Size-contrast illusions deceive the eye but not the hand

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Background: When we reach out to pick up an object, not only do we direct our moving limb towards the location of the object, but the opening between our fingers and thumb is scaled in flight to the object's size. Evidence obtained from patients with neurological disorders has shown that the visual processing underlying the calibration of grip aperture and other movement parameters during grasping is mediated by visual mechanisms located in the cerebral cortex that are quite distinct from those underlying the experiential perception of object size and other object features. Under appropriate conditions, such dissociations can also be observed in individuals with normal vision. Here we present evidence that the calibration of grasp is quite refractory to pictorial illusions that have large effects on perceptual judgements of size.

Results: We used a variation of the familiar 'Titchener circles' illusion in which two target circles of equal size, each surrounded by a circular array of either smaller or larger circles, are presented side by side. Subjects typically report that the target circle surrounded by the array of smaller circles appears to be larger than the target surrounded by larger circles. In our test, two thin 'poker-chip' discs were used as the target circles. The relative size of the two discs was randomly varied so that on some trials the discs appeared perceptually different but were physically equivalent in size, and on other trials they were physically different but appeared perceptually equivalent. The perceptual judgements made by the 14 subjects in our experiment were strongly affected by this size-contrast illusion. However, when asked to pick up a disc, the scaling of the subjects grip aperture (measured opto-electronically before contact with the disc) was largely determined by the true size of the target disc and not its illusory size.

Conclusions: It would seem that the automatic and metrically accurate calibrations required for skilled actions are mediated by visual processes that are separate from those mediating our conscious experiential perception. Earlier studies on patients with neurological deficits suggest that these two types of processing may depend on quite separate, but interacting, visual pathways in the cerebral cortex.

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Background

Our perception of the visual world is by its very nature relative. As we gaze across a room, some of the objects within our field of view will be perceived, in an obligatory fashion, as larger or closer than others. But although we might perceive that one object is larger or closer than another, such relative judgements of size and distance are not enough to calibrate the grasping movement that might be directed at that object — to grasp the object accurately, our visuomotor system must access information concerning its exact size and distance. In fact, it is possible to show that normal subjects often make perceptual judgements about the location (or apparent change in location) of a visual stimulus that are at odds with the motor acts that they direct towards those stimuli.

Bridgeman *et al.* [1] have shown, for example, that even though a fixed visual target surrounded by a moving frame is perceived to drift in a direction opposite to that of the frame (which seems to be stationary), when asked, the subjects persist in pointing to the actual location of the target. Wong and Mack [2] obtained similar dissociations between a perceptual judgement and the control of a motor act, but monitored saccadic eye movements rather than pointing. In their experiments, a small target was presented within a surrounding frame and, after a 500 millisecond blank period, the frame and target reappeared, but now the frame was displaced a few degrees to the left or right. The target itself was presented in exactly the same location as before. Yet instead of perceiving the frame as having changed position, subjects had the strong illusion that it was the target that had changed position, in a direction opposite to that of the actual displacement of the frame. This illusion was maintained even when the target was displaced in the same direction as the frame, but by only one third the distance. In this latter condition the perceived change in target position, after the blank period, was still in the direction opposite to the change in frame position, and thus, even more remarkably, in the direction opposite to the actual change in position of the target. Yet despite the presence of this strong illusory displacement of the target, subjects consistently directed their saccades to the true location of the target (in other words, to its location with respect to the eye rather than to its location with respect to the frame).

The complementary dissociation was observed when a target was moved unpredictably during a saccadic eye movement [3]; here it was found that subjects were unable

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to report, even in a forced-choice situation, whether or not the target had changed position, even though the correction saccades and manual-aiming movements directed at the target showed near-perfect adjustments for the unpredictable target shift. In other words, an illusory perceptual constancy of target position was maintained in the face of large amendments in visuomotor control.

The results of all these experiments suggest that the visual mechanisms mediating the perception of object location operate largely in allocentric coordinates, whereas those mediating the visual control of object-directed actions operate in egocentric coordinates. In other words, visual perception seems to use a coordinate system that is world-based, in which objects are seen as changing location relative to a stable or constant world; the systems controlling actions, however, cannot afford these kinds of constancies and must compute the location of the object with respect to the effector that is directed at that target. Thus, in the experiments by Bridgeman *et al.* [1] and Wong and Mack [2], the target within the moving or displaced frame was perceived as moving relative to the frame, whereas the frame itself, the only large visible feature in the field of view, was perceived as a stable background. The visuomotor systems computing the saccadic (or aiming) eye movements directed at the target simply ignored the movement of the frame and computed the actual position of the target in retinocentric (and perhaps also in head- and/or shoulder-centred) coordinates.

In the experiments by Goodale *et al.* [3] in which the position of the target was sometimes changed during a saccade, the subjects' failure to perceive the displacement of the target was probably a reflection of the broad tuning of perceptual constancy mechanisms that preserve the identity of a target as its position is shifted on the retina during an eye movement. When no other reference points are available in the field of view, the perceptual system assumes that the position of the target, which was stable at the beginning of the saccade, has not changed. Such an assumption has little consequence for perception and is computationally efficient. But the visuomotor systems controlling saccadic eye movements and manual aiming movements cannot afford that luxury. At the end of the first saccade, they must re-compute the position of the target (within egocentric frames of reference), so that the appropriate correction saccade and amendment to the trajectory of the moving hand can be made. In short, different types of visual computation are required for visual perception and visuomotor control.

Just as the perception of object location seems to operate within allocentric frames of reference, so does the perception of object size. Although we often make subtle relative judgements of object size, we rarely make absolute judgements. Indeed, our judgements of size appear to be so inherently relative that we can sometimes be fooled by visual displays in which visual stimuli of the same size are positioned next to comparator stimuli that are either much smaller or much larger than the target

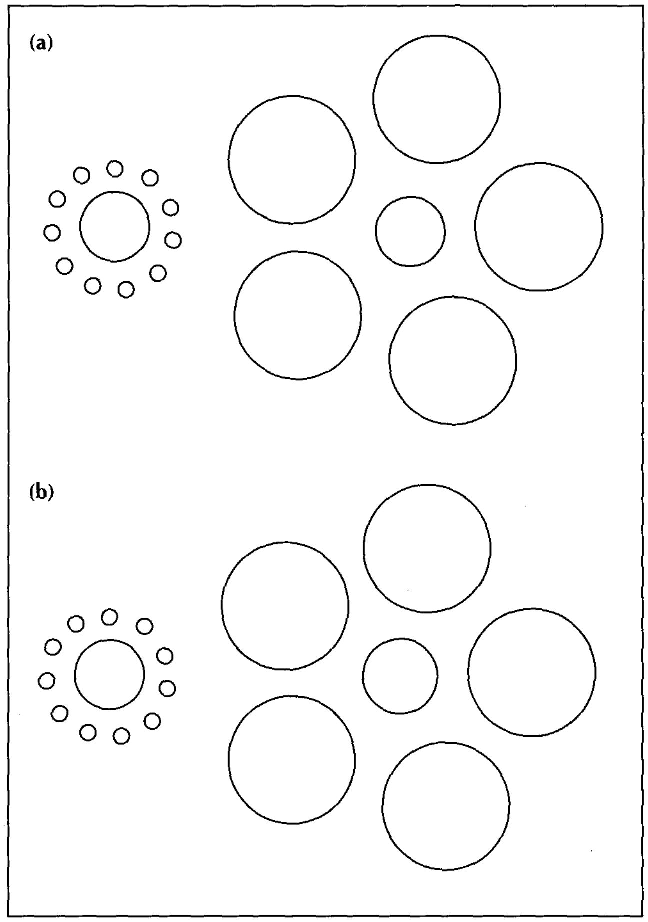

Fig. 1. The Titchener circles illusion. **(a)** The standard version of the illusion. The target circles in the centre of the two arrays appear to be different in size even though they are physically identical. For most people, the circle in the annulus of smaller circles appears to be larger than the circle in the annulus of larger circles. **(b)** A version of the illusion in which the target circle in the array of larger circles has been made physically larger than the other target circle. The two target circles should now appear to be perceptually equivalent in size.

stimuli. Such size-contrast illusions are popular examples used in many introductory textbooks in psychology and perception. One such illusion is the 'Titchener circles' (or 'Ebbinghaus') illusion, in which two target circles of equal size, each surrounded by a circular array of either smaller or larger circles, are presented side by side (Fig. 1a). Subjects typically report that the target circle surrounded by the array of smaller circles appears larger than the one surrounded by the array of larger circles, presumably because of the difference in the size contrast between the target circles and the surrounding circles. Although the illusion is usually depicted as we have just described, it is also possible to make the two target circles appear identical in size by increasing the actual size of the target circle surrounded by the array of larger circles (Fig. 1b).

Although perception is clearly affected by these manipulations of the stimulus array, there is good reason to believe that the calibration of size-dependent motor outputs — such as grip aperture during grasping — would not be. After all, when we reach out to pick up an object, particularly one we have not seen before, our visuomotor system must compute its size accurately if we are to pick it up efficiently, that is, without fumbling or re-adjusting our grip. It is not enough to know that the target object is larger or smaller than surrounding objects; the visuomotor systems controlling hand aperture must compute its real size. For this reason, one might expect the calibration of grip aperture to be refractory to size-contrast illusions. It was this idea that we tested in the present study.

Results

We designed a three-dimensional version of the Titchener circles illusion, in which two thin 'poker-chip' discs were used as the target circles (Fig. 2). The discs were arranged as pairs on a standard Titchener annular circle display drawn on a white background and positioned directly in front of the subject. Before being tested in the grasping paradigm, each of the 14 subjects in the study was presented with a range of different discs (27–33 mm in diameter) in order to find a pair that would be reliably identified as identical in size. To be judged equivalent in size, the disc in the array of larger circles had to be, on average, 2.5 mm wider than the disc in the array of smaller circles.

During the actual testing, trials in which the two discs appeared perceptually identical but were physically different in size were randomly alternated with trials in which the discs appeared perceptually different but were physically identical; for half of these latter trials a pair of small discs was used, and for the other half a pair of larger discs was used. On each trial, the two discs were presented for 3 seconds by illuminating the table with an overhead lamp. Subjects were given the following instructions: 'if you think the two discs are the same size, pick up the one on the left; if you think they are different in size, pick up the one on the right'. In a subsequent test session, these instructions were reversed. All subjects were asked to pick up the disc with the index finger and thumb of their right hand.

The trajectory of the grasping movement was recorded with two cameras that tracked three infrared light-emitting diodes (IREDs), which were attached to the ends of the index finger and thumb as well as to the wrist (Fig. 2). Using these recordings, we were able to reconstruct the change in grip aperture — the opening between the index finger and thumb — as subjects reached out and picked up the target disc. The main kinematic variable we measured was the maximum grip aperture, which is typically achieved about 70 % of the way through a grasping movement and has been shown to be well-correlated with the size of the goal object [4–6]. The calibration of maximum grip aperture has also been shown to be largely refractory to visual information that is available during the execution of the movement, relying instead on the motor programming that occurs before the movement begins [4–6].

Our version of the Titchener circles illusion proved to be quite effective, and all the subjects remained sensitive to the illusion throughout testing. In other words, they

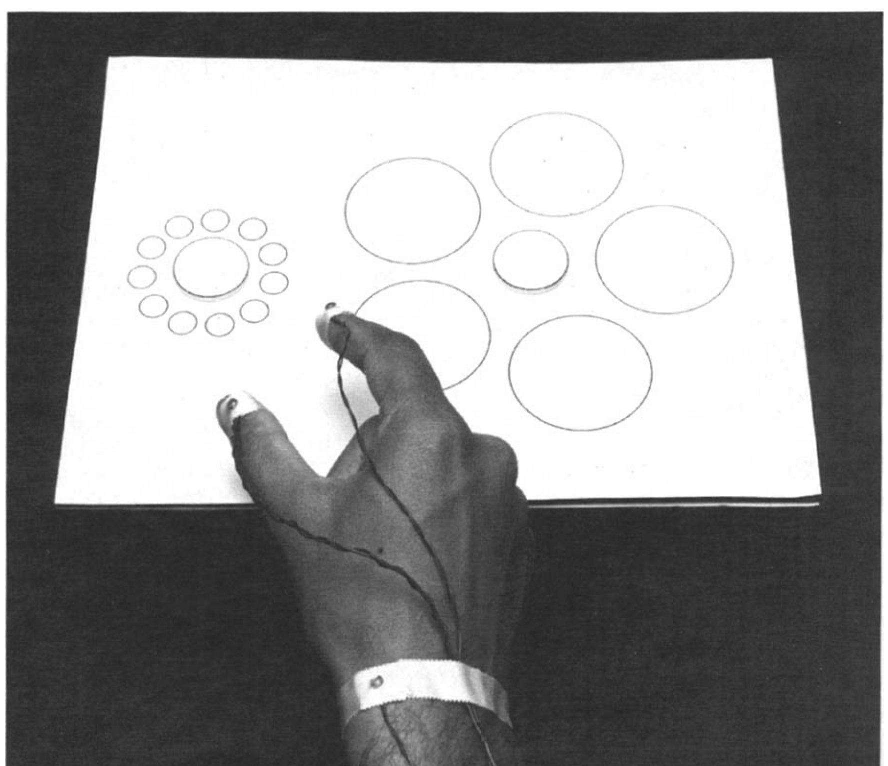

Fig. 2. A photograph of our three-dimensional version of the Titchener circles illusion. Note the infrared light-emitting diodes (IREDs) attached to the finger, thumb and wrist of the subject.

treated discs that were actually physically different in size as perceptually equivalent, and discs that were physically identical were judged to be perceptually different. Indeed, these observations are reflected by the finding that the subjects took significantly longer to initiate their movement on trials in which they judged the two discs to be identical — a familiar finding in 'same/different' judgement tasks — even though, in this case, the discs were actually physically different in size (Fig. 3).

Remarkably, however, the scaling of the subjects grasp was affected very little by these illusory perceptions. Instead, the maximum aperture of their grip was largely determined by the true size of the disc. Thus, on trials in which the two discs were perceived as being the same size, subjects opened their hand wider for the larger disc than they did for the smaller one (Fig. 4a). Moreover, as illustrated in Figure 4b, the relationship between true size and maximum grip aperture was as evident on trials in which the two discs were judged to be the same size (but were physically different) as it was on trials in which the two discs were judged to be different (but were actually both small or both large). In short, the calibration of grip size seemed to be largely impervious to the effects of the size-contrast illusion.

Of course, the control of skilled movements is clearly not isolated from perceptual information. The perceived function of an object (such as a hammer or telephone for example) has clear effects on the nature of the grasp we adopt when we pick it up. Even in this task, one could detect some influence of the perceptual judgements on grip scaling — at least on those trials in which subjects perceived the two discs to be different in size when in fact they were identical. On some of these trials, some subjects did open their fingers slightly more for the disc surrounded by the small circles than they did for the disc surrounded by the large circles. Nevertheless, as Figure 5

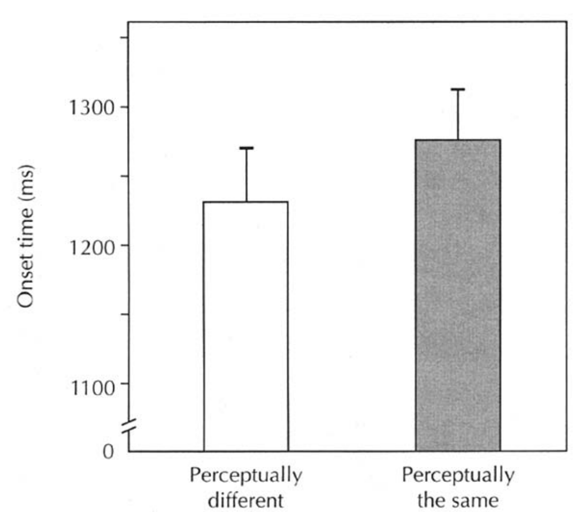

Fig. 3. The mean movement-onset times for trials in which subjects judged the two discs to be perceptually different in size (even though the discs at the center of each annulus of circles were actually of the same diameter), and trials in which they perceived the discs to be the same size (even though the discs at the center of each annulus of circles were actually of different diameters).

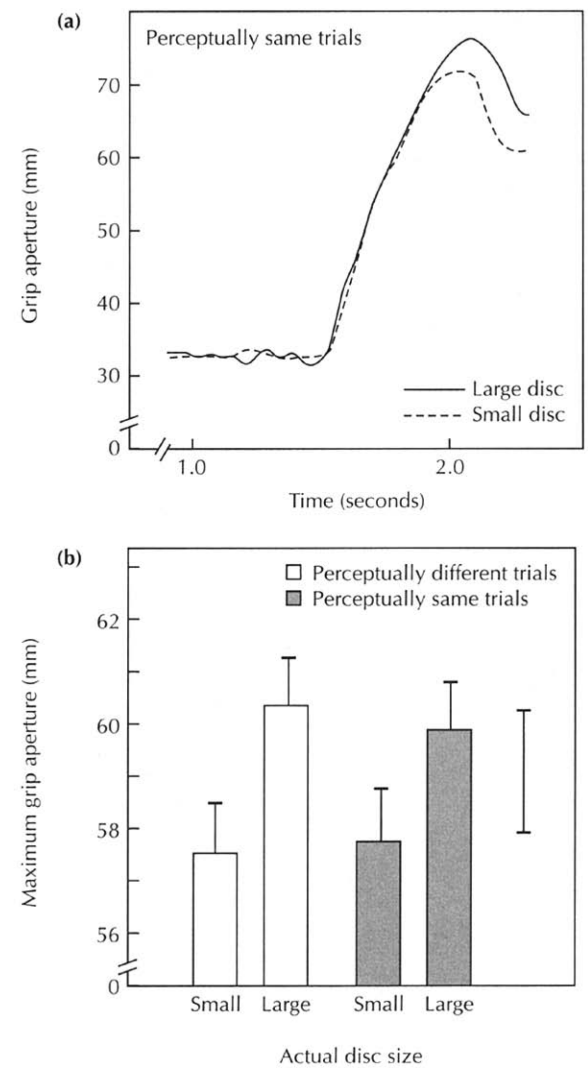

Fig. 4. Graphs illustrating grip aperture under different testing conditions. **(a)** Representative grip-aperture profiles for one subject picking up a large disc and a small disc on separate trials in which he judged the two discs to be identical in size (even though, of course, the two discs were physically quite different). In both cases, the disc was located on the left hand side of the display. **(b)** The mean maximum grip aperture for the 14 subjects in different testing conditions. The grey bars indicate the maximum aperture on trials in which the two discs were judged to be perceptually the same, even though they were physically different in size. The open bars indicate the mean maximum aperture on trials in which the two discs were judged to be perceptually different, even though they were physically the same size (either two large discs or two small discs). The line to the extreme right of the graph indicates the average difference in disc size that was required to achieve perceptual equivalence in the pre-test. The difference between the maximum grip aperture achieved for large discs was significantly greater than the maximum grip aperture achieved for small discs, independent of whether or not the subject believed the discs were the same or different sizes ($p < 0.001$). No other comparisons were significant. Error bars indicate the standard error of the mean.

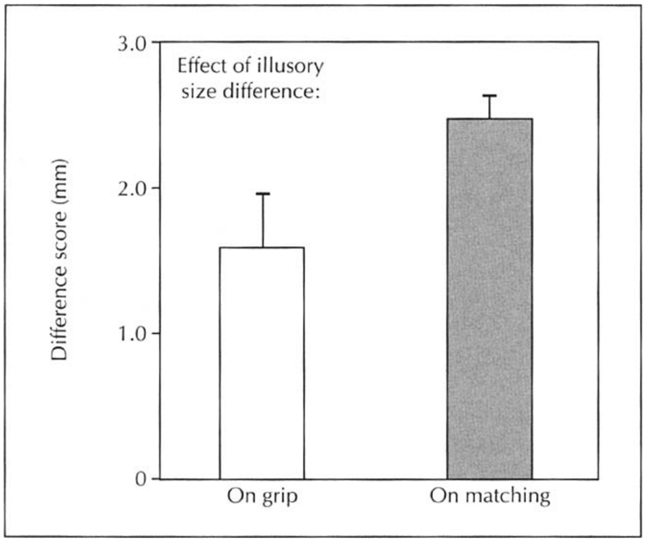

Fig. 5. The effect of the size-contrast illusion on the calibration of the grasp and on perceptual matching of disc size. The open bar shows the average difference between maximum grip aperture for discs surrounded by an array of small circles, and the maximum grip aperture for identical discs surrounded by an array of large circles; that is, the effect of the illusion on grip size. For half these trials, the two discs were both large and for the other half they were both small. The difference score was an average of all trials — that is, when both discs were large, and when both were small. This effect was significantly smaller ($p < 0.02$) and more variable than the average difference in disc size that was required to obtain a judgement of perceptual equivalence with such arrays (the grey bar). Error bars indicate the standard error of the mean.

illustrates, the effect of the perceptual judgement on grip aperture was quite variable, and was significantly smaller than the size difference that was required to achieve perceptual equivalence between the two discs in the matching test that had been carried out earlier. In other words, the effect of the illusion on grip size was much smaller and more variable than the effect of the illusion on perceptual judgements of size. In contrast, as we have already seen, the calibration of grip was strongly influenced by the real object size in all subjects — independent of whether or not the grasp was initiated on perceptually different or perceptually identical trials.

Discussion

The results of these experiments make it clear that although size-contrast illusions have a powerful effect on the perceptual judgements of an object's size, grasping movements directed at that same object remain metrically accurate. Thus, the very act by which subjects indicated their susceptibility to the illusion (that is, picking up one of the two target discs) was itself unaffected by the visual information driving that illusion.

It should be emphasized that the accurate scaling of the grasp was not due to the fact that the subjects were somehow comparing their grip aperture with the diameter of the target disc during the grasping movement. Firstly, as can be seen in Figure 4, the maximum grip aperture was actually much larger than the diameter of the disc — more than twice as large on most trials. But, as reported in many previous studies (see for example [4–6]), maximum grip aperture still correlated well with the size of the target. Secondly, subjects remained susceptible to the illusion throughout the experiment, despite the fact that they were scaling their grasp to the real size of the target disc. If the subjects were adjusting their grasp on the basis of information delivered by the same visual networks that they used to make their perceptual judgements, then one might expect to see some weakening of the illusion over the course of the experiment. No such weakening was observed. Thirdly, as mentioned earlier, the calibration of maximum grip aperture is largely determined by motor programming that is carried out before the hand has actually started to move [4–6]. In fact, on a few occasions, subjects expressed surprise when they handled the disc after they had picked it up — claiming that it seemed larger or smaller than they had expected — even though their grasp had been calibrated accurately in flight.

But why should perception be so susceptible to the illusion while the calibration of grasp is not? It is possible that the illusion arises from a straightforward relative-size scaling mechanism, whereby an object that is smaller than its immediate neighbours is assumed to be smaller than a similar object that is larger than its immediate neighbours [7]. It is also possible that some sort of image-distance equation is contributing to the illusion, in which the array of smaller circles is assumed to be more distant than the array of larger circles; as a consequence, the target circle within the array of smaller circles will also be perceived as more distant (and therefore larger) than the target circle of equivalent retinal-image size within the array of larger circles. In other words, the illusion may be simply a consequence of the perceptual system's attempt to make size-constancy judgments on the basis of an analysis of the entire visual array [8].

Mechanisms such as these, in which the relationships between objects in a visual array play a crucial role in scene interpretation, are clearly central to perception. In contrast, the execution of a goal-directed act, such as prehension, depends on metrical computations that are centred on the target itself. As a consequence, computation of the retinal-image size of the object coupled with an accurate estimate of distance will deliver the true size of the object for calibrating the grip — such computations may be quite insensitive to the kinds of pictorial cues that drive our perception of familiar illusions.

The distinction between visual perception and the visual control of skilled motor acts has also been observed in patients who have sustained selective damage to different visual areas of the cerebral cortex. Thus, patients with damage in the superior regions of the posterior parietal cortex are often unable to use information about the size, shape, orientation and location of an object to control the posture of the hand and fingers and/or the trajectory of their moving limb during a grasping movement [5,9–12]. Yet these same patients can usually identify and describe the very objects they cannot grasp. The opposite dissociation has been observed in another patient (D.F.) who can direct accurate and well-formed grasping movements towards objects that she cannot identify or discriminate [11–13]. Although the damage in D.F.'s brain is quite diffuse, the ventrolateral regions of her occipital lobe are particularly compromised. These neuropsychological data, together with the results of electrophysiological and behavioural studies in the monkey, have led to the proposal that the ventral stream of visual projections from primary visual cortex to inferotemporal cortex is critical for the visual perception of objects, whereas the dorsal stream, which projects from primary visual cortex to the posterior parietal region, mediates the required sensorimotor transformations for visually-guided actions directed at those objects [11,14]. It is possible that the dissociation between perceptual judgements of object size and the calibration of grasp that we have reported here is a reflection of the different computations carried out by these two visual processing streams in the normal brain.

Conclusions

By recording the kinematics of a grasping movement directed at discs presented in a three-dimensional version of the Titchener circles illusion, we have shown that the calibration of grip aperture is quite refractory to the compelling size-contrast illusion induced by the display. This result suggests that the automatic and metrically accurate calibrations required for skilled actions may depend on visual computations that are different from those driving our perceptual judgements about objects in the world. In short, what we think we see may not always be what guides our actions.

Materials and methods

The target discs were constructed of 3 mm thick white plastic with a thin black line drawn around the circumference on their top surface (Fig. 2). The discs ranged in size from 27–33 mm (in 1 mm steps). During presentation, two discs were positioned on a Titchener circles display, one disc in the centre of an array of small circles (each 10 mm in diameter) and the other in an array of large circles (each 58 mm in diameter). The overall diameter of the array of small circles (through the centre of circles) was 47 mm; the overall diameter of the array of large circles was 110 mm (Fig. 2). The centres of the two arrays were 120 mm apart. The entire display was mounted on a turntable so that the left/right position of the arrays could be easily changed.

The 14 subjects (9 males and 5 females) ranged in age from 19 to 41 years (mean 22.2 years) and were all strongly right-handed as assessed by a modified version of the Edinburgh Handedness Inventory [15]. Their vision was normal or corrected-to-normal and their stereoacuity was at least 40" of arc as measured by the Randot Stereotest (Stereo Optical, Chicago).

During testing, subjects stood in front of the table on which the Titchener circles display was placed. This gave them a bird's-eye view of the display that was very nearly orthogonal to the display surface. They were instructed that they could move their eyes but should try to keep from moving their head. During a pre-test phase, subjects were systematically tested with different pairs of discs in order to establish which pairs would be reliably judged as equivalent in size. On average, the disc centered in the array of large circles had to be 2.5 mm larger than the disc centered in the array of small circles in order to achieve perceptual equivalence. For 8 subjects the required difference was 2 mm, for 5 subjects it was 3 mm, and for 1 subject it was 4 mm. Each subject was then tested with his or her particular disc pair during subsequent testing.

During the testing we used two types of trial. In the first type, which was repeated 36 times, the large disc was placed in the array of large circles, and the small disc in the array of small circles, to create the illusion that the discs were in fact the same size. The second type of trial, in which two discs of the same size were used to create the illusion that the discs were different sizes, was subdivided into two further types — each repeated 18 times — in which both discs were either small or large. The left/right position of the arrays was randomly varied. At the beginning of each trial, subjects placed the tips of their index finger and thumb of their right hand on a start button positioned on the table at their midline about 160 mm from the centre of each of the discs. The display on each trial was arranged out of the subject's field of view and before each trial began the room lights were extinguished. An overhead lamp was then turned on, thus illuminating the Titchener circles display for 3 seconds. The subjects were instructed that on each trial they were to pick up the disc on the left if they thought the discs were the same size, and the disc on the right if they thought the discs were different. These instructions were reversed halfway through the testing.

The movements of the hand and fingers during grasping were tracked by conventional opto-electronic recording. Infrared light-emitting diodes (IREDs) were attached to the index finger, thumb, and wrist with small pieces of adhesive tape (Fig. 2). The position of each IRED was tracked with two infrared-sensitive cameras and this information was stored on a WATSMART computer (Northern Digital, Waterloo, Canada) at a sampling rate of 100 Hz. The kinematics of the grasping movement on each trial were reconstructed off-line at the end of the experiment. Movement onset was defined as the point at which the velocity of the wrist IRED first reached a resultant velocity of more than 5.0 cm s^{-1}. Maximum grip aperture was defined as the maximum vectored distance between the index finger and thumb.

Differences in maximum grip aperture across conditions were analyzed using standard repeated-measures analysis of variants. Variable factors included perceptual condition (same/different), physical size (large disc/small disc), position (left/right), and array type (large circles/small circles). When appropriate, post-hoc tests were carried out by applying paired t-tests using Bonferroni corrections.

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