the subject group, and shows that in the matching condition there is a wide spread of resulting responses across the group: from a positive effect of 14.17 degrees of net illusion (indicating a stronger STI over RFI effect - subject 2) to an almost equally high opposite effect (RFI dominating the STI) in subject 6.

Subject	Closed-loop posting	Matching	Open-loop posting
1	-1.63	-5.17	-0.58
2	0.74	14.17	0.85
3	-1.00	-1.17	2.79
4	2.03	-1.17	0.10
5	-1.65	-2.00	6.50
6	0.17	-13.83	1.99
7	-0.96	-1.17	-0.21
8	0.87	7.83	2.81
9	-0.30	-1.17	-2.02
10	-0.09	0.17	2.34
mean	-0.18	-0.35	1.46
s.e.	0.37	2.33	0.76

Table 6.1: Individual magnitudes of illusion for the opposing array calculated as the mean response (over 6 trials) to stimulus 105/75/90 minus the mean response (over 6 trials) to stimulus 75/105/90. Positive results indicate a stronger effect of the STI over the RFI, negative results indicate the opposite effect.

When the illusion strength (comparing responses to stimuli 105/75/90 versus 75/105/90) was examined for each response condition in order to determine the difference from baseline, only the open-loop posting measure showed a reliable illusion: $t(9) = 1.93$; $p = .04$. However, when correction for multiple comparisons was applied, this effect too was rendered unreliable. In effect, therefore, the composite oppositional arrays failed to produce a statistically reliable effect on any measure. A comparison of the difference in magnitude of illusion between the matching and the open-loop posting conditions similarly failed to show any reliable difference: t(9) = .74; n.s. Therefore, although overall the pattern of effects follows our predictions, it fails to confirm reliably the study hypotheses.

<u>Comparisons between the RFI/STI opposing and RFI/STI complementary arrays</u>

Again under the assumption that the frame orientation would affect the matching measure more than the open-loop posting measure, a 2 x 2 repeated measures ANOVA was conducted looking at array type (opposing versus complementary arrays) and response type (matching versus open-loop posting). Figure 6.9 illustrates this comparison.

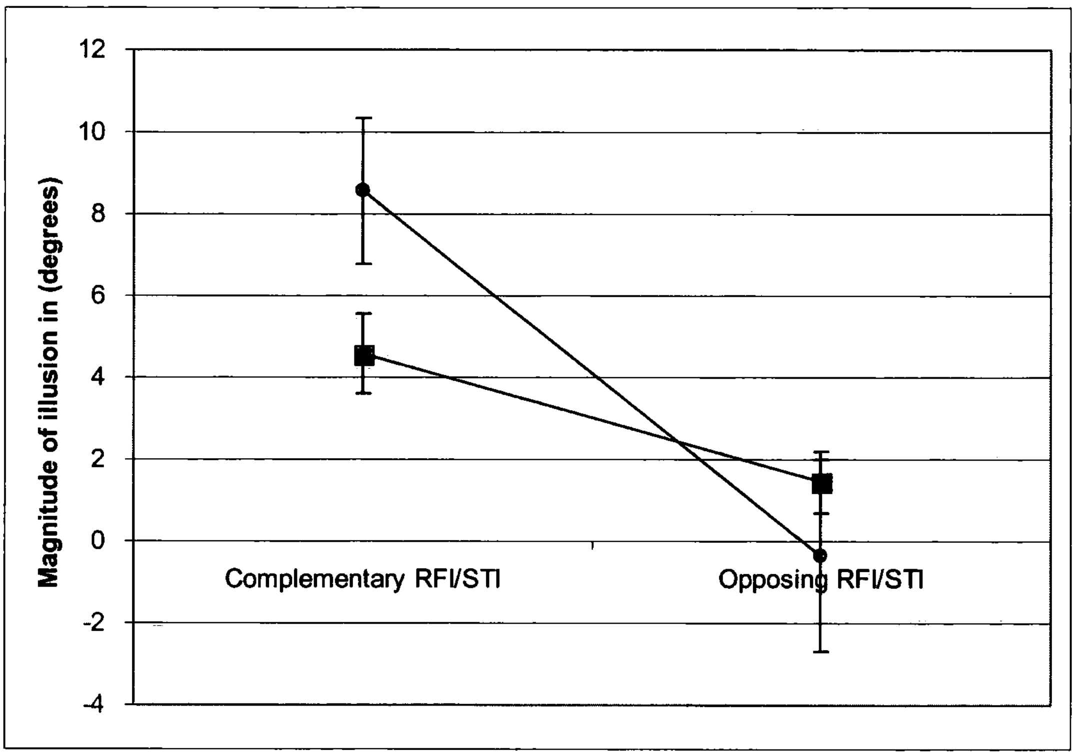

Figure 6.9 Group mean (n = 10) illusion magnitudes for open loop posting (square) and matching (circle) measures in the complementary STI/RFI and opposing RFI/STI arrays. Error bars indicate one standard error of the mean.

There is a significant main affect of array type $F(1,9) = 8.29$; $p < .05$ indicating that overall the complementary array returns a higher magnitude of illusion than the opposing array. However, the interaction that is indicated in figure 6.8 is statistically non-significant: $F(1,9) = 2.64$; $p = .138$ (n.s.). This fails to confirm reliably our prediction that there should be a greater effect of frame orientation on the matching measure than on the open-loop posting measure. A planned comparison (contrasting the magnitude of illusion for complementary and opposing arrays in both conditions) indicated that both matching and visuo-motor measures showed a significantly higher magnitude of illusion in the complementary than in the opposing array: $t(9) = 2.38$; $p =.021$(one-tailed) in the matching measure; $t(9) = 2.81$; $p = .010$ (one tailed) in the visuo-motor measure. After Bonferroni correction both these comparisons remain reliably different. This result indicates once more that the magnitude of illusion in both measures is being influenced by the surrounding frame, although the (albeit non-significant) trend towards an interaction indicates perhaps a greater influence in the matching measure than the visuo-motor measure.

In summary these comparisons seem to indicate a similar pattern of effects to previous results in this study. There is evidence for a strong effect of frame on the matching measure but a smaller residual effect of frame on the open-loop visuo motor task as well. There are only some non-significant indications (in terms of the patterns of interactions) for the predicted difference in favour of a greater effect of frame on the perceptual response.

Discussion

Illusion refraction in the closed-loop posting measure

In general the closed-loop (full vision) posting response was largely refractory to illusory effects in all conditions. This is most likely to be as the result of direct comparison between the palette orientation and the target grating on closure. It illustrates that closed-loop visuo-motor responses (where the dependent variable is taken late in the response) may not be valid comparison with perceptual measures as the result of online correction, and in particular late corrections as the target and the effector converge.

Frame tilt effects on the visuo-motor measure

Taken overall the results indicate that there is evidence for a strong effect of both STI and tilted frame on the perceptual measure. There was, however, also evidence that suggests that the open-loop posting task is also influenced by both illusions, although it would appear that the effects of 'frame-of-reference' were considerably smaller in the visuo-motor measure. This would suggest a partial-dissociation between measures in terms of effect of the tilted frame in the posting visuo-motor task. This result again suggests that the full dissociation in the grasping versus matching comparison of study 4 may have been confounded by differences in task demands of the compared conditions (potentially grasp point coding; Brenner and Smeets, 1996).

The framed-STI array showed evidence for association of effects between the two key measures (matching and open-loop posting) and represents a replication of studies 1 and 2. The presence of a positive correlation in magnitudes of effect for the complementary array between these measures also suggests that even when both illusion types are present that this associative relationship persists. This may be a further indication of some contributory effect of the frame on the action measure.

Upright frame effects on the visuo-motor and perceptual measures

There was also evidence for a reduction in overall magnitude of effect in this study's framed-STI array compared to the unframed STI of studies 1 and 2. There was also an indication of a different effect on the perception measure in comparison with the action measure in this change in magnitude between the STI arrays of study 2, versus that of the framed-STI in this study.

There were, however, a number of changes between the STI presented in studies 1 and 2 and the framed-STI array in this study. The STI in the earlier studies had a target grating 74.6 mm in diameter, and annulus diameter 115mm, whereas the STI in this study had a target grating 93 mm in diameter and the surrounding annulus was 166 mm diameter. This change had been made because early pilots of the framed-STI array with the original STI dimensions of studies 1 and 2 indicated a very small illusion – and the grating dimension was increased in order to ensure a measurable illusory effect (in line with the findings of Wenderoth and Johnstone 1988a). As such this change should be expected to increase the illusory affect (rather than decrease it). Secondly the STI in Studies 1 and 2 was presented on a phospholuminescent screen whereas in this study the STI was presented in dimly lit room conditions. It is likely therefore that the grating contrast of the STI in studies 1 and 2 was considerably higher than in the current study. Tolhurst and Thompson (1973) and Wenderoth and Johnstone (1988a) have reported a *decrease* in illusory magnitude for both the after-effect and simultaneous versions of the illusion as contrast *increases*, and as such this again would suggest that the illusion strength in the current study should be higher than that of studies 1 and 2. A third change in the stimulus was that the difference between target and annulus had been 12 degrees in study 2 whereas (in order to limit the number of differently oriented contours) this had been changed to 15 degrees for this study. No studies have specifically compared illusion strengths at these two orientations: previous work merely places the peak effects at target/annulus differences greater than 10 degree and smaller than 20 degree. The change in inducing orientation may be a contributory cause to the reduction in effect, but the large difference observed is unlikely to be fully accounted for by this small alteration in target/annulus orientation difference.

Finally, of course the STI in this study was framed, whereas in studies 1 and 2 all proximal visual cues to horizontal and vertical were excluded as a result of the obscuring annular mask. If the presence of the upright frame *was* the chief causal factor in the reduction in illusion magnitude, we would predict a larger reduction in matching measures than visuo-motor measures (which should be largely unaffected by the distal stimulus). The presence of an interaction between STI type and response condition (the ANOVA comparing the results of study 2 and the current study) does support the suggestion that the frame is having a larger effect on the perception measure (in this case an effect that reduces illusory magnitude). However the changes in the STI from the earlier studies preclude any firm conclusions as to the effect of the upright frame. In order to investigate this further, a replication of study 2 was planned using the current STI form.

Evidence for a greater effect of frame tilt on the perceptual measure

In the complementary array where both illusions are assumed to be to some extent additive, there was evidence for a larger illusion in matching measure over the open-loop posting measure. This is in line with predictions of a greater effect of framing on perception than visuo-motor control. The comparison of illusion magnitudes between the framed-STI and the complementary array showed clear evidence for an interaction between array type and response condition. As the key difference between array types is the tilt (in the complementary array) of the frame, this would again follow our predictions of a larger effect of frame tilt on perception than on visuo-motor control.

The opposing arrays

The results from the opposing array were inconclusive. Although the trend was in the direction predicted (of a larger illusory effect in open-loop posting than the matching measure), firm conclusions cannot be drawn mainly because of extreme individual variation in responses in the perception measure. This would indicate that if the opposing array is to be used, then a substantially larger subject group should be tested in order to reduce the effects of individual differences in responding to this composite display.

Conclusions

In summary the weight of evidence clearly points to a larger influence of the frame on the perception measure but there are suggestions that there may be some residual effects of frame orientation on the visuo-motor measures. In order to examine more clearly the use of the composite arrays, a further study was undertaken. This sought to directly address the issues raised in this study, and to specifically examine the potential for a two-way interaction in illusion strength between perceptual and visuo-motor measures.

Chapter 7: Study 6 - Composite RFI/STI and the 'rods-and-frame' illusion.

Introduction

The results from study 5 suggest it may be possible that a larger illusion could be generated in an open-loop posting measure in comparison with a measure of perception through embedding the STI within a counter-tilted frame. However it appears that individual differences in response to the opposing composite array of study 5 may have been masking any effects of this kind. As such a larger subject group would be required to determine if a reliable illusory effect could be produced using a composite array.

Also there seems to be evidence that the posting measure against a target grating is, to some extent, influenced by the frame (in contrast to the almost complete resistance of the rod-grasping response in study 4). This would be in line with the suggestion from Chapter 1 that a partial, rather than a complete dissociation between perception and action measures may be present in healthy subjects where the illusion paradigm is employed. It may also indicate and that the grasping response of study 4 has access to additional cues to allowing a more veridical response (e.g. grasp point coding: Brenner and Smeets, 1996, 2000).

Study 5 also indicated that placing the STI within an upright reduced the STI illusion strength. However because of a number of changes that were made to the STI sub-array between studies 2 and 5 it was unclear whether differences in the stimulus may have accounted for these. A replication of the study 2 design using the STI variant from study 5 (without cues to horizontal or vertical) would help determine the source of the apparent reduction in illusion strength found between study 2 and study 5.

A novel perceptual measure: "adjust to vertical"

One source of criticism in terms of the illusion paradigm itself in looking at differences between perception and visuo-motor responses is that the task demands of the two measures may account for any dissociations found. Although the results from study 2 would appear to refute this claim, the paradigm still involves differences between conditions in order to differentially tap the dorsal and ventral visual streams.

A key remaining difference is that the visuo-motor task involves no shift in gaze between the position of stimulus presentation and response location, whereas the perceptual measure involves making a response at another point in visual space, and so involves potentially multiple visual shifts. These shifts cause not only effects associated with shifts in visual attention, but also results in different elements of the visual array passing across the retinae during potentially multiple shifts in gaze. To ensure that differential results cannot be attributed to gaze shifts, an additional perceptual measure that involves singular attention to the target is required.

If a subject were to rotate the STI sub-array so as to match their perception of gravitational vertical, this would control for aspects of the different responses between conditions that could be attributed to shifts in visual gaze, and still be likely to tap the perceptual system's processing of orientation. Additionally this response allows testing of the assumption concerning the underlying causal mechanisms involved in the 'frame of reference effect'. Adjusting the target grating to gravitational vertical indicates whether the subject's internal representation of vertical (or their ability to adjust a grating to be in line with it) has been altered as a result of frame tilt. In the matching condition subjects may well have been using their model of gravitational vertical as a reference frame, but may also have been using corporeal reference frames (which may have been distorted by either actual self-tilt as a result of the tilted frame, or assumptions of self-tilt). An adjust to vertical response would more directly measure potential changes in subject's coding of the vertical meridian.

Additionally the 'adjust to vertical' task demands a response in the opposite direction to the matching response. An anti-clockwise tilted frame induces a matching response in which the rod in the matching apparatus is typically rotated in a **clockwise** direction from vertical (as a vertical rod is perceived as being inclined in the opposite direction from vertical to the frame tilt). In the 'adjust to vertical' response the same frame orientation (i.e. anti-clockwise tilt) typically induces a response to rotate the target grating (and the entire STI sub-array) in an **anti-clockwise** direction from vertical (so as to be in-line with the shift in perceived gravitational vertical that has been altered towards the frame tilt). As such the 'adjust to vertical' measure addresses additional potentially uncontrolled effects: e.g. artefacts that may stem from the fact that the matching apparatus was always positioned to the right of the frame, and no-counter-balancing for target frame/matching frame position is normally practical in the testing time available.

Study Predictions

The present study proposed that in perceptual measures (whether with or without a shift in visual attention), a target stimulus surrounded by a distal tilted visual frame will show a larger magnitude of tilt illusion than any illusory effect evident in a visuo-motor measure.

In contrast, a target surrounded by contiguous contours of one orientation, with a distal tilted frame of the opposite tilt (achieved by embedding the STI in a counter-acting tilted frame as in study 5) should show the opposite pattern of differences in terms of relative illusory magnitude on the two measures: there should now be a larger illusion in visuo-motor control than in subjective perception. This pattern, it is suggested, results from a strong counter-acting effect of both illusory inducers on perception, whereas visuo-motor control should be more refractory to the 'correcting' influence of the tilted frame and be subject to the illusory effect of the grating annulus alone.

The study therefore predicts a two-way interaction between measures with a greater illusory effect in the perception measure using the RFI, and a greater illusory effect in the visuo-motor measure using the opposing RFI/STI array. Such an interaction would present strong evidence for the different processing of orientation for the two measures.

Additionally the study aims at determining whether the revised STI sub-array (as used in study 5) induces a smaller illusion magnitude than that found for the STI variant used in studies 1 and 2.

Method

Subjects

The subject group comprised of 17 subjects (11 female, 6 male, age range 19–42 years) who were undergraduate psychology students. All were right-hand dominant with normal or corrected-to-normal vision, and were naïve to the illusion. None had taken part in any related studies.

Stimuli/Apparatus

The frame apparatus and room conditions were identical to those in study 5.

As in study 5, in referring to stimuli there are 3 elements: the orientation of the surrounding frame, the orientation of the grating annulus and the orientation of the target grating. Stimuli are labelled in terms of these 3 orientations from outermost to innermost, thus an array with a frame of 105 degrees, an annulus of 75 degrees and a target grating of 90 degrees (all as measured from the left hand horizontal as presented to the subject) would be labelled "105/75/90". Where either the annulus or the frame are masked, this is indicated by ascribing an orientation of '0' to that element.

Nineteen stimuli were presented (see appendix A, figure a14 for illustrations):

105/75/90 and 75/105/90 (the **opposing pair**)

105/0/90 and 75/0/90 (the **rods-and-frame illusion pair**)

0/75/90 and 0/105/90 (the **STI alone pair**).

12 filler stimuli:	0/103/88, 0/107/92, 0/77/88, 0/77/92, 105/103/88, 105/73/88, 105/0/88, 105/105/90, 75/107/92, 75/77/92, 75/0/92, 75/75/90 (note that where the STI is presented either alone or embedded within a frame, that all target grating/annulus orientation differences are 15 degrees).
1 control stimulus:	0/0/90.

In order to mask the annulus of the STI to form the 'rods-and-frame' pair, a black, opaque annular mask was fixed in front of the annulus grating of the STI leaving the central target grating alone visible within the frame.

In order to mask the frame, a large, black, opaque torus-shaped mask was placed over the frame, with the STI presented centrally within the torus aperture (figure 7.1 illustrates this in the 'adjust' condition).

A closed-loop (full-vision) posting task, as well as adjust, match and post (open-loop) tasks were conducted to the 0/0/90 control stimulus in order to generate control data.

Design

The dependent variable was the magnitude of illusion in three conditions: adjusting to vertical ('adjust'), matching the target grating using the matching apparatus ('match'), and open-loop posting ('post'). The dependent variable (illusion magnitude) was calculated by the difference between the mean response to each stimulus of each stimulus pair (opposing, rods-and-frame, and STI).

Procedure

Testing this number of conditions and stimuli involved each subject in a lengthy testing process (usually approaching 2 hours). In order to ensure that the key comparison was completed - the predicted 2-way interaction between the perception measures and open-loop posting for the 'rods-and-frame' and the opposing array- initially time allowed for only the trial blocks for these to be completed. As the study progressed it was found that the additional trials necessary for STI (alone) could also be included within the time available. As such the entire subject pool was split into those where the STI arrays were excluded (the standard set) and where the STI arrays were included (the superset).

Trials were run in blocks counterbalanced by response type. Within each trial block, stimuli were pseudo-randomised so that no stimulus was presented consecutively on any two trials. The response to each test stimulus was taken as the mean over either 5 or 7 trials for each subject in each condition. Results from study 5 had indicated that the opposing array might provide a wide spread of results in the subject group. To ensure that inter-trial variance was minimised as far as possible the mean for any one stimulus was calculated over 7 trials for the opposing arrays and over 5 trials for all other stimuli (the complementary arrays, the STI alone, the rods-and-frame array and control stimuli).

Prior to each trial the subject closed their eyes whilst the stimulus was adjusted. At the beginning of each trial the experimenter initiated the control software and instructed the subject to open their eyes and fixate the target grating. After 2000 ms a tone sounded which acted as the response cue.

The open-loop posting task and the matching task were performed in an identical manner to that described for study 5.

The adjust task was performed within the same 2 second response window as applied in the matching task. The task required the subject to adjust the whole STI sub-array so that the central target grating matched gravitational vertical. This was performed by the subject rotating the STI array so as to line up the target grating with 'gravitational vertical'. The annulus and target gratings were firmly connected, so that when the outer annulus was rotated, the central target grating could be adjusted to the perceived vertical.

As in the matching task, the STI-sub array was randomly adjusted so that the central target grating was initially either 7 degrees clockwise or anti-clockwise from vertical before each trial. The dependent variable was taken by reference to the scale on the reverse side of the target apparatus (unseen by the subject). Figure 7.1 illustrates this task.

As in the posting task, the matching apparatus was masked during to avoid it being used as a cue to gravitational vertical/horizontal.

Figure 7.1. Schematic of the 'adjust' perceptual measure to stimulus "0/105/90"

Results

Interaction effects between the matching and the posting conditions

It was predicted that in the 'rods-and-frame' array (stimuli 75/0/90 and 105/0/90) that there would be a larger illusion in the perception than the visuo-motor conditions.

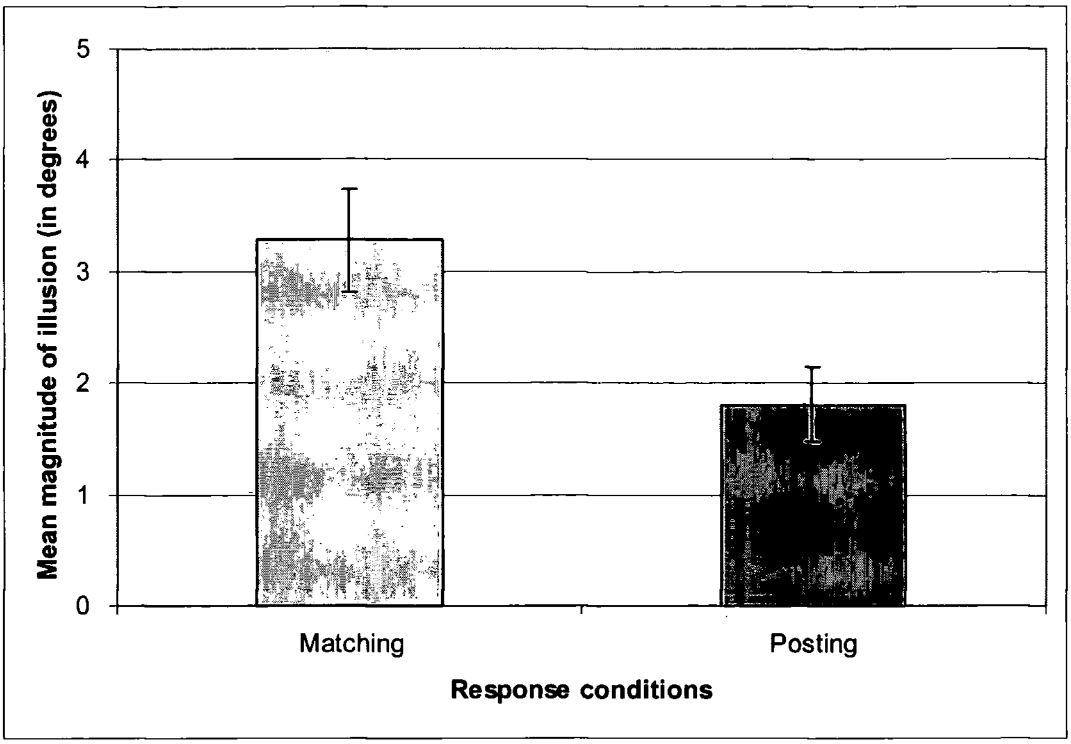

Figure 7.2: Group mean magnitude of illusion (n= 17) for the match and post measures to the 'rods-and-frame" arrays - calculated as the mean response to stimulus 75/0/90 minus mean response to stimulus 105/0/90. Error bars show one standard error of the mean.

Figure 7.2 illustrates the predicted larger magnitude of illusion in the matching condition. A statistical analysis showed that the difference in mean magnitudes across the two measures to be reliable: $t(16) = 3.25$; $p < .01$. The matching measures shows a reliable effect above baseline - comparing mean responses to stimuli 75/0/90 and 105/0/90 : $t(16) = 7.37$; $p < .00000001$ (one-tailed). Of note, however, is that in the posting measure this effect is also reliably above baseline: a comparison of the responses to stimuli 75/0/90 and 105/0/90 in the measure shows a difference that is highly unlikely to be the result of chance: $t(16) = 6.15$; $p < .00001$ (one-tailed). This is in line with the suggestion from study 5, which indicated that the open-loop posting measure might be influenced by the tilted frame.

We had predicted the opposite pattern of differences in the composite opposing array (stimuli 75/105/90 and 105/75/90): that of a larger effect in the visuo-motor measure than the perceptual measure. The study results again supported this prediction.

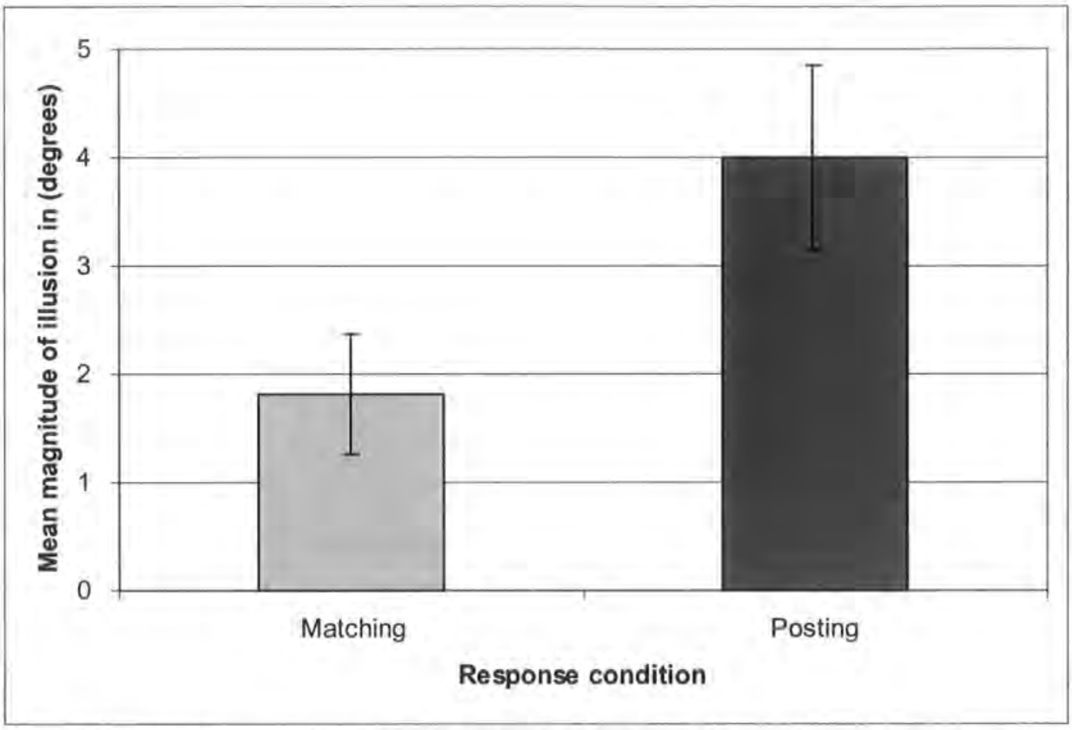

Figure 7.3: Group mean magnitude of illusion (n= 17) for the matching and open-loop posting measures to the composite opposing array (STI embedded within the counter-titled frame) - calculated as the mean response to stimulus 75/105/90 minus mean response to stimulus 75/105/90. Error bars show one standard error of the mean.

Figure 7.3 illustrates that both effects differed significantly from baseline (comparing mean responses to stimuli 75/105/90 and 105/75/90) – indicating that the STI effect outweighed the tilted frame effect (as can be predicted from comparisons of illusion magnitudes from study 2 and study 4). In the match measure, comparing mean response to 75/105/90 and 105/75/90, $t(16) = 4.86$; $p < .0001$ (one tailed). The same comparison for the post measure gives $t(16) = 5.60$; $p < .0001$ (one-tailed). Most importantly the comparison of magnitudes shows that the effect in the post measure is reliably larger than the match measure: $t(16) = 2.63$; $p < .01$.When combining the results from the opposing pair and the rods-and-frame pair, a clear interaction of effects can be seen (figure 7.4).

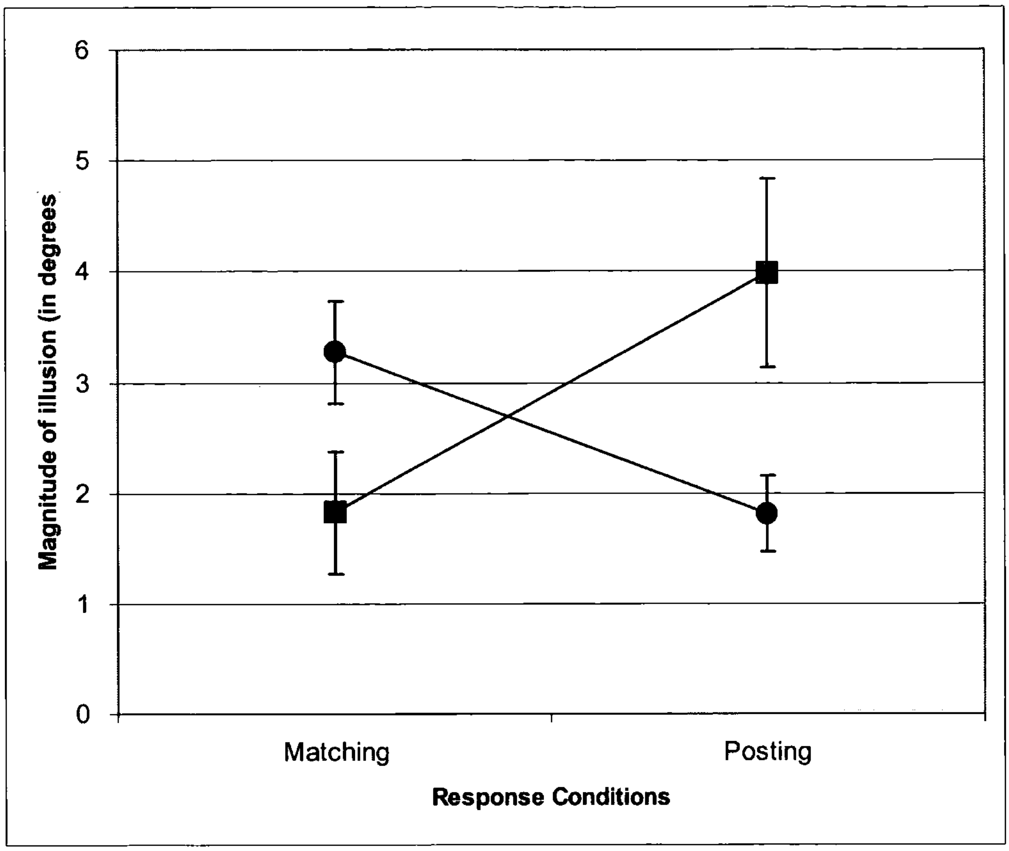

Figure 7.4: Pattern of magnitudes of illusion for the rods-and-frame array (round) and composite opposing array (square) across the match and post conditions. Error bars indicate one standard error of the mean.

A 2 x 2 repeated measures ANOVA was performed on array type (rods-and-frame .vs. opposing) and response condition (matching .vs. posting) and this showed the interaction to be highly reliable: $F(1, 16) = 16.90$; $p = .001$. This result strongly suggests that the match and post response conditions were differently influenced by the rods-and-frame and opposing arrays, in line with our predictions.

Interaction of illusory effects between adjust to vertical and posting measures.

Our predictions for the adjust to vertical and posting comparison are identical to those for the previous comparison between the matching and posting conditions: namely that the rods and frame array should result in the larger illusion in the perception (now the adjusting) measure whereas the opposing array should show the larger illusion in the visuo-motor posting measure.

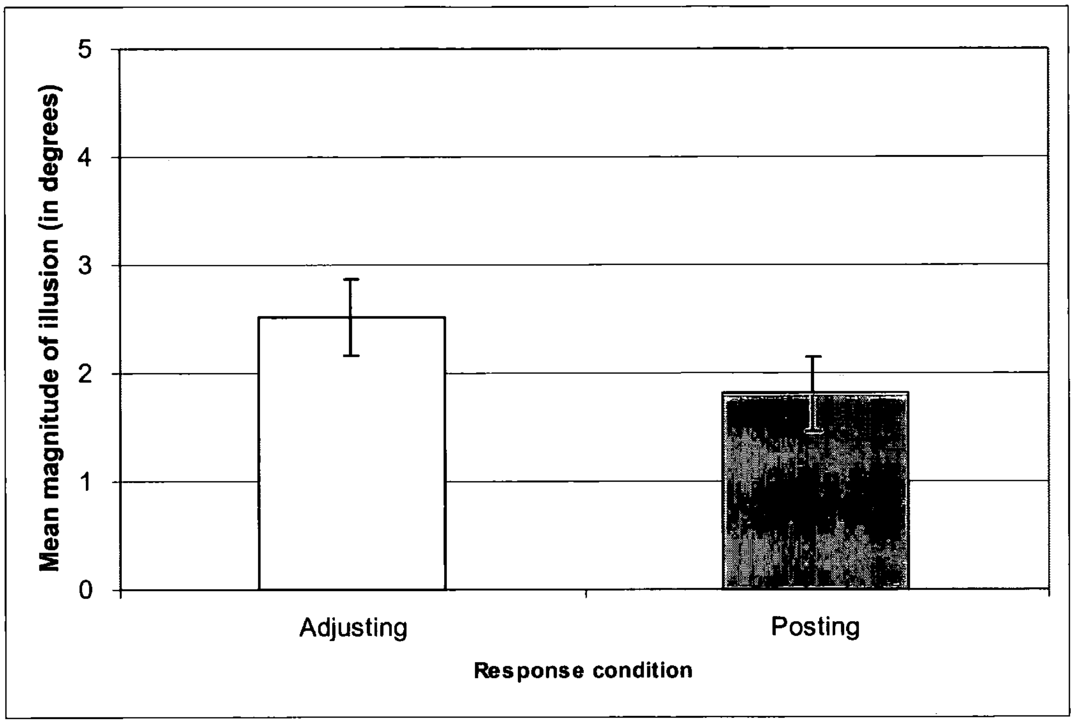

Figure 7.5: Group mean magnitude of illusion (n= 17) for the adjust and post measures to the rods-and-frame array - calculated as the mean response to stimulus 75/0/90 minus mean response to stimulus 105/0/90. Error bars show one standard error of the mean.

Figure 7.5 illustrates the pattern of differences between the adjust to vertical and the posting measure for the rods-and-frame array. As predicted the adjust measure shows a reliably larger illusion magnitude than the post measure: $t(16) = 1.94$; $p < .05$ (one-tailed). Figure 7.6 illustrates the predicted reversal of effects for the opposing composite array.

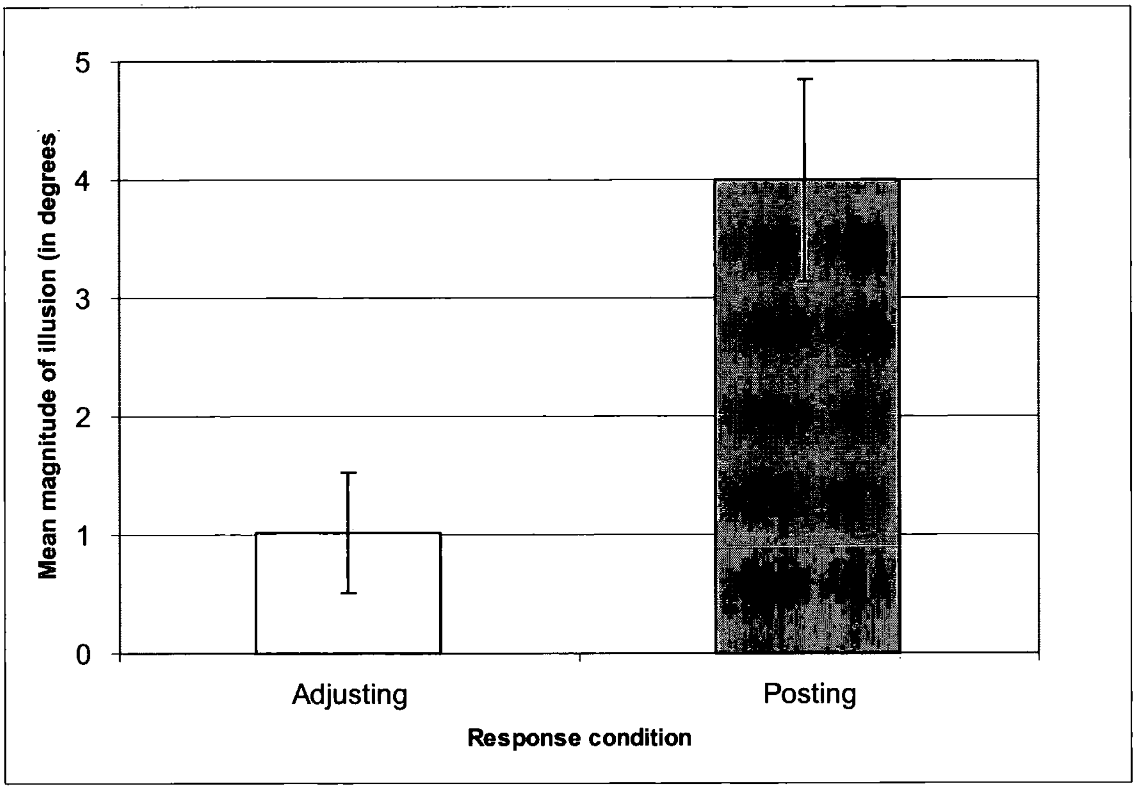

Figure 7.6: Group mean magnitude of illusion (n= 17) for the adjust and post measures to the composite opposing array (STI embedded within the counter-titled frame) - calculated as the mean response to stimulus 75/105/90 minus mean response to stimulus 75/105/90. Error bars show one standard error of the mean.

A statistical analysis of the difference in illusion magnitudes between conditions again shows this to be statistically reliable: $t(16) = 3.06$; $p < .01$ (one-tailed).

Figure 7.7 illustrates the interaction of array type and response condition. A 2 x 2 repeated measures ANOVA was performed on array type (rods-and-frame .vs. opposing) and response condition (adjust .vs. posting) and this showed the interaction to be reliable: $F(1, 16) = 10.48$; $p = .01$. This again suggests that the perceptual (in this case the adjust) measure and the visuo-motor open-loop post response conditions were differently influenced by the rods-and-frame and opposing arrays, in line with our predictions once more.

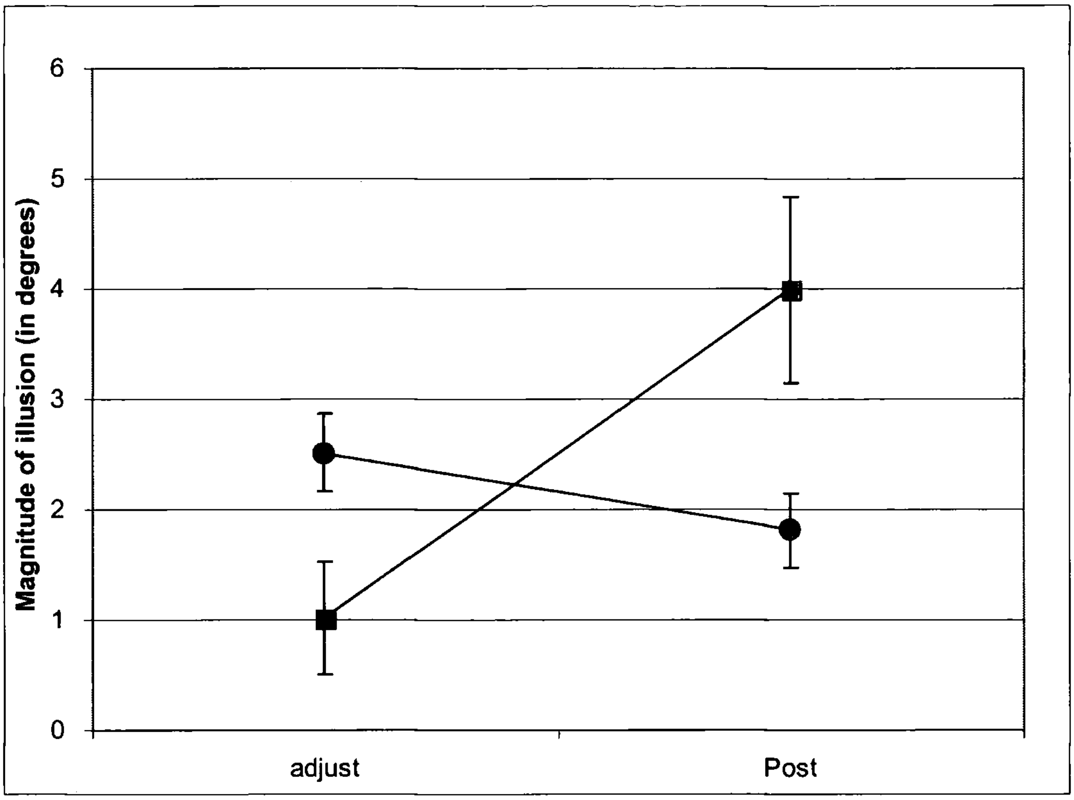

Figure 7.7: Pattern of magnitude of illusion for the rods-and-frame array (round) and composite opposing array (square) across the adjust and post conditions. Error bars indicate one standard error of the mean.

array type	rods-and-frame array			opposing array		
response type	Adjusting	Matching	Posting	Adjusting	Matching	Posting
Subject						
1	3.20	2.00	0.16	4.86	3.18	3.39
2	4.90	4.63	5.35	-1.29	3.50	5.08
3	2.80	7.40	3.02	0.00	0.70	-0.77
4	2.80	3.97	2.56	-0.29	0.30	2.83
5	1.20	4.38	-0.81	0.64	2.30	0.28
6	2.20	3.80	0.81	-1.19	-1.71	2.58
7	2.00	3.00	1.88	0.07	-1.79	2.56
8	5.00	6.23	3.48	0.14	5.75	5.74
9	3.10	5.10	2.81	5.36	5.71	5.82
10	1.40	2.00	1.14	-0.64	0.50	1.06
11	0.80	-0.30	2.00	3.21	5.43	7.32
12	2.10	3.40	1.45	-0.57	1.86	10.28
13	5.20	2.90	0.65	0.29	1.14	11.68
14	1.60	1.40	2.14	3.79	1.14	0.68
15	2.70	1.80	1.71	-0.43	0.46	0.13
16	1.60	1.80	1.15	0.57	0.64	5.58
17	0.10	2.20	1.31	2.71	1.86	3.65
mean	2.51	3.28	1.81	1.01	1.82	3.99
s.e.	0.35	0.46	0.34	0.51	0.55	0.85

Table: 7.1: Magnitudes of illusion (in degrees) for each subject in all conditions and array types, including group mean and standard error of the mean. Results derive from the subtraction of each array pair (rods-and-frame and opposing). Negative results indicate a response in the opposite direction to that predicted *a priori*: namely the direct effect for the rods-and frame array, and a larger 'STI' effect than tilted frame effect in the opposing array pair.

Table7.1 shows the results for each subject from which all analyses have been derived.

Correlatory analyses of magnitude of illusion

Evidence for common processes underlying adjust and match measures

It had been our conjecture that the adjust to vertical and the matching measures were both tapping the perceptual visual system. As such, if the magnitude of illusion found in these measures are compared for each subject, there should be a positive correlation found between them. Correlational analyses were carried out and these resulted in a positive and reliable correlation between the two conditions when responding to the 'rods-and-frame' array: Pearsons $r(16) = +.507$; $p = .019$ (one-tailed). A similar reliable positive correlation was found when the adjust to vertical and the matching measures were compared for the opposing array: Pearsons $r(16) = .519$; $p = .016$ (one tailed). This would indicate a shared causal affect of both the tilted frame alone and the composite array on these measures.

Evidence for shared causality in the rods-and-frame illusion

It is suggested that the residual effect found in the posting measure to the rods-and-frame array is as the result of only partial resistance of the action measure to the tilted frame. If this is the case there should be some evidence of shared causality between the illusory effect found in the perception measures and the action measure. This should result in a positive correlatory relationship in the illusion magnitude between measures for any one subject. A correlational analysis of the magnitude of illusion in the adjust to vertical and the posting tasks was performed for the rods-and-frame data. This showed a reliable, positive correlation in line with the suggestion that there is some shared effect of the tilted frame across measures: Pearsons $r(16) = + 0.465$; $p = .030$ (one-tailed). The same analysis, now comparing the matching and the posting measure, although showing a strong trend, just failed to reach statistical reliability: Pearsons $r(16) = +.404$; $p = 0.054$ (one-tailed). In spite of the lack of a consistently reliable positive correlation across measures for this residual effect, the presence of one statistically reliable correlation, and a second that indicates a strong trend, it seems reasonable to conclude that the illusion found in the posting measure in response to the rods-and-frame array shares some causality with the same effect found in the perceptual measures.

Results summary for perception and action measures comparisons

The results from the use of the two array types: 'rods-and-frame' and the opposing array indicate a clear reversal of effects across conditions. This pattern appears reliable even where the perceptual measure of 'adjust to vertical' is used, excluding the shift in gaze involved in the matching perception measure.

STI replication

In order to replicate previous results, and to determine what factors may have been underlying the reduced magnitude of the revised and framed-STI display in study 5, a number of subjects in the current study (n=9) were also tested on the STI alone, with the frame masked (see figure 7.1 above). However it was found that the visuo-motor measure could not be calculated as there appeared to be missing IRED data points as the posting card approached the target. The likely explanation for this was that the large mask around the display, which was back-lit, became warm over the testing session and emitted enough infra-red radiation as to interfere with the markers as they approached the target, a problem that had not been apparent in the piloting of the design. This had been noted during testing but only on later analysis was it found that one marker had been consistently missing for some considerable distance from the target, and as such the dependent measure of orientation could not be calculated for the open-loop measure. However the perceptual data were available (as these had been recorded manually by reference to the scale on the reverse of the apparatus).

Figure 7.8 illustrates the magnitude of illusion found in response to the STI for the matching measures in studies 2 and 5 and the current study

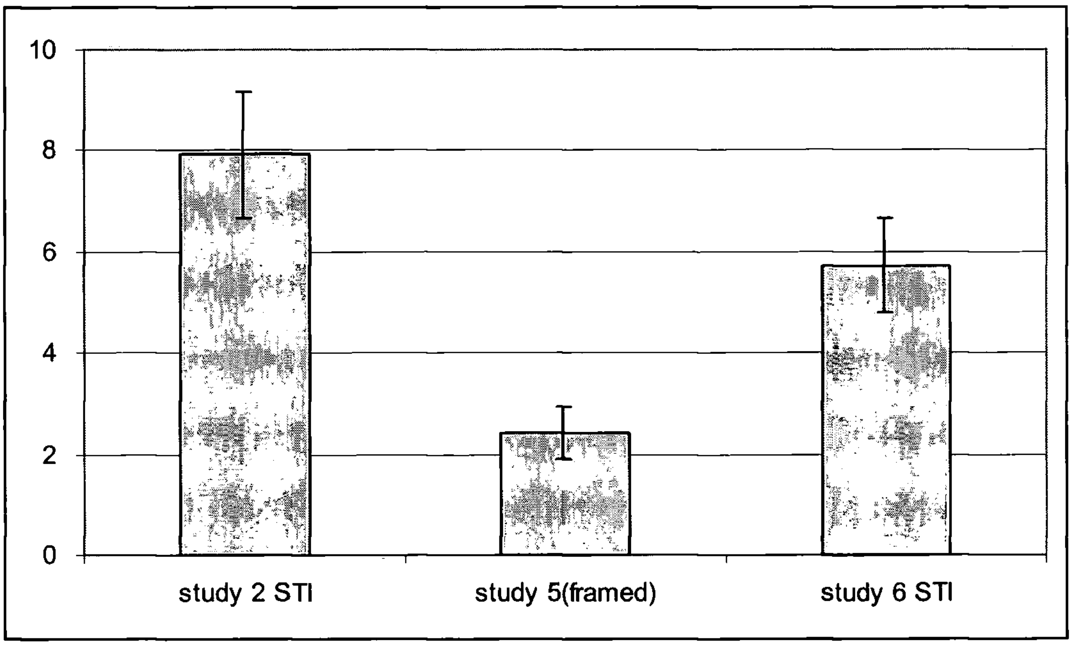

Figure 7.8: Mean magnitude in the matching measures in study 2 (n = 12); study 5 which used the framed-STI (n =10), and study 6 using the printed and modified STI (n = 9). Error bars indicate one standard error of the mean.

Although the mean magnitude of illusion for the framed-STI in study 5 was significantly smaller than *both* the magnitude in study 2 (Kolmogorov-Smirnov Z = 1.56; p .016, two-tailed) *and* the magnitude in study 6 (Kolmogorov-Smirnov Z = 1.45; p = .030, two-tailed), there was *no* reliable difference in illusion magnitudes when the results from study 2 and study 6 were compared (Kolmogorov-Smirnov Z = 1.34; n.s.). This pattern of results would suggest that the reduction in magnitude for the framed-STI in study 5 was a result, in part at least, of the presence of the upright frame providing veridical cues to horizontal and vertical, rather than the number of changes made to the STI array itself between study 2 and the subsequent studies. The presence of this effect would suggest that in measures of perception, the presence of an upright frame reduces the magnitude of illusion for the STI.

The suggestion that a frame cueing true orientation does reduce the illusion strength found in the STI indicates that the perception system incorporates cues from the wider visual scene that ameliorates the effects of even this low-level distortion of visual orientation processing.

Comparison of perceptual measures for STI and rods-and-frame illusions

A comparison between the two available perceptual measures showed a notable result (as illustrated in figure 7.9). The apparent larger illusion of magnitude in the match measure when compared to the adjust measure (figure 7.9) is highly reliable: $t(8) = 3.97$; $p < .01$; two tailed.

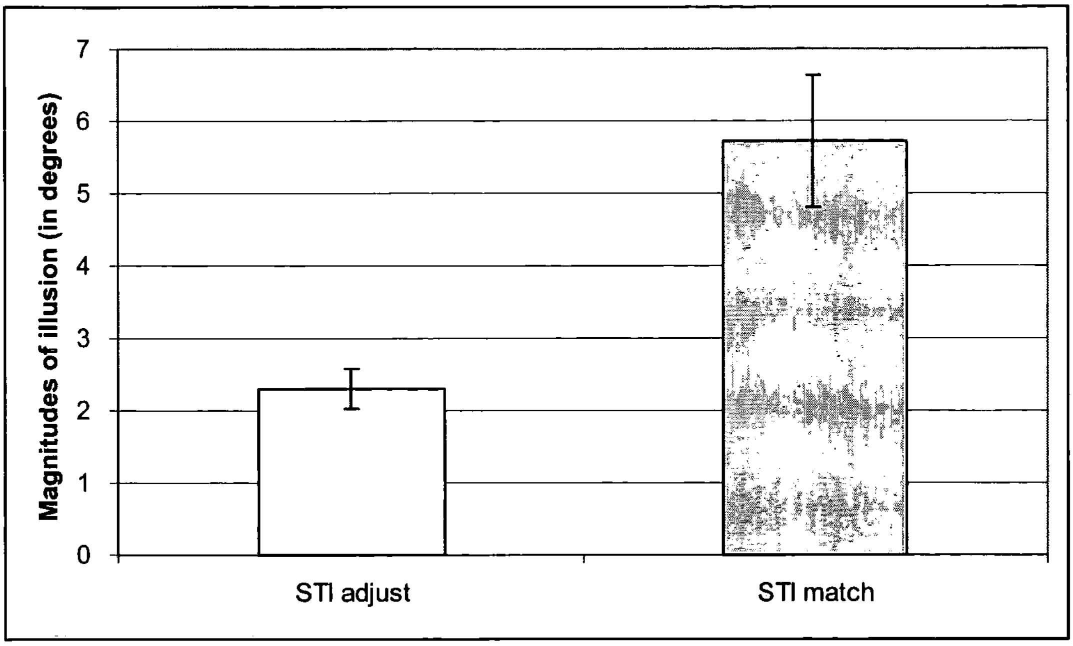

Figure 7.9. Mean magnitudes of illusion (n= 9) for the 'STI alone' display in the two perceptual measures of adjust and match. Calculated as the mean difference between the stimuli 0/75/90 and 0/105/90. Error bars indicate one standard error of the mean.

A correlatory analysis comparing adjust and match magnitudes of illusion for the STI, however failed to show a reliable correlation (Pearson r = .342; n.s.) – although the smaller subject group size (n = 9) may have contributed towards an unreliable result.

In order to examine this apparent difference between these two measures of perception, a similar comparison was carried out between the magnitude of illusion to the rods-and-frame illusion (figure 7.10) where a larger sample size was available.

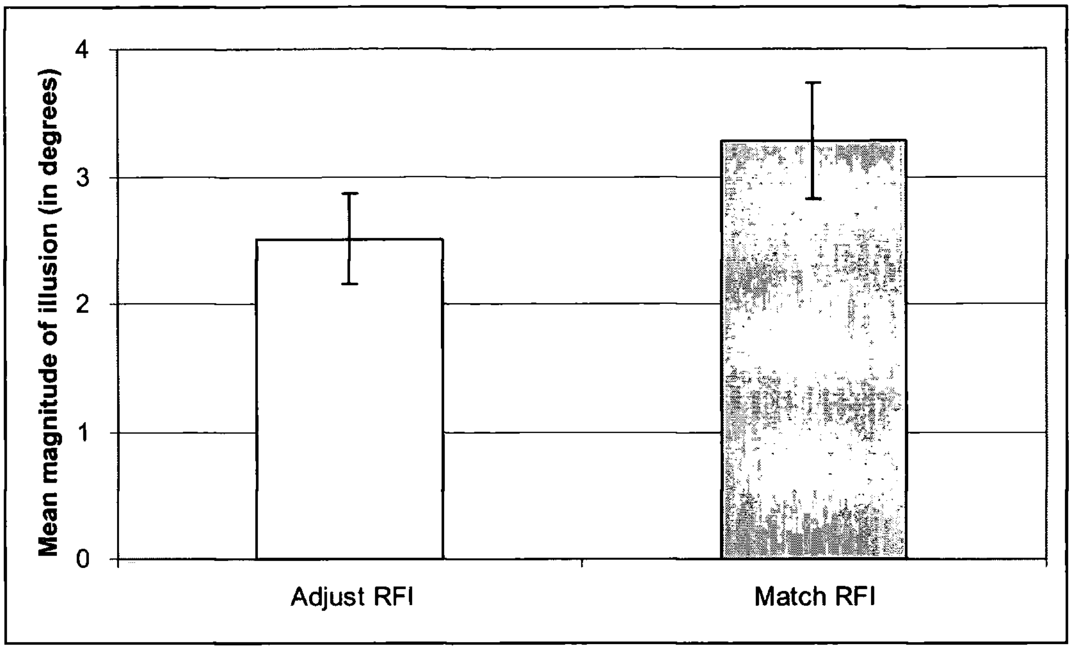

Figure 7.10 Group mean (n= 17) magnitudes of illusion for the rods-and-frame alone array in the two perceptual measures of adjust and match. Calculated as the mean difference between the stimuli 75/0/90 and 105/0/90. Error bars indicate one standard error of the mean.

The apparent difference in illusion magnitude illustrated in figure 7.10 marginally failed to reach criterion: $t(16) = 1.84$; $p = .085$, two tailed.

Overall there does seem, however, to be some indication that the 'adjust' measure may generally return a lower magnitude of illusion that the matching measure. As is reported in the analysis above, there is evidence of a strong, positive correlation between illusion magnitude to the RFI in the two perceptual conditions (although a weaker, unreliable correlation in the same comparison for the smaller sample size available for the STI). The presence of both correlatory evidence for shared causality and evidence for a difference in overall effect would suggest that although sharing a common cause, that secondary factors seem to be affecting the overall magnitude in each condition.

Discussion

Interaction of effects between action and perception measures

The study results indicate strong evidence to suggest that differences in task demands across measures of perception and visuo-motor control cannot explain the different effects found in these two measures. The presence of a clear interaction between measures can be taken as evidence for different processing of orientation being dominant in the perception and action. Such evidence strongly supports the predictions made by the perception .vs. action model as to the likely pattern of effects found between measures where the causal mechanisms underlying illusions is taken into account.

It can also be strongly argued that the presence of a shift in gaze does not account for the difference in effects found in the two measures, as the same interactive pattern of results is found in a measure suggested to be tapping the perceptual system without a shift in visual fixation (the adjust task). The suggestion that the adjust to vertical and matching tasks are tapping a unitary (perceptual) system is supported by the reliable positive correlation of effects across these two measures for both the rods-and-frame and the oppositional arrays.

Partial-dissociation between action and perception measures

The presence of a clearly reliable illusion in the open-loop posting measure where the rods-and-frame illusion is the target stimulus indicates that the posting measure is not wholly refractory to the tilted frame. This evidence supports some of the conjectures from study 5, that the tilted frame may be having some affect on the action response. This issue will be dealt with in some detail in the general discussion.

Potential differences between perception measures

There seems to be evidence to suggest that the adjust task may return a lower magnitude of illusion than the match measure. This may be due to the availability of vestibular and somatosensory cues in the adjust measure, as it demands direct reference to the coding of gravitational vertical (whereas in the matching measure gravitational vertical is at best a potential secondary reference cue). The presence of a reliable illusion in the rods and frame array in the adjust measure indicates that the representation of gravitational vertical is influenced by the tilted frame. The indications of a smaller illusion in the adjust to vertical task, however, suggests that the integration of visual, vestibular and somatosensory cues ameliorates this illusory affect in comparison with the match measure where such cues cannot be as directly incorporated into the response (and which may be dominated by the visual array alone).

Chapter 8: General Discussion

Evidence supporting the perception .vs. action model

Our conscious experience of the visual world is marked by its consistency and stability. This is achieved in spite of the fact that in a dynamic world the stimuli which are projected onto the retinae are radically changing over time. The aim of the perceptual system must be to provide a predictable framework into which changing visual stimuli are mapped. A perceptual system based solely on a rote processing of the changing array of visual stimuli presented to it would be potentially unsustainable. As such it is perhaps a truism that perception must be based on a product strongly *guided* by the visual information which it receives, but not wholly *dictated* by it: what you get, is not what you see.

In addition to the visual world being dynamic, the visual system resides within a corporeal framework that is itself in motion. In spite of this added layer of complexity, changes in body, head and eye position do not radically alter our visual experience, nor do they profoundly alter our ability to make discriminations within it:

"It may be that, in ordinary surroundings, humans can correctly judge the vertical when they tilt the head... because they rely on the perceived stability of the visual framework." (Howard, 1982, p. 431).

The visuo-motor system, on the other hand, in order to achieve its aim of accurate interaction with the concrete world, must be driven by the veridical relationship between the action object and the effector. Anything less than such accurate coding would result in a failed motor act. The visuo-motor system cannot afford the luxury of a set of generalised models, it requires a timely and accurate representation of the goal object. It may be unnecessary for the observer to consciously experience the processes that guide action, in fact there may be positive disadvantages in introducing contradictions between the perception of the world and its actual form. Wong and Mack (1981, p. 130) concluded their study which reported the dominance of actual location over perceived location in driving saccades by saying "...permitting perception to determine eye movements when there is conflicting retinal (or spatial) information, would cause the eye to be placed where the target was not".

Early cortical vision demands the decomposition of stimuli into low level discriminable features, and there are a number of mechanisms that amplify the different attributes of visual elements. A by-product of these processes may be effects that actually distort veridical characteristics in order to achieve the required discriminations. Such a process is suggested to be involved in the underlying mechanisms from which the tilt contrast effects found in the simultaneous tilt illusion (STI) are derived.

Following these low-level discriminations, visual elements must then be reconstructed for a conscious percept to be established. It is in these 'reconstructive' processes (it is suggested in the ventral stream) that further illusory effects can be manifest, and the rod-and-frame illusion (RFI), may be an example of distortions that arise as a result of such relativistic processing associated with the 'frame of reference effect'.

In terms of the studies published to date using healthy subjects to examine the effects of illusions on measures of perception and action, there has been no systematic determination of the underlying causal mechanisms involved. In many cases there are likely to be a number of interacting factors that contribute to the overall net effect of an illusion, and perhaps the two tilt illusions examined in this dissertation are also the result of more than one contributing factor. However there seems to be consistent evidence to suggest that the STI effect arises chiefly as the result of the processes involved in orientation discriminations within the earliest stages of cortical vision. Whenever an illusion arises as a result of processes prior to the bifurcation of the ventral and dorsal streams (optical, sub-cortical or early cortical) the perception .vs. action model would predict that both streams should be equally affected by such 'mis-processing'. The results from studies 1 and 2, and 5 strongly support this prediction, showing not only reliable and large illusions in both perceptual and visuo-motor measures, but strong evidence for shared causality of these effects between conditions.

Where illusory effects arise solely from the incorporation of the set of processes necessary to establish visual perception *per se*, the perception .vs. action model predicts a pattern of *dissociation* of effects across measures and little or no evidence for shared causality. This prediction is supported from the results found in study 4 where the rod and frame illusion (RFI) was found to have a reliable effect only in the perceptual measure.

However the presence of a dissociative pattern in study 4 does not exclude the potential effects associated with differences in task demands in the two measures, although the results from study 2 clearly indicate that such factors are not consistently a confound.

One means of strengthening the argument for different processing underlying the two measures would be a two-way interaction between measures, analogous to the neuropsychological double dissociation found between subjects presenting with the syndromes of optic ataxia and visual form agnosia. The results from study 6 show just such an interaction. The dissociative pattern of effects found using the 'rods-and-frame' variant of the RFI was a replication of the results found in study 4. The *a priori* prediction of a larger illusory effect in a visuo motor response where the STI and RFI are counter-acting was derived from the results of studies 2 and 4, a prediction that was supported by the study 6 results. The reversing patterns of dissociation within a single subject group represents a two-way interaction between measures and array type. This same interaction was shown even where a perceptual measure involved no shift in gaze and was performed within the same referential framework as the visuo-motor measure (the 'adjust to vertical' and the posting comparison). These findings represent compelling evidence to suggest that visual perception and visuo-motor control are reliant on differing processes.

Criticisms

The use of the illusion paradigm is predicated on the assumption that an immediate response to a stimulus with a goal-directed visuo-motor act that relies solely on the available visual characteristics of the action object will be dominated by dorsal stream processing, and that such a response will be largely resistant to illusory effects generated as a result of visual context. Essentially effects associated with changes in a distal stimulus or context will not be incorporated within the processing necessary to generate the motor response. This measure is contrasted with one dominated by the perceptual processing which it is suggested codes the characteristic of the goal stimuli within the context of the wider visual scene, and as such is influenced by distal illusion inducers. In order to ensure that the measure is ventral stream dominated, it must be characterised by displacement spatially or temporally from the goal directed visuo-motor act.

There have been strong criticisms raised which suggest that comparison of visuo-motor measures and perception are not comparing 'like with like' and any differences between the two cannot rule out artefacts associated with the inherent differences between measures *per se*. A number of issues remain to be resolved, notwithstanding the aim of the series of studies conducted here to specifically minimise, if not excluding them.

Absolute versus relative metrics

Although the Vishton *et al* (1999) study does not provide unequivocal evidence that the different "strategies" applied in each measure accounts for differences between them, it does raise the issue as to whether they may be having some reliable influence. From their results it would appear that the application of metric, absolute perceptual techniques do effect a considerable reduction in illusion magnitudes in responses, although the conclusion that it nullifies any difference between perception and action is open to question.

If visuo-motor measures are dominated by absolute coding of visual characteristics, be it size, shape, location or orientation, this alone could account for lower illusory effects compared with those found in perception measures, which usually incorporate relativistic processing. It would require no reference to different processing to account for dissociations between measures, beyond the tendency for the visuo-motor response to be dominated by absolute coding and perceptual responses to be driven by relative processing. The Vishton *et al* (1999) study may in fact be illustrating the inherent flexibility of conscious perception, whereby more than one strategy can be adopted as a result of training or direction, whereas the visuo-motor act demonstrates its inherent autonomy, being driven without conscious control by visual characteristics; although such an argument seems reminiscent of the suggested differentiation between perception and action made by Milner and Goodale.

The domain of orientation is perhaps the least appropriate one in which this point can be addressed, as there no 'absolute orientation' only a displacement from any given meridian. Even if corporeal orientation could be taken as an 'absolute' reference point, evidence for small, but persistent effects of judgements of self-tilt (e.g. the Aubert and Mueller effects, see chapter 1) and optical effects such as cyclotorsion may mask the small differences that there may be between measures. Judgements of gravitational vertical are likely to be influenced by somatosensory, vestibular and visuo-vestibular effects. Perhaps, therefore, this issue is best addressed through pointing/saccade paradigms and manipulations of location, harking back to Bridgeman and colleagues' earliest work in the area.

In general the question that this issue raises is whether absolute .vs. relative coding is in some way a re-description of the perception .vs. action model, or a falsification of it. If the differences found in illusion studies between the two measures arises from the spontaneous application of absolute coding for action, but relative coding for perception, then in effect the pursuit of this line of enquiry may be less than useful. In order for the Milner and Goodale model to be falsified, it would require a demonstration that the coding technique applied was independent of the neural substrates suggested to be dominant in each measure.

The question may be: is absolute coding *only* generated through dorsal stream processing ? If the chief characteristic of this stream is its 'hard-wired' dependence on actual metrics and the automatic application of this coding in effecting action, whereas perceptual processing in the ventral stream allows a degree of conscious selectivity in terms of the strategies applied (potentially using either relative *and/or* absolute coding) then specific predictions can be made when dorsal stream processes are damaged. It could be argued that, in the absence of an intact posterior parietal complex, optic ataxic patients should show an inability to apply absolute coding to reduce illusory effects in perception measures, even where training in this technique is applied. If this group were able to apply this method as effectively as controls, this would argue the case that absolute coding was not an inherent characteristic of dorsal stream processing *per se*, but merely one that in most cases dominates the visuo-motor response. An inability to apply this technique to reduce illusion magnitudes in the clinical group would suggest that the damage to dorsal stream structures disrupts absolute visual coding and therefore denies the products of such processing to both visuo-motor *and* perceptual measures. If such a deficit was found, it could be inferred that where metric techniques are applied in a perceptual measure in healthy subjects to reduce illusory effects, the reduction in illusion magnitude is as a result of the recruitment of absolute coding derived from processing in a separable visual sub-system. This is suggested to be the case with 'DF's use of motor imagery to assist in perceptual responses (see below).

A corollary of this would be to use neuroimaging techniques in healthy subjects to determine whether there was higher activation in the posterior parietal cortex and/or its major projections where techniques of absolute coding were applied in perceptual measures in comparison with instances where relative expressions of perception were performed. A further alternative would be to use TMS to disrupt posterior parietal processing and determine whether this inhibits the application of absolute techniques for perceptual measures in healthy subjects.

Influence of differing visual references on perception and action measures

Another potential means of viewing the results presented in this dissertation is that where there is a difference in the visual context, then differences in illusion magnitude will be present, but where there is no difference in visual context then there will be no difference in illusory effect between perception and action conditions.

Using this argument the presence of *association* between measures in study 2, using the STI, can be explained merely on the basis that in both cases the 'context' (the tilted annulus) was the same in both cases.

In study 4 the visuo-motor condition involved responding directly to a target within a tilted frame, whereas the matching measure was performed within the context of a different visual context: the upright frame. The difference between these environments may potentially account for the unequal effects across conditions. For instance if the tilted frame had induced either an apparent, or an actual corporeal tilt in the same direction, then the egocentric coding of vertical may be shifted in the frame direction (on the implicit assumption that body orientation generally maps onto gravitational vertical). Under these circumstances the rod will have been coded uniquely as tilted in the opposite direction to the frame but the grasp was performed with an orientation at the same offset away from (the now tilted) egocentric coding of vertical, resulting in a response which was now closer to, or at, true vertical. The net result of both these effects (illusory tilt of the rod and body-tilt) was that grasping will be close to the true orientation as a consequence of two counter-acting factors. However in the perception measure, the matching apparatus was fixed at true gravitational vertical/horizontal. Thus the comparison that subjects are invited to perform involves comparing the target rod in the tilted frame, with the matching rod in the upright frame. The upright matching frame may return apparent or actual body tilt to near vertical, and so the response made in the matching condition was performed in the absence of (or with reduced) body tilt. The absence of this second nullifying effect results in a higher net illusion in matching. The presence of an illusion in perception in the absence of an illusion in the action measure may be, therefore, a result of the two differing visual contexts in which each measure is performed and thus represent a task dependent difference, rather than suggesting differences in the underlying visual processing of orientation.

Exactly the same argument can be offered in explaining the results in study 6 for the (now partial) dissociation between the matching and posting measures where the 'rods and frame' variant is used.

Continuing this theme, the net effect on the visuo-motor measure of adding the tilted annulus in opposition to the frame in the composite STI/RFI array was to increase the overall illusion as the counter-acting body tilt/frame tilt equalise, but the annulus adds a third factor resulting in a larger final illusion. However in the matching condition, where the upright frame of the matching array is being referred to, if body tilt is returned to vertical (on fixation of the upright frame), the only two factors acting were the frame and annulus tilts, which are largely counter-acting, resulting in a smaller net illusion. This argument echoes concerns raised by, amongst others, Pavani *et al* (1999) and Franz *et al* (2000) suggesting that where both responses are conducted within an identical visual array that similar illusory effects are found in both measures, but where the surrounding visual contexts are different across conditions then a different effect of illusions may be found in visuo-motor and perceptual tasks.

However this line of argument fails to account for the dissociation (and two-way interaction) found in comparing the 'adjust-to-vertical' and the posting measure of study 6. In this comparison both responses are performed within the same tilted visual context, there is no shift to an upright frame in the perceptual measure to provide a correction for any potential effects of actual or illusory body tilt, yet the same pattern of differences is found as before. This independent confirmation of the two-way interaction in conditions where the visual contexts are *identical* suggests that differing visual contexts alone cannot account for the pattern of results found. However the reduction in illusion strength between the 'adjust to vertical' perceptual measure in comparison with the 'matching' measure is perhaps some indication that there may be other factors acting, and changes in body orientation and its effect on visual coding of orientation may underlie this phenomenon.

In order to address the question of body tilt directly some means of rigidly controlling corporeal orientation could be applied, although physically restraining subjects could make a visuo-motor task awkward and would not in any case control for illusory body tilt. A more elegant procedure would perhaps be to perform two 'adjust' tasks in which subjects are instructed to adjust the target grating to gravitational vertical and also perform a task that involves aligning the target grating with their own body orientation. Performing these responses to illusory *and* control stimuli would allow the presence of body tilt (either actual or illusory) to be determined, and potentially controlled for through co-variance analyses to partial out the effects of body tilt for each subject. This would also assist in determining the underlying cause of the smaller illusion magnitudes found in the 'adjust to vertical' .vs. the matching measures of perception by assessing the relationship between real/apparent corporeal shifts in orientation and their effects on illusion magnitudes.

Although the suggestion of differing visual contexts being a confound is hypothetically one which could cast some doubt about the illusion paradigm in general, the full complement of results from study 6 seems to refute this.

Extensions of findings

Effects of delay

One factor that was not examined in this series of studies was the effects found as a result of introducing delays between stimulus offset and response. The results from Hu and Goodale (2000) replicate earlier findings (e.g. Wong and Mack, 1980; Gentilucci *et al* 1988; Westwood *et al*, 2000) which suggest that illusory effects are increasingly influential in visuo-motor responses where delays are imposed. The findings of study 6 could be further developed through the application of a similar design. The perception .vs. action model would make specific predictions as to the change in illusory effects where responses to the RFI/STI opposing array and the rods-and-frame array follow the imposition of delays.

Using the RFI/STI opposing array, the imposition of a delay before the visuo-motor response should result in a *decrease* in illusory magnitude, as the perceptual system, vulnerable to the counter-acting effects of both illusions, increasingly dominates the response. However a delayed perceptual response to the same opposing array should result in *no change* in illusory magnitude over a 'no delay' perceptual task.

Using the 'rods-and-frame' array, the imposition of a delay in the visuo-motor response should result in an *increase* in illusory magnitude, whereas again there should be no change in illusion strength in the perceptual measure as the result of delay.

Such a design would further strengthen inferences concerning effects of delay on each condition by again showing an interaction of effects between array types and the two measures.

Principled use of depth cues to induce mis-applied size constancy

It is suggested that the Ebbinghaus and Ponzo illusions result, in part at least, from the mis-application of size constancy. The suggestion that the Mueller-Lyer illusion has the same basis (Gregory, 1963) has, however, been unable to account for a number of characteristics of the illusion (Morgan, Hole and Glennerster, 1990; Mack *et al*, 1995). However even in the Ebbinghaus and Ponzo illusions, the assumption concerning the mechanisms involved is by no means proven. and Coren (1995) found that where depth cues were specifically manipulated that some compelling effects could be found (see Appendix A, figure a15)

Figure 8.1 represents an ambiguous figure. It can be viewed as either the view down a shaft at an opening at the far end in which case the central rectangle is regarded as more distal than the outer rectangle, or as a 4 sided pyramid with the top removed in which case the central rectangle is regarded as the more proximal of the two. If the image were manipulated by introducing depth cues to specifically to induce different perceptions of the relative depth of the figure, with respect to the displacement proximally and distally of the two rectangles, then this may invoke size constancy mis-application in terms of judging the size of the central rectangle.

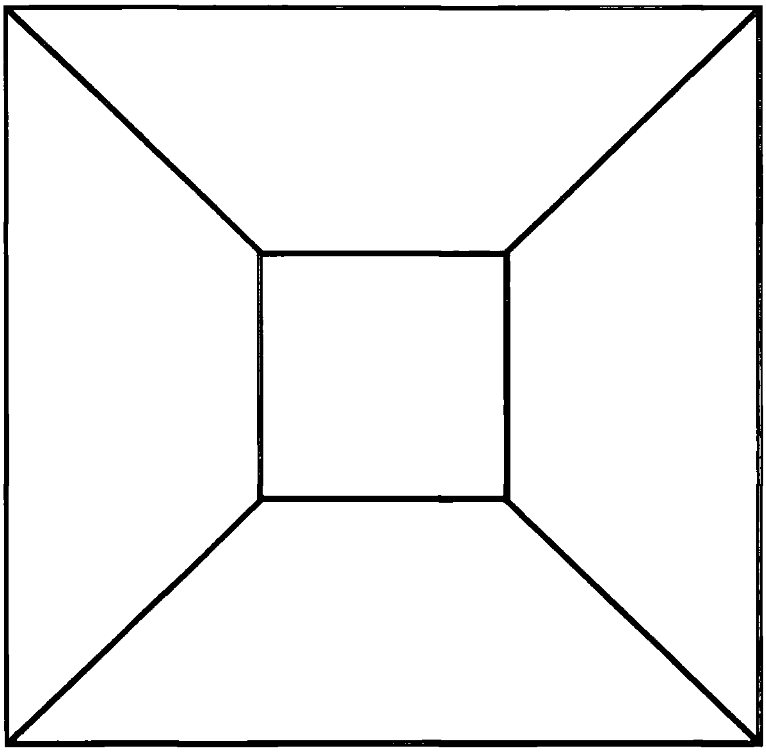

Figure 8.1 An ambiguous figure in regard to the relative distance of the central and outer squares.

The predicted effect would be a larger influence of the depth cues(in terms of the central rectangle size) on perceptual measures than visuo-motor measures (such as maximum grip aperture). This is made on the assumption that mis-applied size constancy effects the perceptual measure more than the action systems. If a delay were to be introduced after stimulus offset then the visuo-motor response should show an increasing effect of the depth-induced size illusion on the assumption of the decay of egocentric coding available as a cue to the grasping response. A lengthy delay should produce a magnitude of illusion of similar proportions to the perceptual measure. If consistent factors of individual differences influence the illusion strength, then there should be evidence for a correlation of illusory effects between the perceptual measure and the delayed visuo-motor measure.

The strength of using such a design is that it makes no assumptions as to the causal mechanisms acting in the illusion, but is a specific manipulation of these factors. Where *multiple* depth cues are applied there should be a corresponding change in the differential of illusory effects on each measure: the more depth cues applied, the larger the difference should be between conditions, and the larger the *increase* in illusory effect between immediate grasping and grasping with an imposed delay.

Examination of the 'direct' and 'indirect' STI effects

Chapter 1 suggested that the two versions of the STI: the direct (repulsion) effect and indirect effect (attraction) may be as a result of early and higher visual processing respectively. However the circumstances under which reliable indirect effects are generated seems at present to be unclear, and the magnitudes of such effects are relatively small. Although using this illusion may be a potential avenue for further research, the generation of suitable stimuli that can reliably generate the required effects would be required.

Visual form agnosia and illusions of tilt

Visual form agnosia results from a disruption to ventral stream processing, in the case of 'DF' through damage in (amongst other areas) the lateral occipital cortex. As the STI is suggested to depend upon processing within the primary visual cortex, which appears to be largely intact (in terms of its function, if not its structure) in the case of DF, then it should be the case that she should be affected by the STI in her visuo-motor responses: she should show the same illusory effect as found in the visuo-motor measures of healthy subjects. A series of studies conducted with DF by the author (not reported here) indicated however, that she has considerable problems in differentiating the target grating from the tilted annulus, even where these were colour differentiated. This result is in line with the findings of Goodale, Jakobson, Milner, Perrett, Benson and Hietanen (1994) which suggested that the most dominant luminance defined visual contours of an array are most influential in mediating DF's visuo-motor responses. Where contours are defined by means other than prominent luminance boundaries, then DF's responses approach chance.

It is suggested that the STI and the tilt-after-effect version of the illusion (see chapter 1) have a common causal mechanism, sited in primary visual cortex (Tolhurst and Thompson, 1975). As such it should be the case that the tilt-after-effect (TAE) version of the tilt illusion should show effects on visuo-motor measures in much the way that the STI showed these in studies 1 and 2. The TAE version should also have a predictable effect on DF. If she was exposed to an inducing grating offset from vertical, and then presented with a vertical grating to which she should respond, then she should show evidence of a tilt illusion in her visuo-motor response. Comparison with a control subject should show that her striatal and visuo-motor systems are acting in much the same way as with healthy subjects, whose visuo-motor responses should be vulnerable to this illusion type. DF should, however, show considerably less illusory effect when responding to the rod-and-frame illusion than a control subject.

Ancillary findings

Hand trajectory

The use of maximum grip aperture as a dependent variable has the advantage that it is sampled relatively early in the response, before visual comparisons between the hand and the target are possible. This excludes simple visual correction on closure to the target from being an experimental confound.

Where orientation is examined, however, the tilt of the effector must be sampled as close to the target as possible, as a dependent measure early in the reach is not readily available. This necessitated the use of open-loop responses in the action responses, by either delaying response until after stimulus offset (studies 1 and 2) or through complete open-loop posting (employed in the later studies). Gentilucci *et al* (1988) and Westwood *et al* (2000) have suggested that even short latencies between stimulus offset and response completion may affect visuo-motor measures: increasing the likelihood of illusory effects emerging in the action measure. If a phenomenon analogous to the relationship between maximum grip aperture and target size were available in the domain of orientation, this would simplify the design of any future research in the area.

There is evidence to suggest that the orientation of the hand follows a predictable trajectory from its starting to its final orientation. However this trajectory seems to include a relatively consistent bias during this movement. There is considerable variation in this bias both across subjects and within subjects over a number of trials, but this observation may have implications not only for its potential use as an early indicator of final orientation, but also in terms of where the dependent variable should be sampled in orientation studies.

Figures 8.2a and 8.2b illustrate 20 posting responses by a single subject to the control stimulus '90/90' (which were pseudo-randomly inter-leaved with other stimuli). There seems to be a consistent abductive roll of the wrist during the movement from the starting orientation of 90 degrees and the final orientation of same tilt, even to this control stimulus that is essentially a single grating oriented at 90 degrees.

Many subjects are not as consistent as the one illustrated: some include smaller adductive rolls (i.e. anti-clockwise with the right hand) prior to an abductive roll, others show less consistent patterns, but evidence for abductive biases is common. Similar patterns can be found in the orientation between finger and thumb in the open loop grasping of study 4 (figures 8.3a and 8.3b) even where the starting orientation of the hand was not controlled.

It may be that as a result of the inconsistencies between trials (and individuals) a large number of repetitions will be required before any potentially correlatory analysis could reveal, for instance, a relationship between the magnitude of the bias and the final orientation of the effector. The search for an early indicator of final orientation may nonetheless be a worthwhile one.

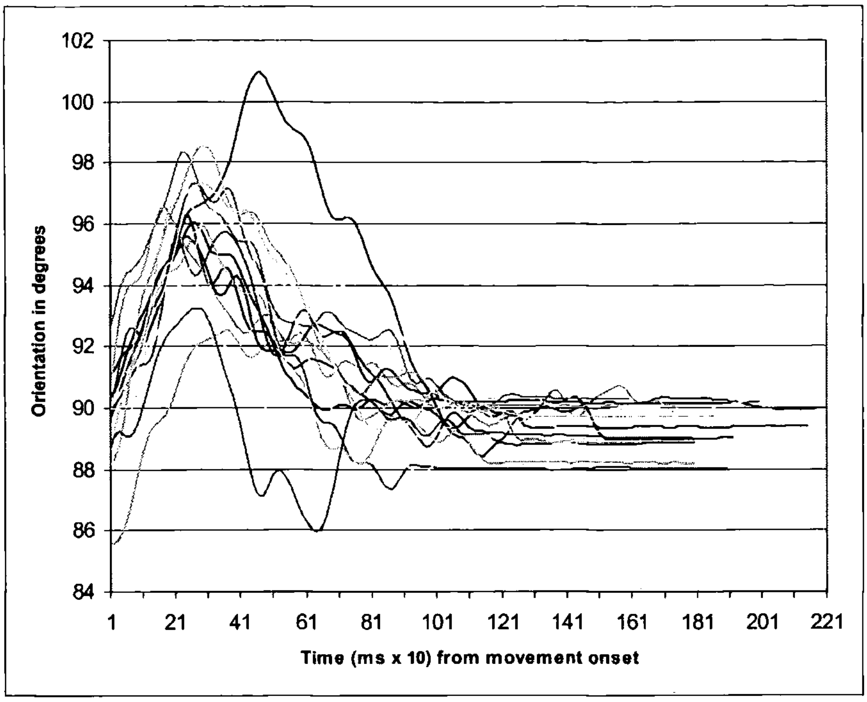

Figure 8.2a: Orientation of the posting 'palette', for a single subject (20 trials) to control stimulus '90/90' in study 2.

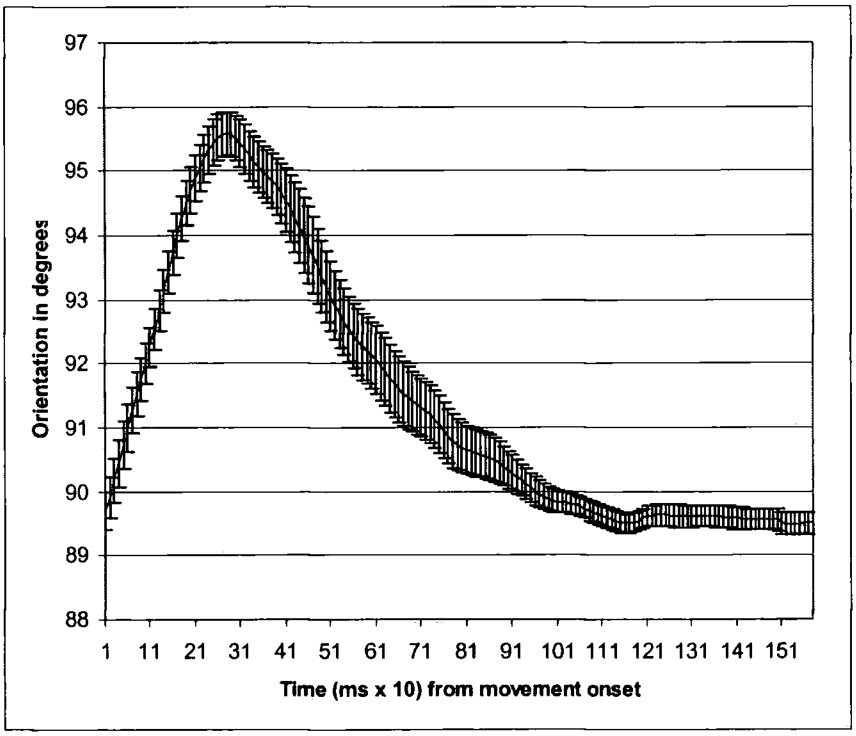

Figure 8.2b: Mean orientation of palette (taken from data in 8.2a): error bars indicate one standard error of the mean.

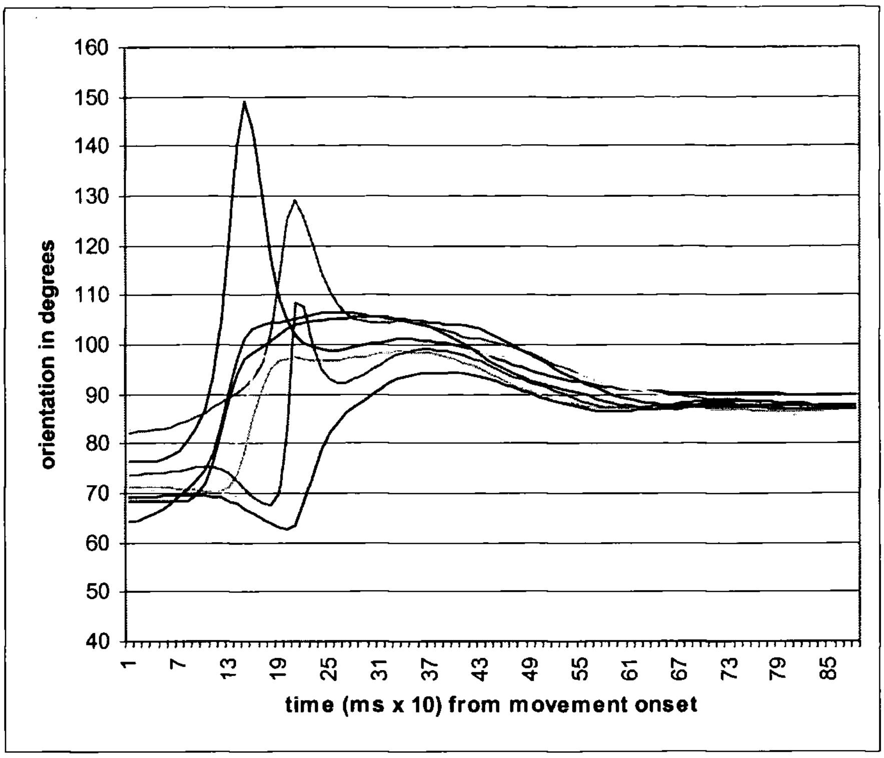

Figure 8.3a: Relative orientation of finger and thumb, for a single subject (over 9 trials) to control stimulus '90/90' in study 4.

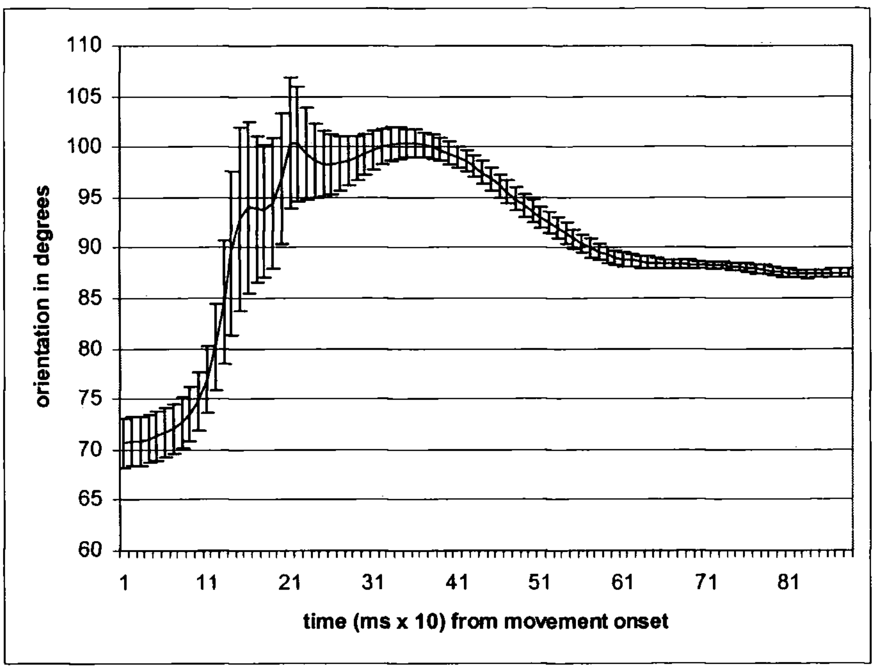

Figure 8.3b: Mean relative orientation finger and thumb (taken from data in 8.3a): error bars indicate one standard error of the mean.

The experimental impact of this artefact of movement is, however, more pressing. It would appear that the earlier the dependent measure of orientation is taken before movement endpoint, the more variable the data are likely to be, depending on the consistency of the bias for any one individual or condition. More importantly if the direction of orientation bias is influential in the study design (e.g. solely looking at biases clockwise or anti clockwise around vertical) then this 'abductive roll' may be a confound: an early sampling of orientation is likely to be contaminated by this bias. In studies 1, 2, 5 and 6 the dependent measure of orientation was taken at, or 10 ms prior to, movement end-time, and so should not be unduly influenced by this effect. In study 4, however, hand orientation was sampled at 50 ms prior to end-point (in order to exclude haptic feedback as a cue in the grasping response) and so may have been influenced by the bias. However the final dependent measure in all studies was taken as the *absolute* magnitude of illusion (calculated as the difference between responses to stimuli with clockwise and anti-clockwise tilted inducers) so it should not have been influenced by this effect (on the assumption that it would, on average, be affecting all responses equally). As such, this does not seem to represent a serious concern for the inferences drawn from the comparisons of illusion magnitude where the two conditions are compared, and in the worst instance this would only be applicable to the results from study 4 where the early sampling of hand orientation was applied.

In general, however, where the orientation of the hand or hand-held card is tracked, the sample forming the dependent measure should be taken as late in the movement as possible in order to avoid any distorting effects of this bias.

The presence of this unreported bias may be of future interest. All subjects in the studies reported here are right-hand dominant and used their dominant hand for all responses, hence the assumption of the bias being 'abductive'. Further studies would be required to determine if there is an equal and opposite effect in left-hand dominant subjects (or right hand-dominant subjects using the left hand).

Variation of illusion magnitude over time

Glover and Dixon (2001) report that there is evidence to suggest that the illusion magnitude in their variant of the STI diminishes over the course of a number of trials. They also report that the illusory effects on hand posture, although pronounced in the early stages of prehension, diminish as the hand approaches the target: although as a closed-loop response was used this can be accounted for purely in terms of late visual correction as the hand approached the target.

In order to determine if a similar effect was present in study 2 a re-analysis of the data was conducted comparing the mean STI illusion magnitudes to trials early (1^{st} epoch) in the testing process for each subject, and those in the later trials (2^{nd} epoch).

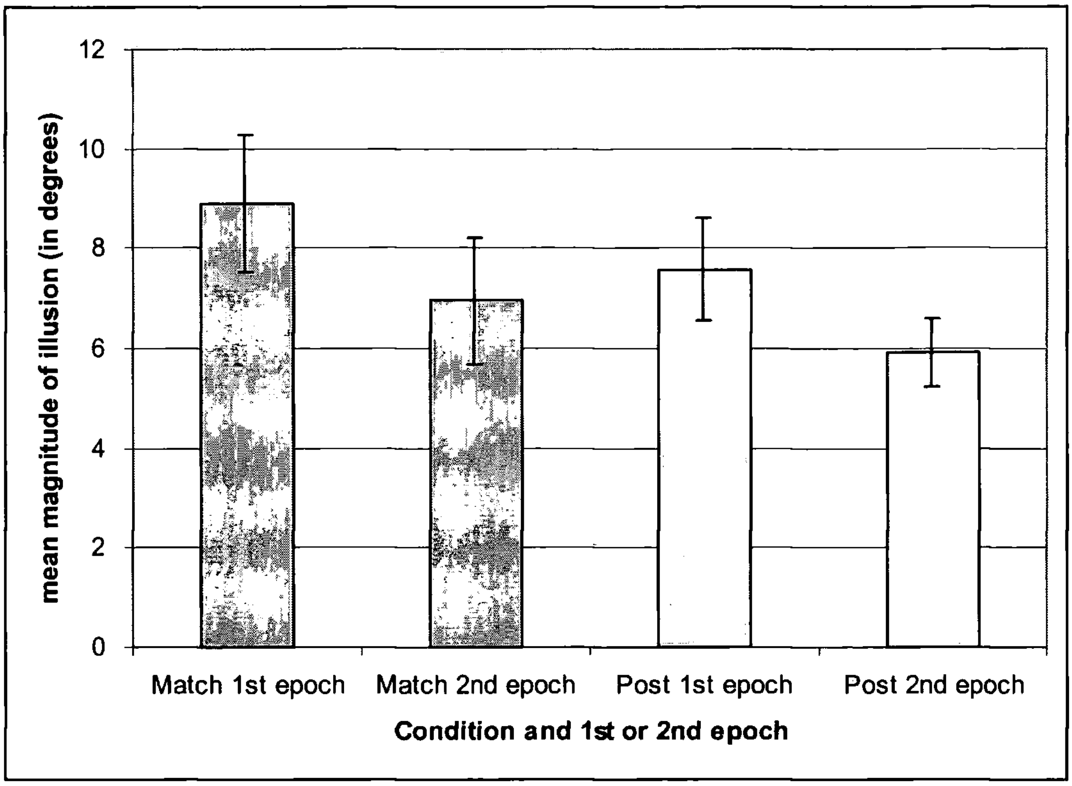

Figure 8.4: Group mean magnitude of STI illusion in degrees of effect (n=12). Darker bars indicate the matching (perceptual) measure and lighter bars the posting (visuo-motor) measure. Bars represent either the mean magnitude of illusion over first half of trials (1^{st} epoch) or second half of trials (2^{nd} epoch). All data extracted from study 2. Error bars indicate one standard error of the mean.

Figure 8.4 illustrates the group mean magnitudes of illusion when 1^{st} epoch trials and 2^{nd} epoch trials are examined for study 2. It shows that there is a reduction in illusion magnitude for both the matching and posting measures between epochs. A statistical analysis of these differences showed that both were statistically reliable: in the matching measure the comparison between illusion magnitude in 1^{st} and 2^{nd} epochs showed a reliable difference: $t(11) = 2.15$; $p < .05$ (one-tailed); the same comparison in the posting measure showed a comparable result: $t(11) = 2.29$; $p < .05$ (one-tailed). This would indicate that there was a reliable reduction in illusion magnitude in both measures as testing progressed.

If the reduction in STI magnitude in both measures was from a common cause, then there should be not only evidence for no differences in illusion magnitude across conditions within each epoch of trials but also evidence of shared causality of illusory effect across conditions within each epoch. In other words when considering the trials of early and late epochs separately, the pattern of effects between measures should show the same evidence for association as when trials were collapsed over both epochs.

Examining the magnitude of illusion between matching and posting conditions in the first epoch there was no reliable difference in illusion strength between measures: t(11) = 1.53; n.s.(two-tailed). There was however a reliable correlation between measures (figure 8.5) Pearson r = +0.78; p = .003 (one-tailed).

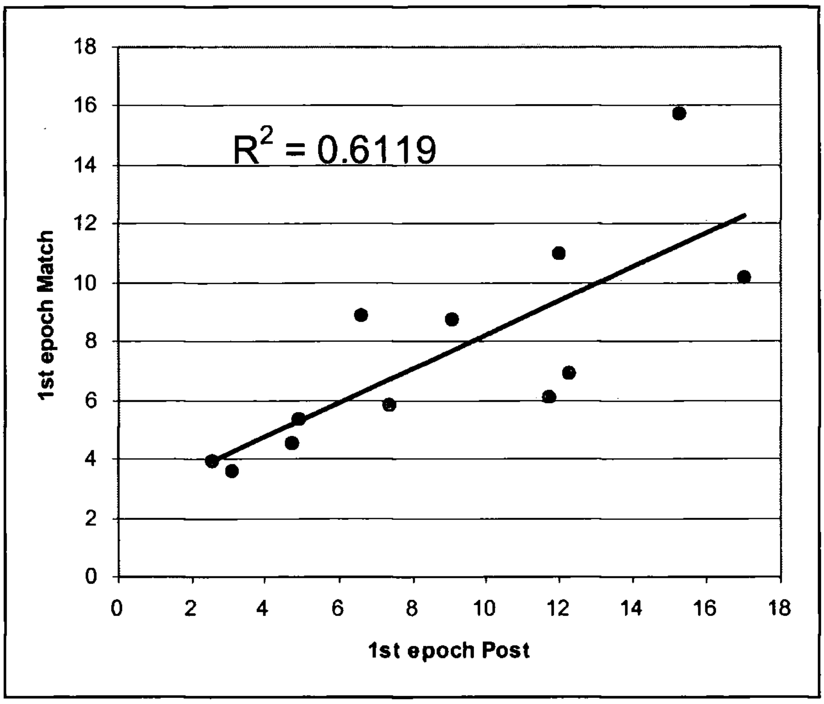

Figure 8.5: Correlation of STI magnitude per subject for 1st epoch trials in the posting and matching conditions, study 2.

The same set of analyses was carried out for the 2nd epoch of trials. This again showed no difference in illusion magnitude between conditions: $t(11) = 1.27$; n.s. (two-tailed) and again a reliable correlation between measures(figure 8.6): Pearsons $r = +0.82$; $p = .001$ (one-tailed).

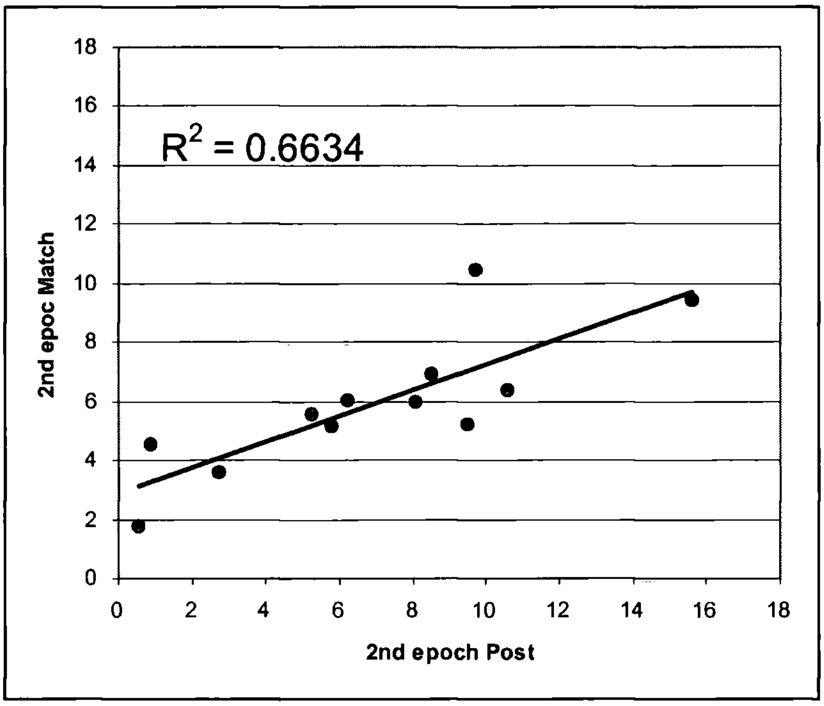

Figure 8.6: Correlation of STI magnitude per subject for 2nd epoch trials in the posting and matching conditions, study 2.

These results confirm that there was a reliable reduction in STI illusion magnitude between the first and second epochs of trials, replicating the findings of Glover and Dixon (2001). This reduction seems to affect both measures in a similar fashion: to the extent that each epoch shows the same pattern of strong correlations across measures and no difference in illusion strength between measures. This result again suggests that both measures are tapping a unitary source of illusion and even when this illusory effect reduces as a result of repeated exposure, the relationship between illusion magnitude is closely tied. Unfortunately, the Glover and Dixon (2001) study does not report whether there was any change in illusion magnitude in their perceptual measure and so an independent verification of this result is unavailable.

Perhaps the reduction in illusion magnitude is merely a result of subjects becoming less prone to tilt illusions over time. However, as reported in the results of study 4, this analysis revealed that there was no evidence for *any* change in magnitude between first and second epoch trials in *either* perceptual *or* visuo-motor measure. It would seem therefore that the variance in illusion strength over time might be associated with the illusion type itself rather than to orientation illusions in general.

The suggested causal mechanisms involved in the STI (lateral inhibition in primary visual cortex) may well be vulnerable to the effects of general adaptation in terms of repeated exposure. If there was a generalised reduction in firing rates of all orientation sensitive populations of cells over time, the difference between any two given populations would diminish, perhaps reducing the strength of the induced illusion which, it is suggested, arises from disparities between firing rates for cells sensitive to neighbouring orientations. However the pseudo-random inter-leaving of different stimuli (controls, filler illusions and target illusory figures) within each trial block should result in a general dishabituation. The inclusion of filler trials of both control stimuli and 'false' illusory ones should also help maintain the naivety of subjects as to the nature of the illusion. However there does seem to be some order effect influencing the illusion, which may in itself warrant further investigation.

One potential explanation may be that all gratings presented (including filler and false illusion stimuli) were between orientations of between 78 degrees and 112 degrees i.e.

confined to a relatively narrow band of orientations around vertical. Perhaps some general habituation occurred in visual cells sensitive to this specific range of orientations as a result of repeated exposure, which did not fully dishabituate when a slightly differing stimulus was presented, but aggregated over time. Glover and Dixon (2001) report that in their second epoch of trials there was essentially *no* illusion in the reaching measure, whereas our study 2 found a reliably strong, though reduced, illusion in the latter epoch. As such it would appear that the Glover and Dixon study demonstrated a dramatically greater reduction in illusion strength over time. However they report that the orientation of the background grating was not altered within each trial block in their study, only the orientation of the target 'handle' was altered to each of the target orientations in a random sequence. The background grating was changed only between trial blocks. As such subjects were repeatedly exposed to a background grating of the same orientation over a number of consecutive trials (forming the early and late epochs). Under these conditions the effects of habituation in reducing illusion strength could be considerably more marked than in the present study 2: which would explain why there was such a greater reduction in illusion strength between early and late epochs in the Glover and Dixon findings in comparison with our results.

Calvert and Harris (1985) reported a similar effect when using the STI: longer exposures were found to induce a smaller illusory magnitude than short tachistoscopic presentations. Their explanation was in terms of parvo and magnocellular visual systems, although their results were only presented in abstract form, and so no further details are available.

Another potential explanation for the reduction in illusion strength may be through normalisation: "...the tendency for prolonged inspection to induce a reduction in disparity between an object characteristic and its norm (curved lines appear straighter, tilted lines appear more vertical/horizontal)." (Howard,1982, p. 148). However this would not explain why there was no corresponding reduction in illusion strength in the RFI, where it would be expected that a similar effect would be manifest. In fact the absence of any evidence for a reduction in illusion strength in the RFI over time is perhaps further evidence to suggest different causal mechanisms involved in the two illusion types.

Overall the mechanisms underlying variation of illusion strength over time do not seem clear, but the persistence in the pattern of association between measures found in the STI and dissociation in the RFI, even when early and late epoch trials are examined, seems to indicate that this effect does not bear critically on the perception .vs. action model's predictions as to the effects of these two illusion types on the two measures.

Differences between two measures of perception

In study 6 two measures of perception were used: the matching measure and the 'adjust to vertical' measure. The presence of a positive correlational relationship between illusion magnitudes in the two measures suggests shared causality but the presence of a reliable difference in illusion (the adjust task returning the smaller illusion) indicates that there may also be differing factors influencing each response.

In effect there were two slightly differing aspects of visual perception being tapped in each case. The matching measure demanded a comparison between the target grating placed within a tilted frame and the matching grating within an upright frame. This task is a variant of the 'parallel setting' technique that has been used extensively in psychophysical testing of orientation, although the separations between the target and matching gratings are greater than is normally the case because of the need to use large 'rod to frame' separations for both the target and the matching arrays. Essentially the subject is attempting to perform a 'stimulus matching' task: to eliminate or minimise the difference in a domain (in this case orientation) between the target and matched stimuli. One cue that is available in such a technique is that, rather than relying solely on the orientation of two gratings, the distances between corresponding points on the two gratings can be used (most prominently the 'top and bottom' of each target stimulus: the rods of study 4, the grating lines of studies 5 and 6) However the large separations between target and matching arrays in studies 4, 5 and 6, and the small shifts in orientations involved, would limit the effectiveness of such a strategy.

The 'adjust to vertical' response demanded mapping orientation onto a largely vestibular/somatosensory representation of 'gravitational' vertical, where there were no prominent cues in the visual environment with which a comparison could be made (and experimentally these were excluded through the use of masking all proximal and many distal cues to vertical). Howard (1982) describes the 'adjust to vertical' task as one of "exocentric orientation...the orientation of an external object with reference to some external reference axis" (p. 10).

One potential explanation for the difference may again turn on the issue of task demands: perhaps the two tasks are not matched in terms of difficulty. The absence of the shift in gaze in the adjust measure may make this task simply easier to perform, and perhaps the difference can be accounted for as a result of more variable responses in the matching measure. However examining the results of both perceptual responses to the control stimulus ('0/0/90') in study 6 shows that both tasks were performed with equal, and quite remarkably high, accuracy and precision. The group mean response to the control stimulus was 89.99 degrees (s.e. 0.27) for the adjust task and 89.59 degrees (s.e. 0.39) for the match task (see table 9.1). A statistical analysis of this small difference showed no evidence for a reliable difference $t(16) = 0.68$; n.s. (two-tailed).

Subject	adjusting	matching
1	89.50	89.70
2	91.00	86.20
3	90.70	90.10
4	90.10	89.60
5	89.20	89.20
6	90.00	90.80
7	89.80	88.20
8	87.86	90.90
9	90.30	86.70
10	88.75	91.30
11	91.20	88.70
12	89.80	89.20
13	87.85	92.80
14	90.75	91.00
15	90.15	90.10
16	91.90	88.80
17	91.00	89.70
mean	89.99	89.59
s.e.	0.27	0.39

Table 8.1: Response (in degrees) to the control stimulus 0/0/90 in the adjust to vertical (adjusting) and matching tasks, study 6.

Bearing in mind the precision with which the target rod could be set to vertical by the experimenter (+- 0.5 degrees), the similar precision for recording the subject's response from the scale on the rear of the apparatus, and the JND for orientation discrimination (c. 0.5 degrees), therefore, there is no evidence to suggest that matching was merely a more difficult task than the adjust measure. In fact both were performed with quite notable accuracy.

The key differentiator between the two tasks may be the ability to use a more direct comparison with gravity in the adjust measure. In the matching measure this cue was, at best, available only as a secondary cue to assist in the task of making the target grating and matching grating parallel.

Conclusions

Three questions were posed in chapter 1:

1. *"to determine whether, in the novel domain of orientation, there is evidence to suggest differentiable effects of visual illusions on measures of perception and visuo-motor control."*

There seems to be substantial evidence to suggest that this is the case. The potential effects of grasp-point coding and task demand differences (as a result of differing visual contexts across conditions) raises some concerns about the results of the dissociation across measures found in the RFI (study 4) if this is taken in isolation. However, the presence, in study 6, of the replication of this result using the rods-and-frame variant of the illusion, even where the contrasted conditions were contained within identical visual contexts, suggests that perception and visuo-motor control are differentially affected by the rod-and-frame illusion.

2. "*to determine whether orientation illusions with differing causal mechanisms will have patterns of effect across perception and action measures that concur with predictions based on separable processing in ventral and dorsal visual streams*."

The presence of *associative* patterns of effect between measures where the simultaneous tilt illusion was utilised and *dissociation* where the rod-and-frame illusion was used, indicates that the underlying mechanisms involved in visual illusions are critical in determining the likely effects on perception and visuo-motor control. There seems to be strong evidence to suggest that the STI is sited within early cortical vision. Although not as compelling, there is convergent support for the suggestion that the RFI is not based on the same causal mechanisms, and that involvement of higher processes within conscious vision may be involved.

A model of an essentially unitary visual system, where both conscious visual perception and visuo-motor control are differentiable only in terms of the differing repertoire of cues available to guide their respective responses, does not readily account for the patterns of association, dissociation and interaction found in this series of studies.

Essentially support for the Milner and Goodale model derives from its parsimony in explaining the patterns of effect found in the two illusion types tested. There are a number of potential explanations of the patterns found: amongst the simplest, however, is the perception vs. action model of dual cortical visual processing.

3. *"to address a number of methodological issues that have been raised concerning the illusion paradigm, in particular to address the different task demands of perception and action measures".*

Visual perception and visuo-motor control are different. It requires no great insight to suggest that they may behave differently in response to the same stimulus. The challenge in successfully applying the illusion paradigm to test the perception .vs. action model is to control for all the confounding differentiators, until the only remaining factor that separates the two measures is the fundamental neural processes that underlie each. It would, however, be unwise to suggest that every *potential* confound had been excluded.

It seems fair to propose that the series of studies reported here do not contain the *same* confounds as has been suggested may have been the case in earlier studies. However addressing the new domain of orientation may mean that new factors have been introduced that can go towards explaining the pattern of results without reference to the Milner and Goodale model. These studies have sought to explicitly exclude previous, and some emerging, artefacts of task demand differences in terms of methods applied, and have provided novel evidence through the two-way interactions of study 6, to suggest that there are differentiable processes involved in the two measures. This finding, in a previously little investigated domain, has at the very least been a genuine attempt to directly incorporate the issues raised by those studies critical of this work's theoretical context.

Partial or full dissociation between perception and action in healthy cortex?

Having suggested that a pattern of dissociation does appear present between action and perception this brings us onto the concluding question: does the evidence suggest a partial or a full dissociation between measures, and what explanation may there be for only a stronger *tendency* for action measures to be resistant to illusory effects ?

There seems to be evidence to indicate that figural illusions may influence aspects of even the low-level kinematics of movement. Illusory effects on action measures may have been under-reported in the literature as a result of higher noise to effect ratios in visuo-motor measures (see chapter 1), as well as some potential publishing biases against studies where no dissociation between measures was found (as suggested by Carey, 2001). However there seems consistent evidence that illusions *are* having reliable, if smaller, effects on visuo-motor acts. This pattern of results has a number of potential explanations.

First, of course, it could be that illusions are acting equally on both measures and it is only the differences in task demands that account for any differences found between measures. Essentially the visuo-motor response has a far larger repertoire of corrective strategies with which to effect a veridical response. It seems reasonable to suggest that such factors are acting in some cases, and are, in fact, difficult to design controls for. However this does not seem to be a comprehensive explanation for the pattern of effects reported here: e.g. the pattern of association in study 2 and the two-way interaction of effects found in study 6.

A second explanation for the presence of illusory effects in action is that the ventral and dorsal processing streams interact and that illusory effects pass between the two systems. It has already been suggested that there are potentially a number of instances where a visuo-motor act recruits perceptual processing in order to plan and execute a response. This occurs where an isomorphic transformation of contemporaneous visual coding cannot be applied in the action response: e.g. lift force coding, 'novel posture' grasping, pantomimed responses, or where delays are imposed before the visuo-motor response. There is also anatomical evidence for cross-connections between ventral and dorsal streams in the primate cortex (e.g. Ungerleider, 1995) and some behavioural evidence for cross-talk between the two streams in humans (Van Donkelaar, 2000). There is also evidence for the reduction of illusion magnitudes in perception through applying metric strategies (Vishton *et al*, 2000) which may be an example of perceptual recruitment of dorsal stream coding.

There is also evidence that, in the absence of an intact perceptual system, visuo-motor representations may be recruited to inform perceptual responses. Visual form agnosic patient 'DF' has been shown to utilise her largely intact visuo-motor system as a compensatory technique to assist in perceptual tasks as found in Murphy, Racicot and Goodale (1996) and Dijkerman and Milner (1997). The suggestion in Dijkerman and Milner (1997) is that DF uses a 'pure form of motor imagery' in the perceptual task, which would imply that, if suitably refreshed (in the case of DF through sub-motor rehearsal), the visuo-motor representation of orientation can be applied in what is considered a measure of perception. Murphy *et al* (1996) propose a related technique may be adopted by DF in judgements of size, perhaps self-cueing through monitoring her own sensorimotor responses to inform the perceptual measure

These exceptions to the separate processing for perception and action suggest that conventional tasks may not exclusively tap two wholly isolated systems, but rather have a tendency to be dominated by one or the other, and that in some instances the systems can interact. It may be the case that in the intact visual cortex the processing of the two streams is less delineated than would be suggested by the neuropsychological evidence alone.

A third explanation is that the Milner and Goodale model of separable visual systems dominating the two measures is largely correct, but that where the causal mechanisms involved in the illusory effect are as the result of optical, sub-cortical or early cortical processes that it would be expected that the illusory effect will be carried downstream to both perception and action systems. Ward and Coren (1976) suggest that the Mueller-Lyer illusion is enhanced through blurring, and it is suggested that this points to some optical processing being involved in the effect. This is suggested by Gentilucci *et al* (1996) as accounting for illusory effects they found in a grasping response. There is strong evidence to suggest that the simultaneous tilt illusion is sited early in visual cortex, and this illusion has consistently showed its effects in visuo-motor measures in all reported studies: both here, and by Van der Willigen *et al* (2000) and Glover and Dixon (2001).

The rod and frame illusion also potentially contains early-sited effects, perhaps the most clear is the effect of cyclotorsion. Goodenough *et al* (1979) report that for large arrays an effect attributable to cyclotorsion could be expected to induce around 1 degree of bias. In fact the results from study 6 indicate that the illusion magnitude in the visuo-motor posting measure is close to this predicted effect (which would be around 2 degrees as we calculate illusion magnitude as the difference between the two opposing pairs of illusions).

Where suggestions are made that effects in visuo-motor responses result from early sited processing, this argument is credible only where there is independent evidence or rationale for the existence, and siting, of such processing. This argument is greatly strengthened where the suggestion of shared causality between perception and visuo-motor measures is be supported through the presence of positive inter-correlations between illusions found in the two measures.

In the studies using the STI both these criteria appear to be met. There is convergent evidence for STI siting from a range of independent studies and strong evidence for both equal magnitude of effect and shared causality across measures

The RFI appears to be a potential cocktail of effects: contour interaction (where rod/frame gaps are small), illusory and actual body tilts, cyclotorsion and the perceptual 'frame of reference effect'. There seems to be evidence that these first two effects (contour interaction and body tilt) may not be acting, or if present they are not biasing the results as a whole. We would expect that both cyclotorsion and 'frame of reference' were acting in the arrays of studies 4, 5 and 6. Both perception and action would be affected by cyclotorsion, but the perception .vs. action model would predict that the visuo-motor posting measure would be immune to the 'frame of reference' effect. There is evidence for some shared causality between perception and action measures in studies 5 and 6, where grasp-point coding is excluded as a cue for the visuo-motor measure (which may explain the absence of any illusory effect on grasping in study 4). However overall the perception measures are reliably more influenced by either the correcting effect of the upright frame (study 5), its biasing effect when tilted (study 6) or its counter-acting effect where a tilted frame surrounds an oppositionally tilted annulus (studies 5 and 6). In addition to these effects, there is consistent evidence for some shared effect of the tilted frame on both perception and visuo-motor control.

This pattern of results seems consistent with the presence, of two separable effects:

> the first effect, **cyclotorsion**, influences both measures and is evidenced by the presence of some shared causality between perception and action, but the correlatory relationship between measures is relatively depressed as a result of...

> ...the second effect, **the frame of reference**, which is variable across subjects (and may have no relationship with cyclotorsion) but which compounds the cyclotorsion *only* in the perception measure, as evidenced by a greater overall illusory effect in this condition.

Closing commentary

The series of experiments conducted here indicate an explanation for the mixed pattern of results in the illusion paradigm:

- Action measures will consistently return small or no illusions where they have access to cues denied to the perception measure.
- Where both conditions are matched in terms of task demands, the absence or presence of illusory effects in action is critically dependent on the causal mechanisms of the illusion employed.
- Where illusions arise as result of early visual processing, the presence of illusory effects in action is not a criticism of the perception .vs. action model, but is in fact a confirmation of its predictions.

The experiments conducted within the series of studies reported here (and in those using the illusion paradigm generally) are, of course, far removed from a direct examination of neurological process suggested to be underlying differences between measures. However the results indicate a picture of increasing complexity. In fact suggesting that action and perception measures are solely and exclusively dominated by dorsal and ventral streams in all instances is a caricature of the Milner and Goodale model. Direct neuroimaging or targeted lesioning studies in primates are likely to present the best opportunities to test the extent to which the model can generally applied

The results of these studies have been supportive of the Milner and Goodale model, although suggesting that in healthy cortex the predictions of different effects of illusion on each measure, and the inferences that can be safely drawn from such patterns, are likely to be less clear cut than was originally suggested by earlier studies using the illusion paradigm. We cannot determine, from such an indirect method, the exact nature of the forms of interactions taking place *in vivo.*

> "Although it may seem a paradox, all exact science is dominated by the idea of approximation. When a man tells you that he knows the exact truth about anything, you are safe in assuming he is an *inexact* man." - Bertrand Russell.

However, if the value of a scientific model is judged by its potential to generate empirically testable hypotheses, then I would suggest that the perception .vs. action model of dual visual systems has satisfied this criterion.

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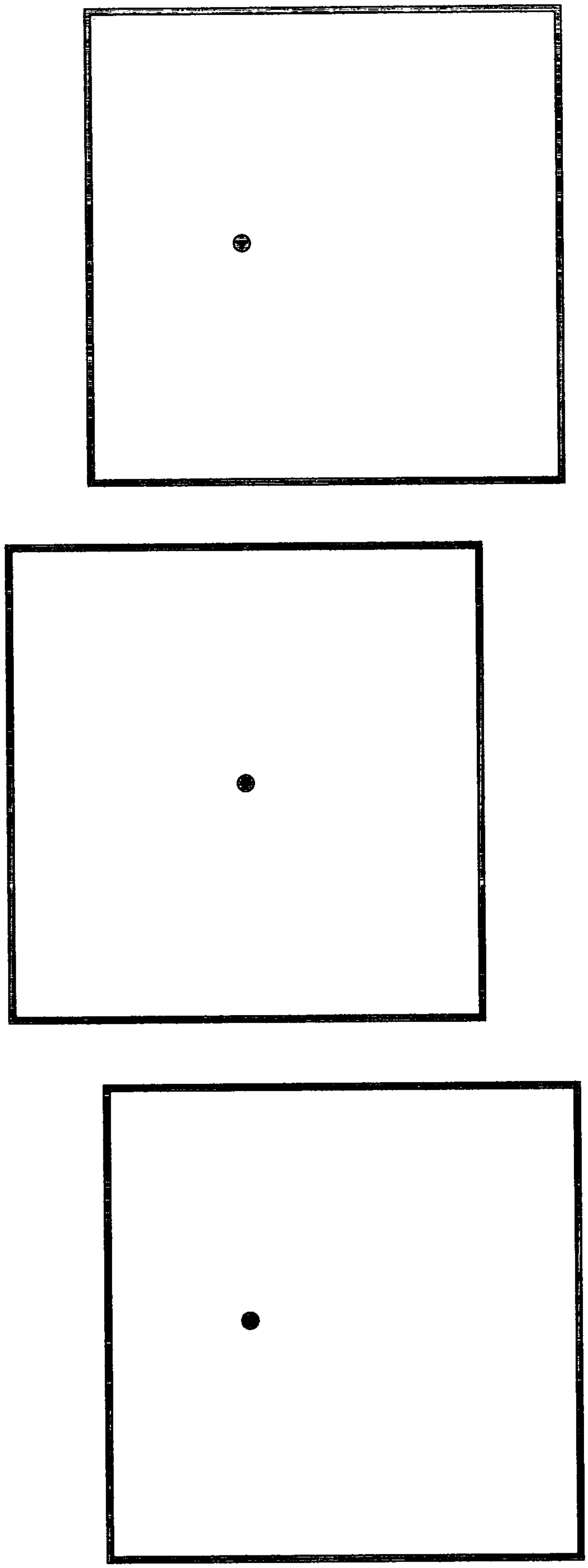
Appendix A: Illustrations of referred illusion types



igure a1: Illustration of form of stimulus used in the Roelofs effect.

Appendix A: Illustrations of referred illusion types

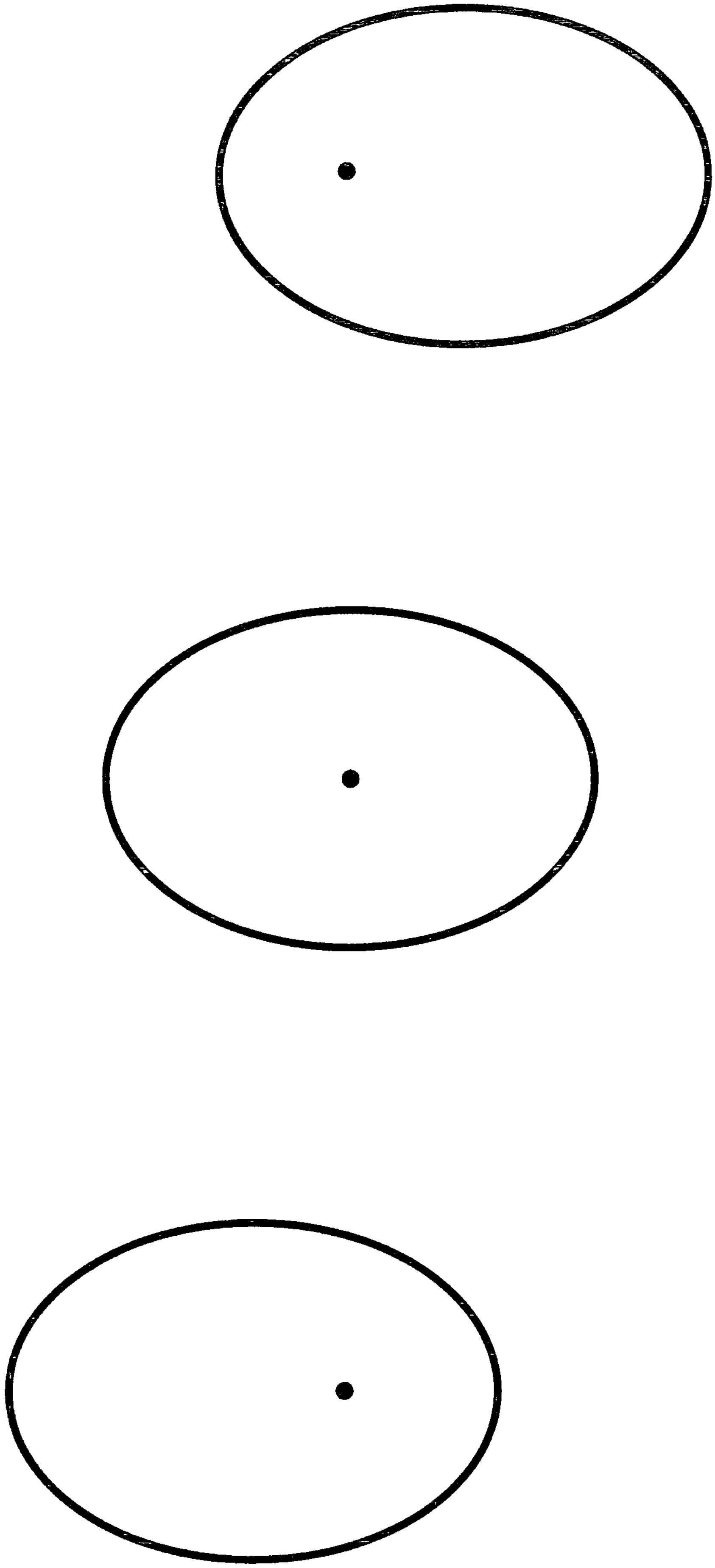


Figure a2: Illustration of the ellipse variant of the Roelofs effect.

Appendix A: Illustrations of referred illusion types

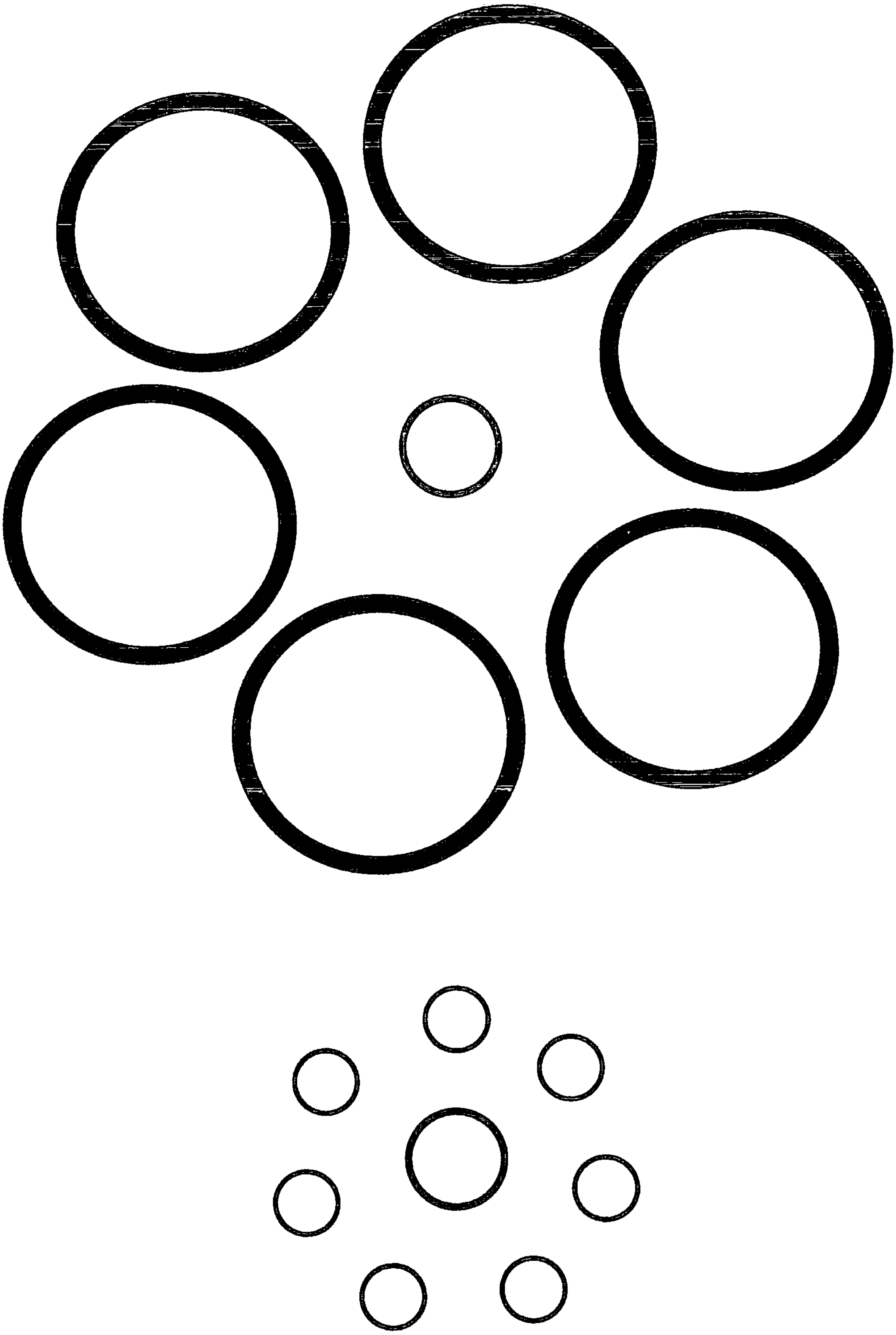


Figure a3: Illustration of the Titchener's Circles/ Ebbinghaus Illusion.

Appendix A: Illustrations of referred illusion types

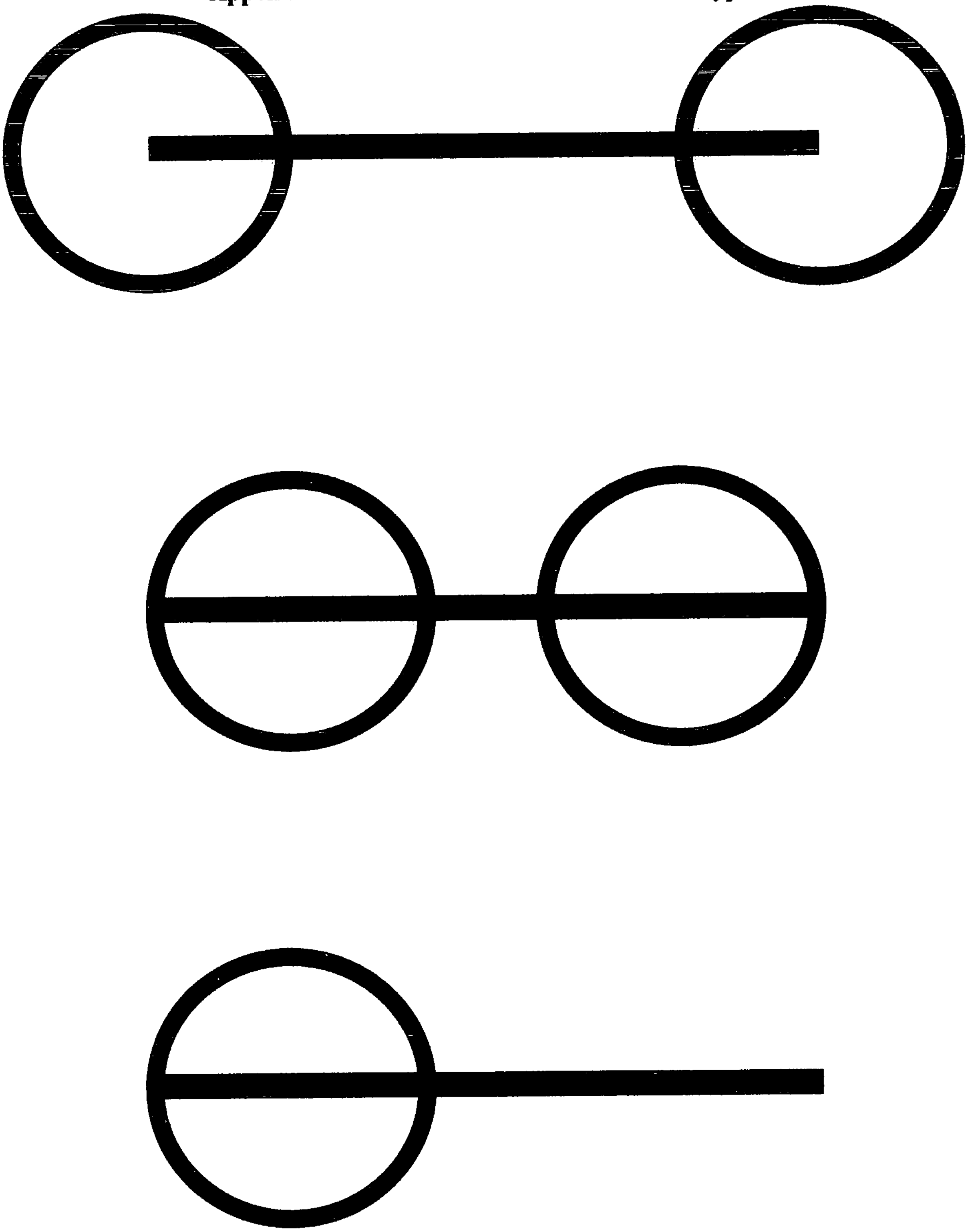


Figure a4: The Delaboeuf variant of the Mueller-Lyer Ilusion (top and middle figures) and the one ended-Delaboeuf variant (bottom figure).

Appendix A: Illustrations of referred illusion types

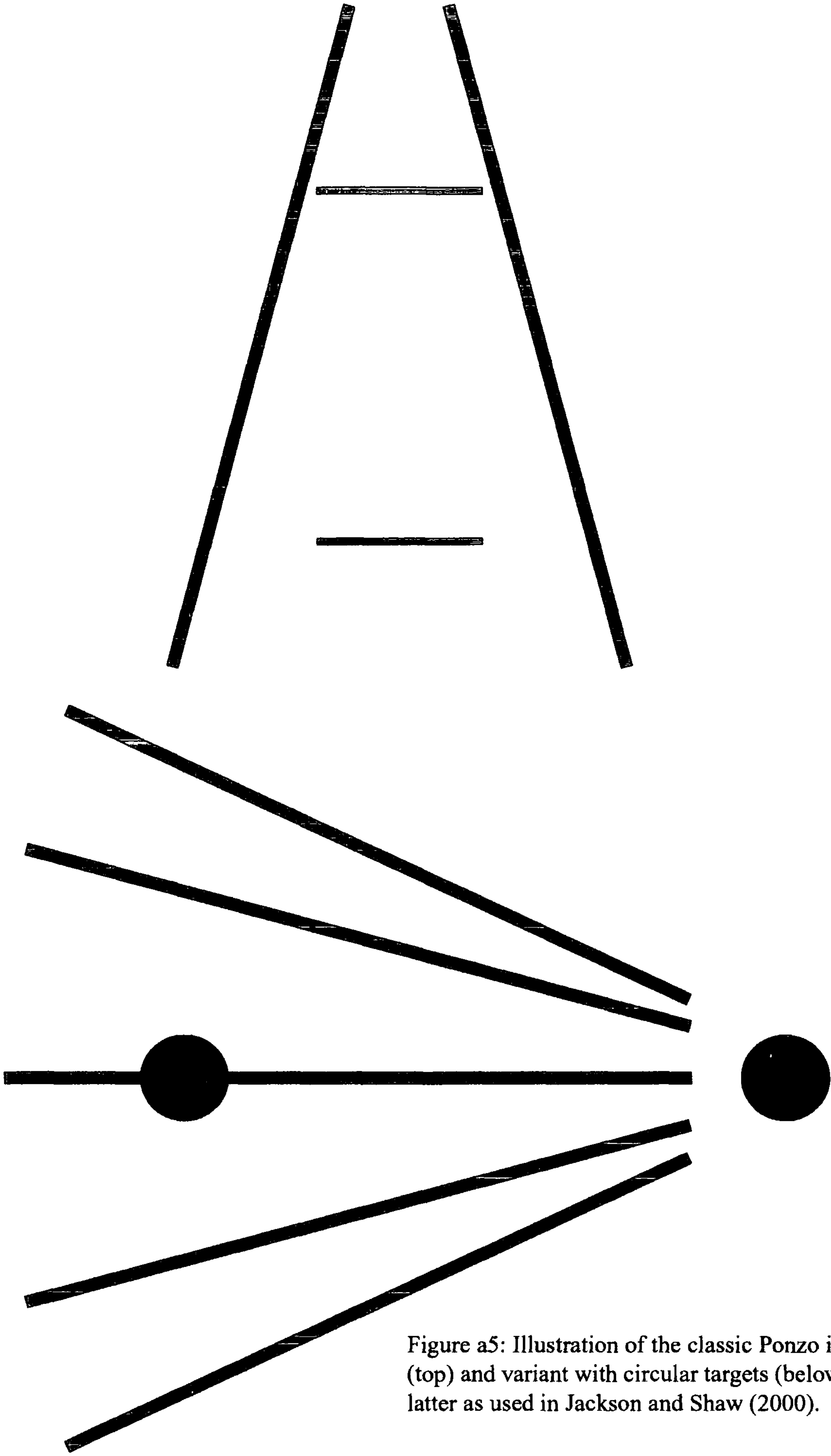


Figure a5: Illustration of the classic Ponzo illusion (top) and variant with circular targets (below): the latter as used in Jackson and Shaw (2000).

Appendix A: Illustrations of referred illusion types

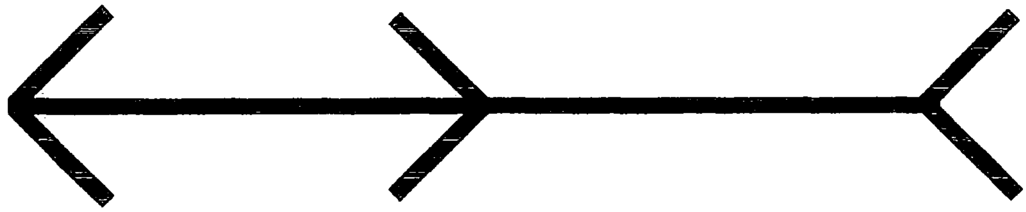


Figure a6: The Brentano variant of the Mueller-Lyer illusion.

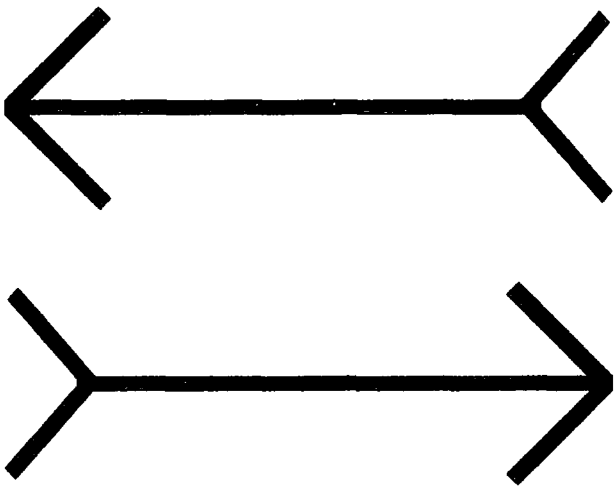


Figure a7: The Judd variant of the Mueller-Lyer illusion.

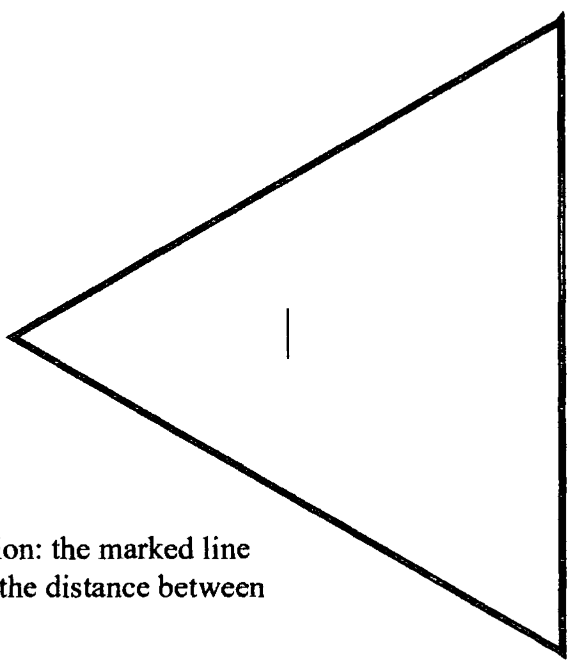


Figure a8: The Triangle illusion: the marked line indicates the true bisector of the distance between base and apex.

Appendix A: Illustrations of referred illusion types

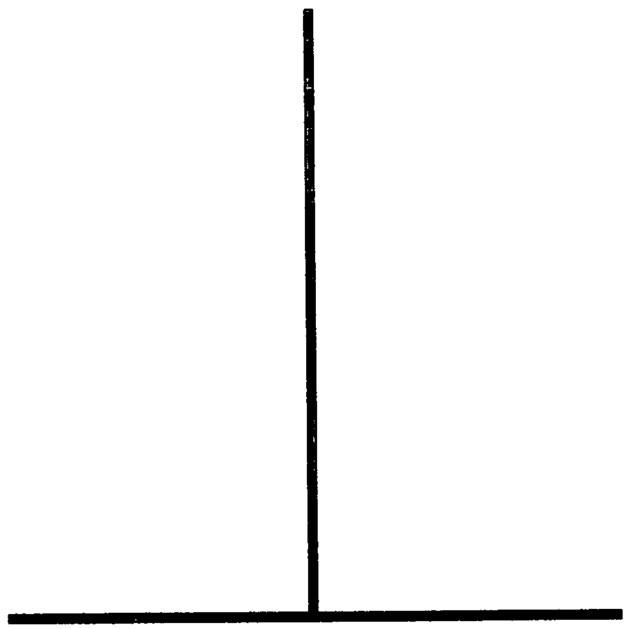


Figure a9: The horizontal/vertical Illusion. Both Lines are of equal length.

Appendix A: Illustrations of referred illusion types

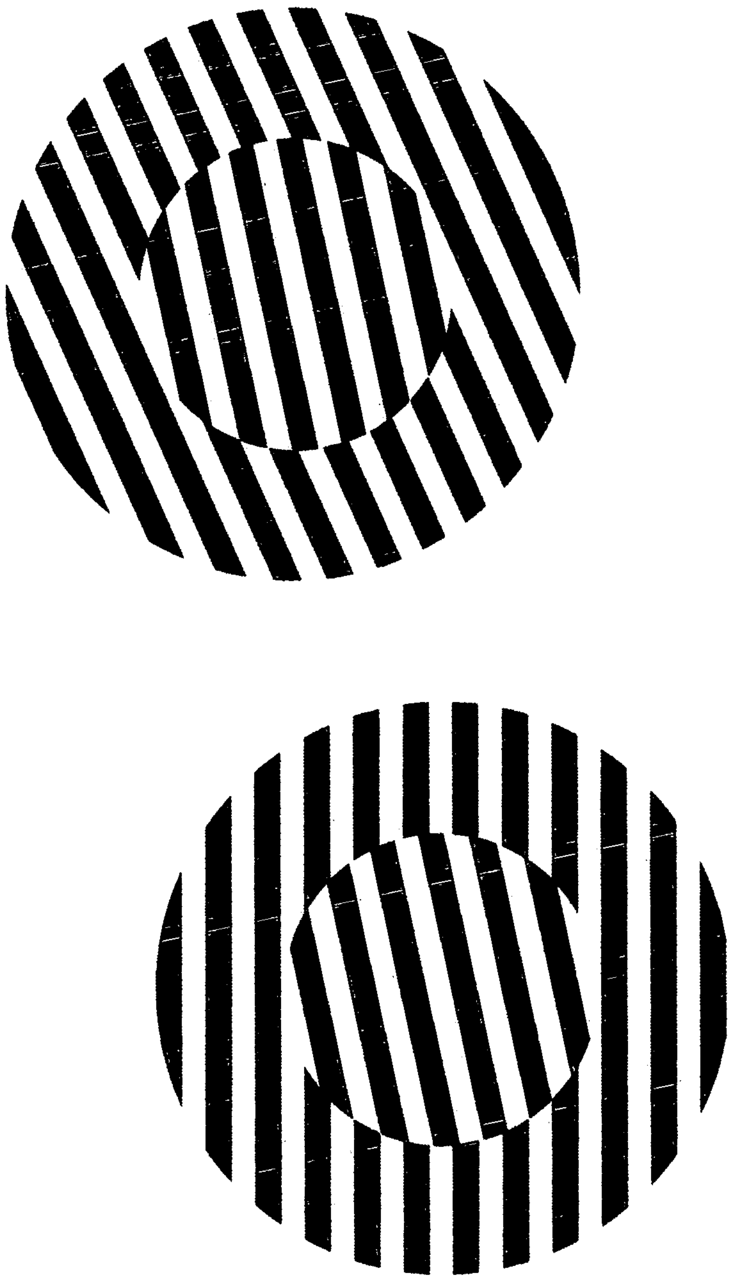


Figure a10: The Simultaneous Tilt illusion (STI).

Appendix A: Illustrations of referred illusion types

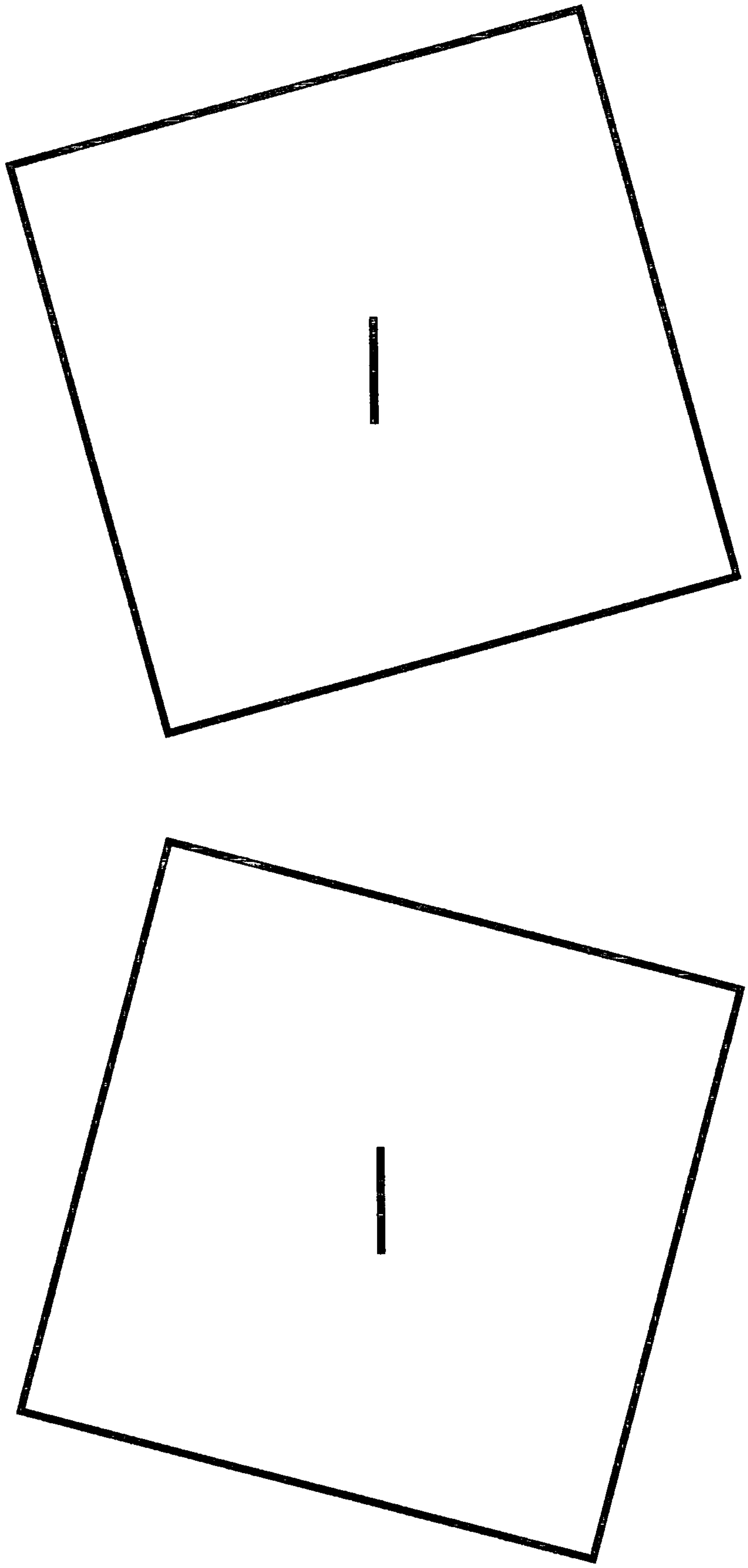


Figure a11: The rod-and frame illustration (RFI). Target stimili (75/90 and 105/90) for the 'rod and frame' pilot study 3. N.B. not to scale.

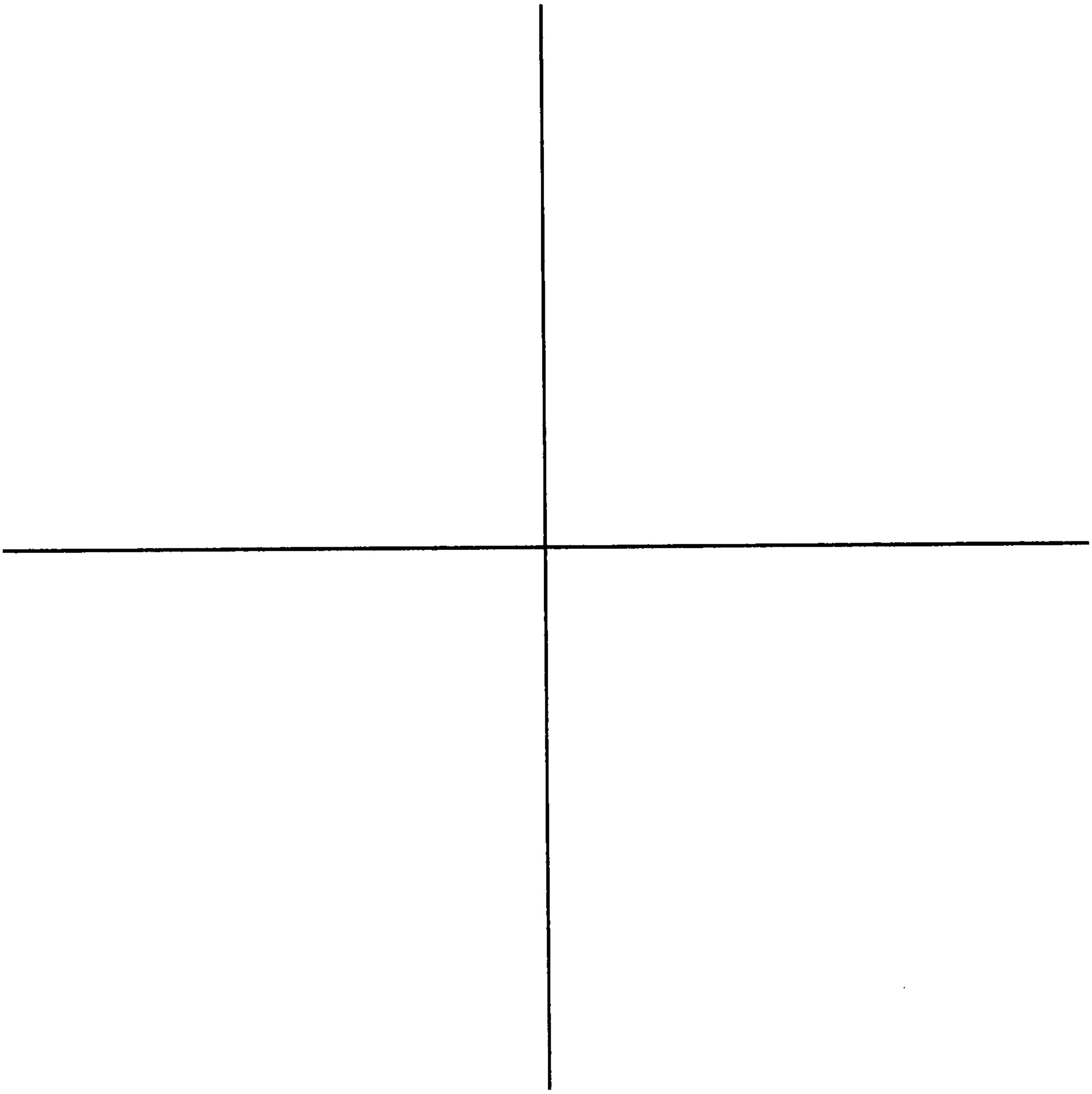


Figure a12: The 'cross-hairs' response sheet used in study 4.

Appendix A: Illustrations of referred illusion types

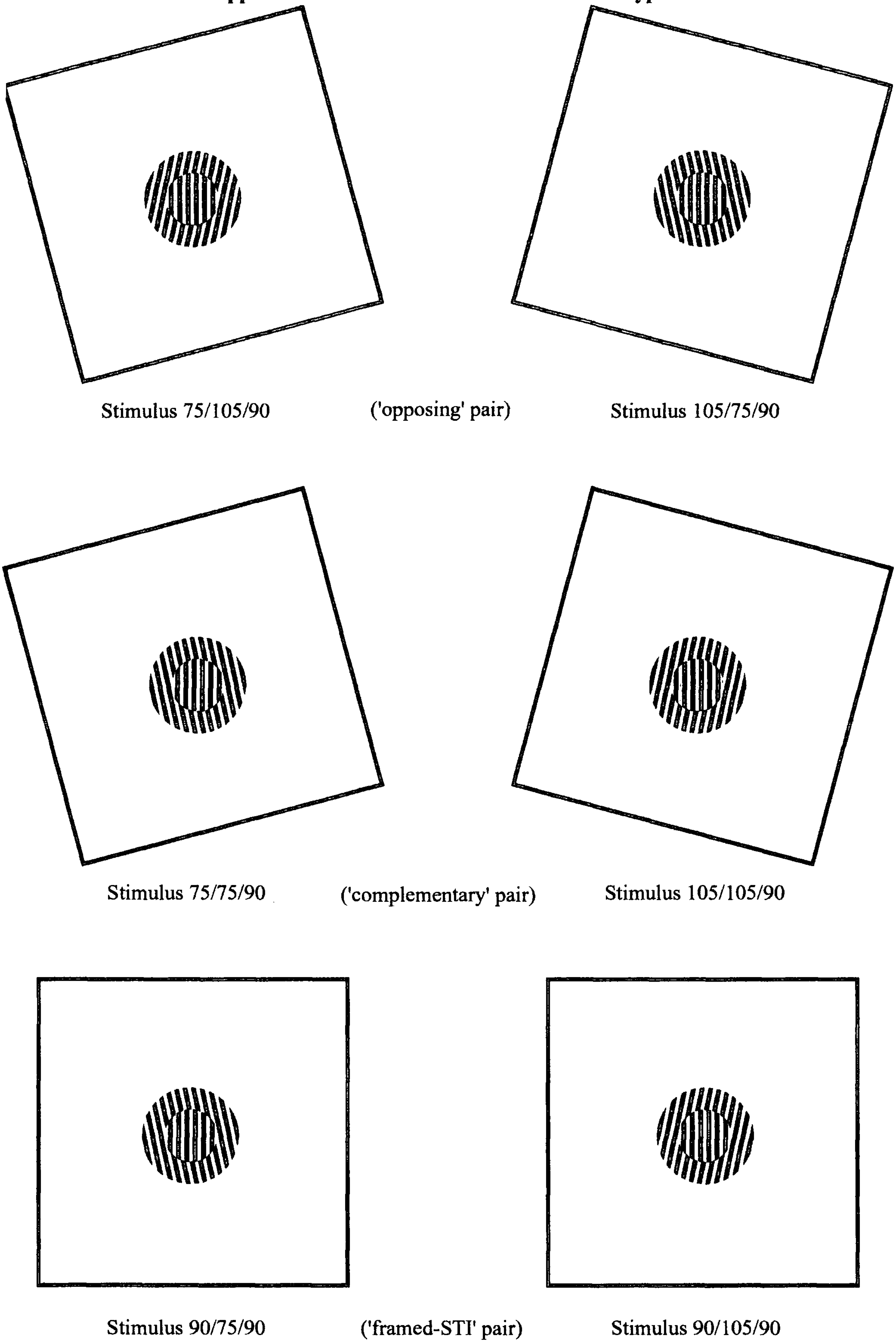
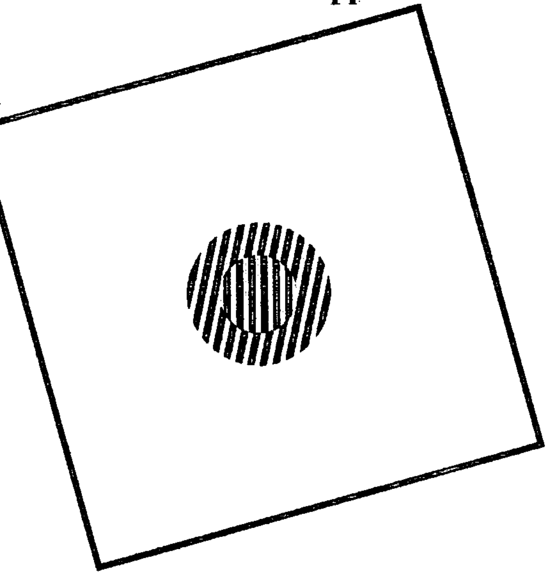
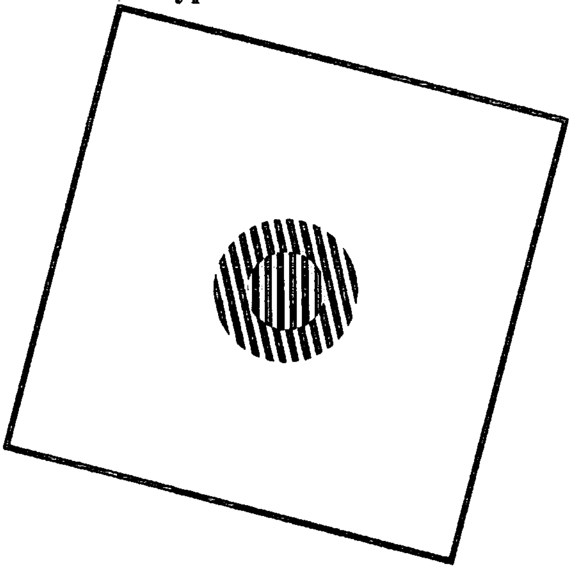
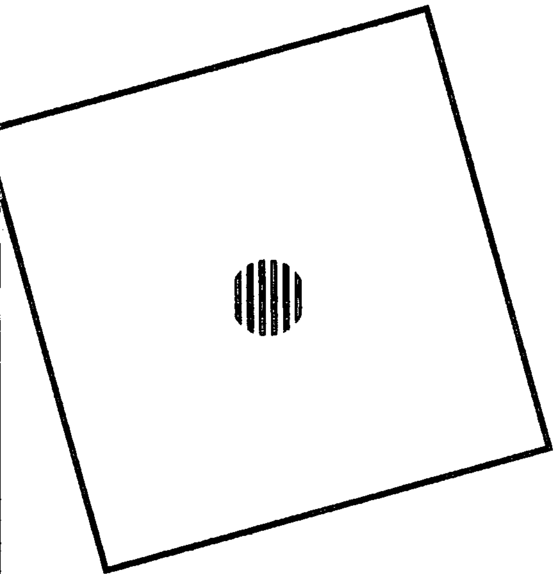


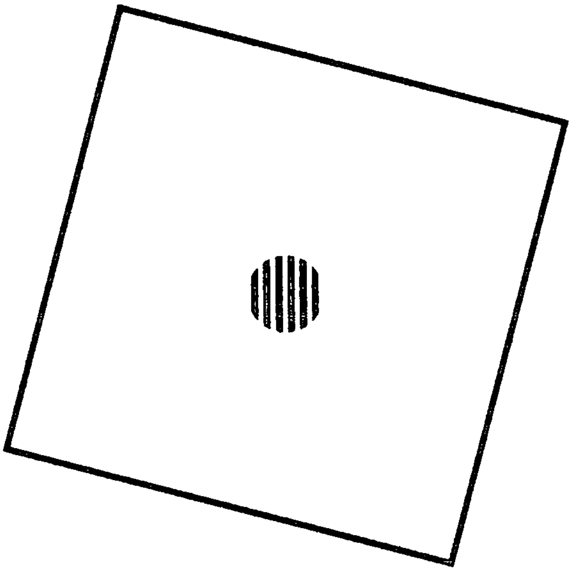
Figure a13: Target stimuli for study 5 (N.B. not to scale)





Stimulus 75/105/90 ('opposing' pair) Stimulus 105/75/90





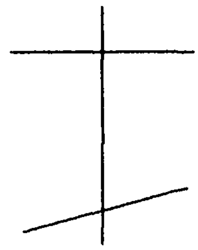
Stimulus 75/0/90 ('rods-and-frame' pair) Stimulus 105/0/90

Stimulus 0/75/90 ('STI' pair) Stimulus 0/105/90

Figure a14: Illustrations of the target stimuli used in study 6 (N.B. not to scale).

Appendix A: Illustrations of referred illusion types

(a)



(b)

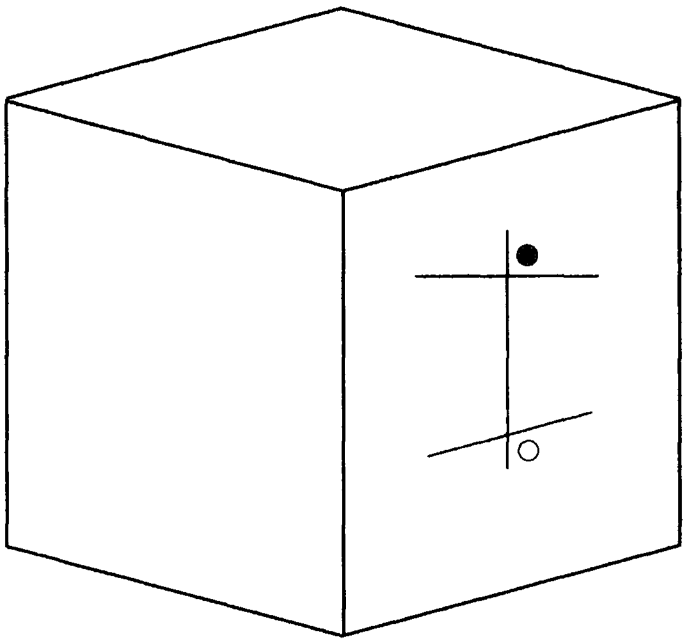


Figure a15: The upper figure (a) clearly shows the upper horizontal line as perpendicular to the vertical line, and the lower line as oblique. When this figure is embedded within a depth cue (b) fixating at the red spot makes the lower vertical/'horizontal' crossing appear perpendicular and the upper crossing oblique - this effect reverses by fixating the blue spot.

From Enns and Coren (1995) p. 1165.

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