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# **Grasping Deficits and Adaptations in Adults with Stereo Vision Losses**

**Dean R Melmoth, Alison L Finlay, Michael J  
Morgan & Simon Grant\***

Department of Optometry & Visual Science, The Henry Wellcome  
Laboratories for Visual Sciences, City University, Northampton Square,  
London EC1V 0HB, UK

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**\*Correspondence to: Simon Grant**

**telephone, 44-(0)20-7040-0187; telefax, 44-(0)20-7040-8494; e-mail, [s.grant@city.ac.uk](mailto:s.grant@city.ac.uk)**

**PURPOSE:** To examine the effects of permanent *versus* brief reductions in binocular stereo vision on reaching and grasping (prehension) skills.

**METHODS:** The first experiment compared prehension proficiency in 20 normal and 20 long-term stereo-deficient adults (10 with coarse, 10 with undetectable disparity sensitivities) when using binocular vision or just their dominant or non-dominant eye. The second experiment examined effects of temporarily mimicking similar stereoacuity losses in normal adults, by placing de-focusing low or high plus lenses over one eye, compared to their control (neutral lens) binocular performance. Kinematic and error measures of prehension planning and execution were quantified from movements of the subjects' preferred hand recorded while they reached, **precision-grasped** and lifted cylindrical objects (two sizes, four locations) on 40-48 trials under each viewing condition.

**RESULTS:** Performance was faster and more accurate with normal compared to reduced binocular vision and least accomplished under monocular conditions. Movement durations were extended (up to ~100 ms) whenever normal stereo vision was permanently (ANOVA  $p<0.05$ ) or briefly (ANOVA  $p<0.001$ ) reduced, with a doubling of **error rates** in executing the grasp (ANOVA  $p<0.001$ ). Binocular deficits in reaching occurred during its end-phase (prolonged final approach, more velocity corrections, poorer coordination with object contact) and generally increased with the existing loss of disparity sensitivity. Binocular grasping was more uniformly impaired by stereoacuity loss and influenced by its duration. Long-term stereo-deficient adults showed increased variability in digit placement at initial object contact and adapted by prolonging (by ~25%) the time spent subsequently applying their grasp (ANOVA  $p<0.001$ ); brief stereo-reductions caused systematic shifts in initial digit placement and 2-3 times more post-contact adjustments in grip position (ANOVA  $p<0.01$ ).

**CONCLUSIONS:** High-grade binocular stereo vision is essential for skilled precision grasping. Reduced disparity sensitivity results in inaccurate grasp-point selection and greater reliance on non-visual (somesthetic) information from object contact to control grip stability.

Wheatstone's (1838)<sup>1</sup> demonstration of the stereoscope established that the human visual system computes horizontal disparities in the two retinal images to help determine the solid shape and relative depths of objects in the environment, a process known as binocular stereopsis. The neural bases of this process and their unique contributions to enhancing 3D-visual perception have since been extensively researched and documented<sup>2-4</sup>. Yet the potential advantages of binocular stereopsis for performing everyday visually-guided actions have received comparatively little attention<sup>4,5</sup>. This issue is of increasing clinical concern, as disparity processing mechanisms are compromised in several common visual disorders, such that a significant proportion of the general population may experience disability as a result of their associated losses in stereoacuity.

Binocular disparity cues are most marked for surfaces and objects located within near, peri-personal space. Partly for this reason, Morgan (1989)<sup>6</sup> suggested that the main pressure to utilize this information may have arisen from requirements for directing reaching and grasping (prehension) movements towards objects close at hand. In support of this conjecture, it is now known that cortical areas on the dorsal (vision-for-action) pathways involved in controlling the hand during grip formation and execution exhibit functional specializations for disparity processing<sup>7-12</sup>. Kinematic analyses of normal adult prehension have also repeatedly shown that performance is faster and more accurate – especially in the final approach to the target and in grasping it – when both eyes are used compared one eye alone<sup>13-17</sup>, with depth cues from disparity specifically implicated as the source of these binocular advantages<sup>18-21</sup>. These studies involved temporarily depriving normally-sighted people of this information. Our present goal was to directly compare the immediate effects of such a brief perturbation with the performance of adults accustomed to living with impaired stereo vision. Does binocular stereopsis make an irreplaceable contribution to prehension abilities or do permanently stereo-deficient subjects compensate for its loss over time?

Early reductions in stereo vision frequently occur in association with the main risk-factors for the development of amblyopia: namely, strabismus (ocular misalignment) and anisometropia (**bilaterally unequal** refractive error). Indeed, it has been argued that the characteristic losses in visual acuity (VA) and contrast sensitivity affecting the amblyopic (i.e., deviated, ametropic) eye in these conditions are secondary to its reduced influence, compared to the fellow (dominant) eye, on the visual cortex during critical periods in its

development<sup>4,22,23</sup>. Recovery of stereoacuity is also generally more refractory than the monocular deficits to the most widely used amblyopia therapy – patching of the dominant eye – possibly because it denies any opportunity for meaningful binocular interactions during occlusion episodes. We recently reported<sup>24</sup> that adults with persistent, moderate-to-severe amblyopia, accompanied by marked reductions in stereo vision, exhibit a range of prehension deficits compared to normal binocular performance, the impairments being most evident during the end-phase reach and grasping actions. The reduced spatial acuity in the amblyopic eye of these patients, however, probably contributed to their impaired binocular performance, as this tended to worsen with increasing VA loss. Here we address the problem by examining the prehension abilities of adults with reduced binocular stereo vision, most of whom were strabismic and/or anisometric, but with relatively normalized vision in their affected eye following ‘successful’ amblyopia treatment in childhood.

## **MATERIALS AND METHODS**

We conducted two experiments designed to assess the effects of reduced stereo vision on prehension movements made under otherwise ‘natural’ viewing conditions: that is, in a well-lit environment containing a rich array of monocular spatial cues which participants might exploit to compensate for their stereo loss. Subjects were free to move their head – potentially generating depth and directional information from motion parallax<sup>19</sup> and optic flow – while reaching and grasping for familiar<sup>25</sup> (household) objects of high-contrast and spatial detail. The objects were placed at different locations on a table bearing colored stickers on its black (ebony veneer) wood-grained surface, with the table edges also visible, thus providing a variety of depth (e.g., texture<sup>26</sup>) and distance (e.g., linear perspective, absolute height-in-scene<sup>27</sup>) information. Subjects gave informed consent for participation in the experiments, which were approved by the City University Senate Ethical Committee and conducted in accordance with the declaration of Helsinki.

### **Experiment 1: permanent developmental reductions in binocular stereo vision**

The first experiment compared the binocular and monocular performance of 20 long-term stereo-deficient adults (aged 19-36 years) with those of 20 normal controls (matched for age, gender and handedness<sup>28</sup>). Participants were pre-screened to determine their existing

binocular visual functions. Inclusion in the control group required: (1) no history of neurological or ocular disorder (other than refractive error); (2) normal or corrected-to-normal logarithm of Minimum Angle of Resolution (logMAR) VAs of  $\leq 0.0$  (Snellen equivalent, equal or better than 6/6) in each eye; and (3) high-grade binocular stereo vision, defined by good motor fusion (of  $\geq 30 \Delta$  Base Out or  $\geq 12 \Delta$  Base In) to challenge with a variable prism bar (Clement Clarke International, Cambridge, UK), and by crossed and uncrossed stereoacuity thresholds of  $\leq 40$  arc secs (Randot test, Stereo Optical Co. Inc., Chicago, USA).

The majority of the stereo-reduced subjects presented with strabismus (n=8), anisometropia (n=4) or a combination of the two (n=6), and with different decrements in stereo vision. For this reason, they were divided into two sub-groups, based on their existing crossed stereoacuity threshold (see Table 1 for further details). All had regained relatively good logMAR VA in their affected (non-dominant) eye through occlusion therapy (alone or combined with refractive correction), although this remained outside the normal range (0.18-0.24, Snellen equivalent ~6/9) in a few members of both sub-groups. Stereo thresholds were initially determined using the Wirt-Titmus test (Stereo Optical Co. Inc, Chicago, USA) which presents solid figures containing some monocular contour information and, arguably, provides the best assessment in relation to the prehension tasks involving real 3D objects. As a secondary check, thresholds were also examined with the TNO test (Laméris Ototech B.V., Nieuwegein, The Netherlands) consisting of random dot stimuli with no monocular cues.

Subjects classed as having ‘Coarse Stereopsis’ (CS) had near-normal fusional capacities, but elevated stereoacuity thresholds (crossed range 100-3000 arc secs). Most of these subjects recorded lower Wirt-Titmus stereo thresholds than on the TNO test (**which has a more dissociating anaglyph format**), consistent with previous reports in normal<sup>29</sup> and stereo-impaired subjects<sup>30</sup>. A major exception was case CS9 who passed the Wirt-Titmus Fly (at 3000 arc secs) but failed the contour figure at the next disparity level (800 arc secs), while also perceiving depth in Plate 1 of the TNO test at an intermediate threshold (1700 arc secs). Subjects classed as ‘Stereo-Negative’ (SN) failed both stereo tests. These subjects all had manifest strabismus, as a consequence of which they generally showed reduced motor fusion and some central or intermittent suppression of vision in their non-

dominant (N-D) eye when viewing binocularly (Bagolini striated glasses test), with two alternating fixators (SN9, SN10) showing no evidence of any binocular function (Table 1).

To further examine their visual status, binocular and monocular contrast sensitivities for stimuli with low-to-high spatial frequencies of 0.5, 1, 2, 8 and 16 cycles/deg positioned in foveal and in more peripheral vision (at horizontal eccentricities of 0° and 10°, respectively) were measured using established quantitative (temporal, two-interval forced choice) methods<sup>32</sup> in a selection of the stereo-deficient subjects. Stimuli were vertically oriented Gabor patches (~2° of visual angle) of different spatial frequency and contrast, presented at the center of a computer monitor (mean luminance ~90 cd/m<sup>2</sup>) with a luminance-matched surround (10° x 8°), at a distance of 1 m. For the peripheral measurements, subjects fixated a small spot 10° along the monitor's horizontal meridian. Thresholds were determined using a standard one-up/one-down staircase paradigm, with contrasts divided or multiplied by 1.15 following a correct or incorrect response, respectively, and were defined as the mean contrast of the last 5 reversals. Subjects wore their usual refractive correction, as in all other tests.

[Table 1 & Figure 1, near here]

### **Experiment 2: temporary reductions in binocular stereo vision**

The second experiment assessed the effects of briefly reducing the stereo vision of a group of 12 normally-sighted adults (6 males, 6 females) aged 18-30 years, for whom the same inclusion criteria to those of the first experiment were applied in pre-screening. An additional requirement was that any refractive error was fully corrected by contact lens wear. Procedures used were modified from Melmoth et al<sup>21</sup>. Subjects wore optometric trial-frames (The Norville Group Ltd, Gloucester, UK), with a Plano, Low Plus (LP) or High Plus (HP) spherical lens slotted into the frame in front of the eye opposite their preferred hand. The Plano lens, with no refractive power, allowed for normal binocular vision and served as the control condition. The specific powers of the LP and HP lenses were customized for each subject so as to reduce their crossed disparity sensitivity to between 200-800 arc secs and to ~3000 arc secs, respectively. For the LP condition, this involved determining the lowest power for each subject (which was between +2.00 and +3.50 D) that produced uncertainty about the depth percept in the No.2 or No.3 Wirt-Titmus test circles (at 400 and 200 arc secs, respectively), but not for the No.1 circle (800 arc secs). For the HP condition, it involved finding the lowest power (which was between +3.50 to +5.00 D) that permitted a

just-noticeable depth percept for the Fly stereogram (at 3000 arc secs). These tests were conducted at a similar viewing distance to the prehension experiments.

Stereo thresholds were elevated by these amounts because they showed test-retest reproducibility among participants and simulated the approximate losses in disparity sensitivity experienced, respectively, by the real coarse and stereo negative subjects. The de-focusing lenses mimicked another feature of binocularity in these subjects, in that Low Plus lens viewing had little or no effect on motor fusion thresholds – examined using the variable prism bar – whereas these were reduced in the High Plus condition. One difference, however, is that the Plus lenses induce an optical aniseikonia whereby the image in the ‘affected’ eye is magnified by a factor of  $\sim 1\%$  per dioptre<sup>33</sup>. In earlier work<sup>21</sup>, we showed that this causes subjects to judge near targets as being a few millimetres closer to this eye than to the other. The Plus lenses thus introduce a small bias in estimating the visual direction of objects, as well as reducing the fidelity of depth-from-disparity cues. Another difference is that the de-focusing lenses more closely model anisometric than strabismic conditions, whereas most of the real stereo-deficient subjects had a squint. However, we previously found a similar range and severity of prehension deficits among patients with persistent moderate amblyopia, regardless of whether it was mainly caused by image blur or ocular misalignment<sup>24</sup>.

### **Prehension Recordings and Analyses**

The procedures were similar to those detailed previously<sup>17,21,24</sup>. Subjects were seated at the table with lightweight infrared reflective markers attached to the wrist, thumb- and index finger-nails of their preferred hand. They wore liquid crystal PLATO goggles (Translucent Technologies, Toronto, Canada) to control their viewing condition. The goggles were placed over any everyday corrective lenses usually worn by the participants in experiment 1 and over the optometric trial frames in experiment 2. The goggles were opaque between trials. In the first experiment, sudden opening of one or both goggle lenses cued the subject to begin the reach. In the second experiment, goggle opening was followed by a brief (3 s) delay, allowing the subject to adjust to the given viewing condition, with an auditory tone then delivered to signal that the movement should begin. Subjects reached and precision grasped isolated cylindrical objects (100 mm high) of either ‘small’ (24 mm) or ‘large’ (48 mm) diameter (37g and 148 g, in weight) placed at ‘near’ (20 cm) or ‘far’ (40 cm) locations 10° either side of the midline starting position, while their hand movements were recorded (at 60

Hz) by a 3D motion-capture system (ProReflex, Qualisys AB, Sweden). Temporal and spatial resolutions of the system were 16.67 msec and <0.4 mm, respectively.

Instructions given were to perform the movements as ‘naturally, quickly and accurately as possible’ and to grasp the target between the thumb and index finger at about half its height. Practice trials were conducted to ensure compliance. Subjects in the first experiment then completed six, 24 trial blocks each comprising a single presentation of the three possible viewing conditions (binocular, dominant/sighting eye only, non-dominant eye only) x 2 object size (small, large) x 4 object location (near ipsi-space, near contra-space, far ipsi-space, far contra-space) combinations, in the same random order. Subjects in the second experiment completed 5 blocks of 24 trials involving the 3 possible lens powers (Plano, LP, HP) and the same 8 object combinations, again in an identical random order. Lenses were removed from the trial frames after each completed movement, so that subjects could not anticipate the viewing condition of the up-coming trial. Brief rests occurred between trial-blocks. Both experiments were typically completed in ~45 minutes.

Profiles of the wrist velocity and spatial trajectory, and of the grip aperture between thumb and forefinger were examined for on-line errors or corrections (see Fig. 2), and key dependent measures of the prehension kinematics were determined. Manual prehension has two main components – the reach and the grasp – the planning and execution of which depend on different types of visuospatial information about the goal object and its relations to the moving hand and digits<sup>13-21, 24-27</sup>. We divided the kinematics and errors occurring in each component into several ‘sub-actions’ in our analyses (see Table 2 for detailed definitions), so that we could determine whether there were *selective* effects of reduced stereo vision, and whether these were the same or different in the two experiments. For example, kinematics of the initial reach – its peak velocity and time to peak deceleration – and the timing and position of the initial peak grip aperture at hand ‘pre-shaping’ mainly depend on evaluations of the target’s *absolute distance* during movement preparation, and they all increase with object distance, whereas the width of the programmed peak grip increases according to judgements of the object’s 3D size. Parameters of the terminal reach – its low velocity phase and coordination with object contact (see Table 2) – and of grip execution also increase, respectively, with target distance and size, but are additionally influenced by the quality of ‘online’ feedback about changes in the *relative distance* (i.e., depth) between the approaching hand/digits and the object. Reduced stereopsis would thus

be expected to impair sub-actions of the terminal reach (e.g., low velocity phase duration) and of the grasp (e.g., grip aperture size at peak and at object contact; grip closure and application times) already linked to depth-from-disparity processing.

Main effects of viewing condition on performance *within* each subject group were explored by submitting the averaged data to 3 (views) x 2 (sizes) x 2 (distances) Huynh-Feldt adjusted repeated-measures ANOVA (SPSS UK Ltd., Woking, UK). Differences *between* the binocular and monocular performance of the normal and stereo-deficient sub-groups in experiment 1 were examined by separate one-way ANOVA. Planned pair-wise comparisons were undertaken *post hoc* using Fisher's Least Significant Difference (LSD) test. This procedure applies less adjustment for the error mean square associated with the specific pair of contrasts being examined than more conservative approaches (e.g., Bonferroni test) which add correction for multiple comparisons. We chose the more sensitive LSD test to avoid an anomaly which arose when we applied the Bonferroni correction to some of our data, which was that it revealed no significant differences between any of the paired contrasts, despite the presence of a main effect (e.g., of view or sub-group) identified by the preceding ANOVA. Indeed, only LSD probabilities of less than 1 in 100 generally achieved significance according to the Bonferroni test. Mindful of this, while we set significance at the conventional  $p < 0.05$ , we have been circumspect in presenting LSD results at levels above  $p = 0.01$ .

[Tables 2 & 3, near here]

## RESULTS

### Prehension performance in normal and long-term stereo-deficient adults

Representative examples of contrast sensitivity functions obtained from normal, coarse and negative stereo vision subjects are shown in Figure 1. As would be expected, normal controls (Fig.1A) showed enhanced binocular compared to monocular contrast sensitivities, particularly in foveal vision. Results from the stereo-deficient subjects depended on their existing stereoacuity and recovery of non-dominant (N-D) eye logMAR VA. Those with coarse stereopsis also had enhanced binocular sensitivity across the spatial frequency range tested at the central field location – even when their stereo threshold was quite elevated (Fig.1B) – and both CS and SN subjects with partial or intermittent suppression (Table 1) showed increased binocular sensitivity for lower spatial frequencies (i.e., 0.5-2 cycles/deg)

at 10° eccentricity (Figs.1B, 1C), confirming the presence of functional binocularity more peripherally. Finally, reduced N-D eye VA was associated with loss of contrast sensitivity at the higher spatial frequencies examined, especially in central vision (Fig.1B).

Initial within-subject comparisons revealed differences in the binocular *versus* monocular prehension performance of both normally-sighted and stereo-deficient subjects. But neither movement kinematics or errors committed were affected by non-dominant compared to dominant (DOM) eye viewing in any of these groups, despite an overall mean reduction (of ~1½ lines) in N-D *versus* DOM eye VA among the stereo-impaired subjects (Table 1) and its loss of high spatial frequency contrast sensitivity in some individual cases. This finding is similar to results previously obtained in adult patients with ‘mild’ amblyopia<sup>24</sup>, and confirms that minor spatial acuity losses have little impact on prehension abilities when using the affected eye. For simplicity, therefore, we present direct comparisons only of the binocular and dominant eye performances in the three subject groups studied here.

As in our previous work<sup>17,24</sup>, the normal adults were found to be faster and more accurate on almost every performance indicator when using binocular vision compared to their DOM eye alone, with nearly all of these effects being statistically highly significant (Table 3). Most notably, binocular movements were executed more quickly (by ~100 ms, on average) than when using one eye, yet involved significantly fewer corrections or errors during both the reach and the grasp (all  $F_{(1,19)} > 50.0$ ,  $p < 0.001$ ). The normal subjects programmed a somewhat higher peak velocity to their reach ( $F_{(1,19)} = 17.2$ ,  $p = 0.001$ ) when using both eyes, but the duration of its early phase (up to peak deceleration) was similar with DOM eye viewing, as was the programmed time to peak grip aperture (both  $F_{(1,19)} < 0.3$ ,  $p > 0.6$ ). Instead, their faster binocular movements resulted from shorter times spent in the later (low velocity phase) of the reach, in coordinating its termination with initial object contact, and in closing and applying the grasp (all  $F_{(1,19)} > 40.0$ ,  $p < 0.001$ ). This was reflected in the different time courses of the movements, in that *proportionally* more time was devoted to these later phases when their vision was restricted to one eye (all  $F_{(1,19)} > 13.0$ ,  $p \leq 0.01$ ). Finally, binocular vision improved grasping precision, with the programmed width of the peak grip and its distance from the object, as well as the subsequent grip size at contact better calibrated to the object’s spatial properties than with monocular viewing (all  $F_{(1,19)} > 25.0$ ,  $p < 0.001$ ).

The subjects with coarse stereopsis exhibited a broadly similar pattern of binocular advantages, some of which were also highly significant (Table 3). Indeed, average binocular movement durations were ~100 ms shorter in this sub-group of participants compared to their DOM eye alone ( $F_{(1,9)}=44.7, p<0.001$ ) this, again, being mainly accounted for by relatively faster movement end-phases – in both absolute and percentage terms (all  $F_{(1,9)}>13.0, p\leq 0.01$ ) – with the same three spatial aspects (as in the normal adults) of their binocular grasping also better calibrated for target size and position (all  $F_{(1,9)}>10.0, p\leq 0.01$ ). The binocular performance of the stereo negative subjects, by contrast, differed little from that of their dominant eye, with improvements confined to a marginal reduction (of only ~25 ms) in overall movement duration ( $F_{(1,9)}=5.9, p=0.039$ ) and to a few aspects of control at and after object contact (see Table 3 for details; all  $F_{(1,9)}>9.0, p<0.015$ ). The general lack of binocular advantage among this sub-group was not due to marked improvements in their *monocular* performance. Univariate ANOVA conducted on the data obtained from the dominant eye alone in the normal, CS and SN subjects revealed only two between-group differences. Post hoc comparisons showed that both effects were associated with the coarse stereopsis sub-group, who seemed to time the formation of their peak grip later (by ~100 ms) in the movement and somewhat closer (by ~7 mm) to the target (both  $F_{(2,37)}=3.3, p=0.048$ ; LSD,  $p<0.025$ ) than the controls. But the dominant eye performance of the SN sub-group, who should be accustomed to operating with markedly reduced stereo vision, was indistinguishable from normal.

[Figures 2 & 3, near here]

#### ***Between-subject group differences in binocular performance***

Binocular movement durations were generally prolonged (by 80-100 ms, on average) in the stereo-deficient compared to the normal adults (Table 3, right-most column,  $F_{(2,37)}=3.6, p=0.04$ ; LSD, both  $p<0.05$ ). As illustrated in Figure 2A, an overall impression was that they slowed each sub-action of their movements down, producing lower peak velocity reaches with slightly extended times to peak deceleration and in the later low velocity phase (Table 3). They also tended to form a narrower peak grip later in the movement and closer to the target, and with a less accurate (i.e., wider) grip size at initial contact (see Fig.2B). However, only two of these other differences appeared significant, and were attributable to the CS subjects showing the same alterations in grip programming as with their DOM eye; that is, a somewhat later and nearer peak grip aperture than the normal adults (LSD, both  $p<0.025$ ). The stereo negative subjects, however, made twice as many total reaching errors as the

normal adults (Fig.3A). Further analysis, by error-type (see Supplementary Material, Table 1), revealed that this was entirely due to more velocity corrections in the final approach (LSD,  $p < 0.05$ ), since directional (spatial path) errors were equally uncommon ( $\leq 0.5$  per 48 binocular trials) in all participants ( $F_{(2,37)} = 0.4$ ,  $p = 0.5$ ). Despite these corrections, temporal coordination between initial object contact and the end of their reach was significantly poorer than with normal binocular vision (LSD,  $p = 0.004$ ).

More strikingly, both stereo-deficient sub-groups showed similar deficits in controlling the subsequent *post-contact phase* of their grasp. In particular, their grip application times were increased in absolute and proportional terms compared to normal binocular viewing (LSD, all  $p < 0.05$ ) – which mainly accounted for their prolonged movement durations – and they made over twice as many cumulative grasping errors (Fig.3B) as the control subjects (LSD, both  $p \leq 0.001$ ). Further analyses by error-type (see Supplementary Material, Table 1) showed that the increases were partly caused by adjustments to the grip (e.g., arrowed in Fig.2B) occurring immediately after object contact (LSD, both  $p < 0.02$ ), but predominantly by abnormally prolonged contacts (e.g., arrowed in Fig.2A) prior to lifting the objects (LSD, both  $p < 0.01$ ).

The object's properties had predictable main effects on the binocular performance of all participants, with parameters of the reach increasing with target distance and most of those associated with the grasp increasing with object size. But there were also some significant interactions with viewing condition which differed between the three sub-groups. One representative example is shown in Figure 4, and concerns the overall view (binocular, dominant eye) x object size (small, large) interaction ( $F_{(1,37)} = 10.1$ ,  $p = 0.003$ ) for grip application times. These were always increased when contacting the larger of the two objects, but whereas this effect was pronounced in the normal adults under DOM eye conditions (view x size interaction,  $F_{(1,19)} = 21.7$ ,  $p < 0.001$ ), *differentiation* for this object property by view was less marked for the CS sub-group ( $F_{(1,9)} = 5.9$ ,  $p = 0.03$ ) and was absent among those classed as SN ( $F_{(1,9)} = 0.0$ ,  $p = 1.0$ ). This occurred because their binocular performance became increasingly worse than normal with reducing disparity sensitivity and similar to that of their dominant eye alone. This result was also obtained for low velocity phase, reach-grasp coordination and grip application durations across participants for performance directed at far compared to near targets (view x distance interactions, all  $F_{(1,37)} > 14.0$ ,  $p \leq 0.001$ ), confirming a marked advantage of normal binocular vision for larger amplitude movements<sup>13,17</sup>.

[Figures 4 & 5, near here]

### ***Correlations with deficits in stereoacuity***

Most of the stereo-reduced subjects had binocular deficits in addition to reduced disparity sensitivity, since only 6 of them – all in the coarse sub-group – passed the tests of sensory and motor fusion (Table 1). This raises the question as to whether preservation of these other binocular functions in these subjects was *primarily* responsible for the apparently normal reaching performance of the CS sub-group as a whole. Further analysis indicated that they were not, since the average peak velocity, low velocity phase duration and error-rates of their binocular reaches were similar to those of the 4 remaining CS subjects with partial or intermittent binocular vision and generally reduced vergence ranges ( $F_{(1,9)} < 1.7$ ,  $p > 0.2$  for all comparisons). Their binocular grasping performance was no different either.

Another issue was whether dividing the stereo-reduced participants into 2 ordinal sub-groups may have masked more subtle relationships between their performance and stereo vision loss. To examine this we plotted, for the CS subjects, the mean of some key binocular and dominant eye performance indicators (low velocity phase and grip application times; total grasp errors) against their lowest recorded crossed stereo threshold. For all 3 measures, the correlations were weakly positive, at best ( $R^2 = 0.01-0.1$ ). Further inspection showed that the movements of two cases (CS2, CS5) were consistently slower and more error-prone than the rest, despite their small reductions in stereoacuity (Table 1). Removal of these 2 cases resulted in much stronger positive correlations (see Fig.5) in binocular end-phase reach ( $R^2 = 0.5$ ) and grip application times ( $R^2 = 0.63$ ). In other words, for these 8 subjects, approximately half the variability in these performance measures was related to their stereo threshold, although there remained no correlation with total grasping errors ( $R^2 = 0.03$ ). Interestingly, their dominant eye performance showed similar relationships (Fig.5), with increases in the same two measures (i.e., except total grasping errors) moderately correlated with stereo threshold ( $R^2 = 0.52$  and  $0.81$ ). These findings were independent of how this threshold was determined: that is, they also **occurred** when plotted against the results of the Wirt-Titmus or TNO tests alone, the reason being that these outcomes were, themselves, well correlated ( $R^2 = 0.64$ , for the 9 CS cases with matching data, Table 1).

### **Effects of temporary stereo vision losses in normal adults**

Details of the main effects of briefly reducing stereoacuity on the binocular performance of normal participants with well-established prehension skills are given in Supplementary

Material (Tables 2 & 3). Movement onset times averaged ~450 ms across all three viewing conditions in these subjects ( $F_{(2,22)}=0.3, p=0.8$ ) demonstrating a similar readiness to react to the ‘go’ signal. **But**, as in long-term stereo-deficient adults, movement durations were significantly extended when their disparity sensitivity was reduced with the Low Plus (by ~50 ms) and High Plus (by ~80 ms) lenses compared to normal binocular/Plano lens (mean = 889 ms) viewing ( $F_{(2,22)}=16.7, p<0.001$ ; LSD, both  $p<0.01$ ). Movement errors also showed two notable similarities to the real stereo-deficient subjects. First, simulating conditions of coarse stereopsis with the LP lens had no reliable effect on reaching errors, but these were significantly increased, due to more velocity corrections (both  $F_{(2,22)}>7.5, p<0.01$ ), when stereo vision was further reduced with the HP lens (see Fig.6A). Second, both experimental lenses resulted in a more than 2-fold increase in total grasping errors (Fig.6B) compared to the control condition ( $F_{(2,22)}=19.3, p<0.001$ ), most of which occurred during the period of grip application. Unlike long-term stereo vision loss, however, the predominant error-type involved adjustments to the grip ( $F_{(2,22)}=7.0, p=0.009$ ; LSD, both  $p<0.01$ ), rather than prolonged object contacts ( $F_{(2,22)}=4.9, p=0.02$ ; LSD, both  $p<0.05$ ).

Further inspection revealed some other, more pronounced differences associated with the duration of stereo-impairment. Although both de-focusing lenses extended overall movement durations, there was no hint that the early landmarks of the reach (time to peak deceleration) or grasp (time to peak grip) were delayed, and grip application times only increased significantly ( $F_{(2,22)}=9.9, p=0.001$ ) with more degraded High Plus lens viewing (LSD,  $p=0.001$ ). Instead, the extensions resulted mainly from significant increases in the absolute and proportional times spent in the immediately *pre-contact period* of the movements. For example, the average times spent in the low velocity phase of the reach (268 ms) and in closing the grip (209 ms) in the control condition each increased progressively (by between ~35-65 ms) with LP and HP lens viewing (both  $F_{(2,22)}>11.0, p=0.001$ ; LSD, all  $p\leq 0.01$ ). Subjects also initially opened their hand to a significantly *wider* peak grip aperture ( $F_{(2,22)}=23.8, p<0.001$ ; LSD, both  $p<0.01$ ) slightly *further away* from the object ( $F_{(2,22)}=5.1, p=0.015$ ; LSD, both  $p<0.05$ ) than with normal binocular vision. The direction and approximate magnitude of all these effects more closely resembled those induced by restricting a normal subject’s vision to one eye (Table 3).

[Figure 6, near]

### Exploring the grasping deficits

Stereo vision losses were consistently associated with increased post-contact grasping errors, even though the *width* of the grip at object contact appeared relatively normal according to both kinematic and error measures of this parameter (Table 3; Supplementary Tables 1-3). It is possible, nonetheless, that the precise *positions* of the digit-tips were altered under stereo-reduced conditions. To examine this, we determined the X- and Y-coordinates of the thumb and finger markers at contact relative to the marker centered on top of the objects. Positive or negative values were assigned, respectively, to positions beyond or nearer than this origin in the Y-axis or depth plane, and to the right or left of the origin in the X-axis or picture plane (with this sign reversed for the few left-handed subjects). Means and standard deviations were calculated for each axis in each subject, with the average of the standard deviations also determined, as a measure of trial-by-trial variability. In all cases, mean thumb positions were negative in the depth plane while the finger positions were positive (for details, see Supplementary Material, Table 4). This occurred because initial contact was always made with the thumb at the front of the object and the finger towards its rear.

Comparisons between binocular and dominant eye vision in the normal adults and between normal *versus* coarse and negative stereo-reduced subjects when using both eyes, revealed no differences in the mean positions of either digit at contact or in their variability with respect to the picture plane. The sites of initial thumb contact were, however, more *variable in the depth plane* (by ~1.0-2.5 mm) in all conditions in which binocular stereo vision was absent ( $F_{(1,19)}=29.6, p<0.001$ ) or reduced ( $F_{(2,37)}=5.7, p=0.007$ ; CS LSD,  $p=0.04$ ; SN LSD,  $p=0.009$ ). Variability of the finger contact in depth also increased significantly ( $F_{(1,19)}=31.6, p<0.001$ ) with normal dominant eye viewing.

A different result was obtained for experiment 2, in that *mean* positions of the two digits – but not their variability – were altered by the de-focusing lenses relative to the control condition (all  $F_{(2,22)}>4.0, p<0.05$ ). Moreover, these positions moved progressively (by ~1 mm, on average) along each axis from Plano to LP to HP lens viewing, the gradual changes being mutually consistent with a systematic shift in both the thumb and finger contact sites to more frontal locations on the objects with each decrement in disparity sensitivity.

## DISCUSSION

Vision plays crucial roles in the control of prehension. Among its primary functions are to identify the optimal contact points on the goal object for successful grasping and to control transport of the hand so that the digits are guided to these favourable landing sites. Binocular stereopsis could, theoretically, enhance each of these functions by extracting essential information not so readily available via alternative visuospatial cues. First, normal binocular observers are reported to accurately judge the surface contours of 3D objects by computing higher-order ‘disparity curvature’<sup>34</sup>, a capacity with obvious advantages for planning where best to place the grip. While other evidence<sup>35</sup> suggests that reliable measures of viewing distance would also be required to ensure correct disparity-scaling, this would be available under natural binocular conditions. Second, disparity processing can provide immediate feedback about changes in the relative positions of the hand/digits and the object when they are together in central vision at the end of the movement<sup>6</sup>. Previous kinematic studies support the general idea that two eyes are much better than one in fulfilling these roles<sup>13-20,24</sup> by showing – as confirmed here – that binocularly-guided reaches and grasps in normal adults are significantly faster and more accurate with fewer overt corrections than equivalent monocular movements. Our new findings concern the effects of permanently or briefly degraded disparity sensitivity on binocular prehension skills.

Real and simulated stereo-deficiency was associated with deficits in terminal reach and grip execution under binocular conditions, the extents of which showed some correlations with the subject’s existing stereoacuity loss. An important issue is whether these problems were specifically attributable to the reductions in stereopsis or to disturbances in other aspects of binocularity. Indeed, there is a suggestion<sup>36</sup> that it is our ability to utilize *matching* information in the two eyes – rather than differences between them – which underpin enhanced binocular motor control, especially when subjects make head movements that generate ‘concordant’ 3D spatial cues in both eyes from motion parallax and optic flow. Using prisms to perturb metric distance information derived from an extra-retinal source – the vergence angle between the two eyes – has also been shown to cause errors in the programmed velocity and amplitude of binocular reaches, with subsequent inaccuracies in implementing the grasp<sup>14,20,21</sup>.

Our participants were unrestrained and typically moved their head to fixate the goal objects at their slightly off-midline locations before commencing the reach. A sub-set of the coarse stereopsis subjects had apparently normal binocular sensory and motor fusion (Table 1, Fig.1B), and so presented with a selective stereoacuity deficit. Moreover, none of them

had a manifest squint, the presence of which is a factor linked to reduced depth sensitivity from motion parallax<sup>37,38</sup>. Since they exhibited similar prehension deficits to the other subset of CS subjects who may have had incomplete binocular concordance – due to partial or intermittent suppression – and generally reduced vergence, we conclude that the availability of these alternative cues made no difference to their performance. This accords with evidence that normal adults specifically required to make head movements to boost self-motion-related cues gain no added advantages for prehension speed or accuracy over static binocular viewing<sup>19</sup>, and that *any* metric distance cue can support proficient reach programming<sup>18,19</sup>, including absolute height-in-scene information<sup>27</sup> available monocularly to all our subjects. On this basis, it is most likely that it was also the disparity losses under stereo negative and the de-focusing lens conditions that mainly accounted for the prehension difficulties.

Briefly degrading stereo vision by means of the de-focusing lenses mainly affected the reach-to-grasp immediately prior to object contact. As their disparity sensitivity was reduced, participants programmed a progressively wider peak grip further from the target and increasingly prolonged and adjusted (Fig.6A) the low velocity phase of their reach. These effects were similar to those occurring in the first experiment when *all* binocular disparity cues were removed by occluding one eye. Indeed, these behavioural changes appear to be the default response of normal adults whenever disparity information is reduced – as when moving to objects in the dark<sup>15,16</sup> or in peripheral vision<sup>39</sup> – and have been attributed to visual uncertainty about the precise 3D shape and location of the target during movement planning. The de-focusing lenses generate all of these uncertainties. We know this as our subjects reported that their assessment of the object's solid properties was unreliable under these conditions, and because we have shown before that the magnifying effect of these lenses causes targets to be judged as slightly nearer the affected eye<sup>21</sup>. Programming a wider and earlier peak grip and prolonging the terminal reach may also be strategies for increasing the spatial and temporal margins available for the recovery of on-line visual feedback required to control the hand in the final approach. A central problem in so doing is that this period is time-limited – usually to around 200-250 ms (Table 3) – so the source(s) of feedback needs to be fast and efficient, to ensure that any adjustments can be smoothly (i.e., covertly) implemented, rather than appearing as obvious corrections in the movement. The normal human stereo system satisfies these requirements, as it can respond – without loss of depth sensitivity – at relative image velocities<sup>40</sup> much greater than those of

the moving hand. Our data suggest that coarse disparity information may be a sufficient source of feedback for controlling the final progress of the hand on-line, since terminal velocity corrections were no more common in the CS and LP lens conditions than with normal binocular vision. But further degradation of disparity sensitivity with SN and HP lens viewing, resulted in poorly coordinated terminal reaching, presumably because the subjects were forced to fall back on less reliable and slower monocular<sup>41</sup> depth cues (e.g., changes in hand-target occlusion) during this period.

An intriguing finding was that the long-term stereo-deficient subjects were mainly impaired during the subsequent post-contact phase of the grasp, the key problem being that their grip application times were uniformly prolonged. Object weight is normally a key determinant of this grasp parameter – with heavier objects associated with extended times in contact – during which the grip and load forces required to lift it are evaluated *via* tactile and kinaesthetic feedback from the digits<sup>42,43</sup>. Application of these forces can be planned in advance, based on prior knowledge of a particular object's size/weight relations acquired from repeatedly handling it. The stereo-deficient subjects appeared to learn these associations, since they showed time-in-contact scaling under all viewing conditions (Fig.4). There were other differences in the binocular grasping of these subjects and the normal adults with temporary stereo losses, suggesting that this was not a simple reflection of their reduced disparity sensitivity, but involved secondary adaptations to this long-term problem. While complicating the story, the nature of these strategic changes warrants further examination.

These subjects tended to programme slightly reduced peak velocities and peak grip apertures (Table 3), rather than initially opening their hand wider as in the simulated cases. This combination of reductions could occur because they judged the objects as being somewhat nearer and smaller than they really were, based on their un-calibrated retinal image sizes. Similar mis-judgments have occasionally been reported in normal monocular observers<sup>13</sup>. If so, then the object's sizes should also have seemed to be *relatively larger* at the far compared to near locations used, and their peak grip would thus be expected to increase accordingly with target distance. But it did not (peak grip aperture x distance effect,  $F_{(1,19)}=0.2, p=0.7$ ). That the CS sub-group formed their peak grip later in the movement is also opposite to the predicted effect of distance under-estimation.

A consequence of this later hand pre-shaping was that it occurred closer to the object, potentially reducing the time available to use visual feedback to control grip closure.

We have argued before<sup>21</sup> that accurately guiding each digit tip to their independent contact points may be enhanced by fine disparity processing channels in the human stereo system, which were compromised in all the real stereo-deficient subjects. We suggest that they probably had difficulty deciding where to place their grip at the preparation stage and largely dispensed with using feedback to rectify the problem. The selective increase in trial-by-trial variability in positioning their thumb in the *depth plane* of the object at initial contact is consistent with this idea, and with evidence that the approach of this digit is normally the more visually controlled of the two in precision grasping<sup>44,45</sup>, partly because the finger landing site is more often hidden from view. The variable thumb positioning could also account for their extended grip application times, as they needed to compensate by spending more time acquiring *non-visual feedback* about the likely success of their grip before attempting to lift the objects. More frequent grip placement inaccuracies may further account for the increased need to adjust the digit positions after contact (e.g., Fig.2B). Similar arguments apply to the increased post-contact grip times and errors occurring in normal subjects with one eye occluded. But the effects of the de-focusing lenses require a different explanation, since these caused a gradual shift in the initial grip placement towards the front of the objects. This may have occurred because the LP and HP lenses made the objects seem compressed in the depth plane or as displaced towards the affected eye due to their introduction of an inter-ocular size disparity. Either way, it would be interesting to determine whether similarly systematic grip placement errors occur under more natural aniseikonic conditions (e.g., in early stages of childhood anisometropia) before any secondary adaptations have the opportunity to occur.

The emergence of high-grade binocular stereopsis and accurate visual control over a versatile hand are considered two pivotal developments in human evolution that may be related<sup>6-8</sup>. Our data support this idea and suggest that the computation of fine binocular disparities makes an irreplaceable contribution to the acquisition of normal precision grasping skills. This was demonstrated by evidence that the ability to process low-grade or coarse disparities in combination with other visuospatial cues cannot completely compensate for its loss, but leads to a greater reliance on non-visual information over the longer-term. Evidence that similarly stereo-reduced subjects make more binocular errors when attempting to catch moving balls, specifically because they close their grip too slowly or too late<sup>46,47</sup>, further suggests that these conclusions apply to interceptive whole-hand grasping abilities.

Our current data also have implications for amblyopia therapy. First, there was a hint of correlations between increasing stereoacuity and improved *dominant eye* performance on some key prehension measures (Fig.5). This implies that stored internal representations of motor *output* skills refined through binocular experience may be accessed, at least in part, by monocular input. Second, we would note that the binocular prehension abilities of the stereo negative subjects with good VA in each eye were generally worse than those with coarse stereopsis and little better than the moderately-to-severely amblyopic patients that we examined in previously<sup>24</sup>. Taken together, these observations suggest that prioritizing the recovery of high-grade binocularity, rather than just vision in the affected eye, should provide generalized benefits for visuomotor control in this disorder.

### **References**

1. Wheatstone C. Contributions to the physiology of vision. On some remarkable and hitherto unobserved phenomena of binocular vision. *Phil Trans Roy Soc Lond.* 1838: 8; 371-394.
2. von Noorden GK. *Binocular vision and ocular motility: theory and management of strabismus.* 4th ed. St. Louis, MO: Mosby; 1990.
3. Howard IP, Rogers BJ. *Binocular Vision and Stereopsis.* Oxford: Oxford University Press; 1995.
4. Parker AJ. Binocular depth perception and the cerebral cortex. *Nature Rev Neurosci.* 2007;8;379-391.
5. Fielder AR, Moseley MJ. Does stereopsis matter in humans? *Eye.* 1996;10:233-238.
6. Morgan MJ. Vision of solid objects. *Nature.* 1989;339:101-103.
7. Sakata H, Taira M, Kusunoki A, Murata A, Tanaka Y. The parietal association cortex in depth perception and visual control of hand action. *Trends Neurosci.* 1997;20;350-357.
8. Castiello U, Begliomini C. The control of visually guided grasping. *The Neuroscientist.* 2008;14:157-170.
9. Dijkerman HC, Milner AD, Carey DP. The perception and prehension of objects oriented in the depth plane. I. Effects of visual form agnosia. *Exp Brain Res.* 1996;112:442-451.
10. Marotta JJ, Behrmann M, Goodale MA. The removal of binocular cues disrupts the calibration of grasping in patients with visual form agnosia. *Exp Brain Res.* 1997;116;113-121.

11. Verhagan L, Dijkerman HC, Grol MJ, Toni I. Perceptuo-motor interactions during prehension movements. *J Neurosci*. 2008;28:4726-4735.
12. Preston TJ, Li S, Kourtzi Z, Welchman AE. Multivoxel pattern selectivity for perceptually relevant binocular disparities in the human brain. *J Neurosci*. 2008;28:1131--11327.
13. Servos P, Goodale MA, Jakobson LS. The role of binocular vision in prehension: a kinematic analysis. *Vision Res*. 1992;32:1513-1521.
14. Mon-Williams M, Dijkerman HC. The use of vergence information in the programming of prehension. *Exp Brain Res*. 1999;128:578-582.
15. Watt SJ, Bradshaw MF. Binocular cues are important in controlling the grasp but not the reach in natural prehension movements. *Neuropsychologica*. 2000;38:1473-1481.
16. Loftus A, Servos P, Goodale MA, Mendarozqueta N, Mon-Williams M. When two eyes are better than one in prehension: monocular viewing and end-point variance. *Exp Brain Res*. 2004;158: 317-327.
17. Melmoth DR, Grant S. Advantages of binocular vision for the control of reaching and grasping. *Exp Brain Res*. 2006;171; 371-388.
18. Bingham GP, Bradley A, Bailey M, Vinner R. Accommodation, occlusion, and disparity matching are used to guide reaching: a comparison of actual versus virtual environments. *J Exp Psychol Hum Percept Perform*. 2001;27:1314-1334.
19. Watt SJ, Bradshaw MF. The visual control of reaching and grasping: binocular disparity and motion parallax. *J Exp Psychol Hum Percept Perform*. 2003;29:404-415.
20. Bradshaw MF, Elliot KM, Watt SJ, Hibbard PB, Davies IR, Simpson PJ. Binocular cues and the control of prehension. *Spatial Vis*. 2004;17:95-110.
21. Melmoth DR, Storoni M, Todd G, Finlay AL, Grant S. Dissociation between vergence and binocular disparity cues in the control of prehension. *Exp Brain Res*. 2007;183:283-298.
22. Daw NW. Critical periods and amblyopia. *Arch Ophthalmol*. 1998;116:502-505.
23. Kiorpes L, McKee SP. Neural mechanisms underlying amblyopia. *Curr Op Neurobiol*. 1999;9:480-486.
24. Grant S, Melmoth DR, Morgan MJ, Finlay AL. Prehension deficits in amblyopia. *Invest Ophthalmol Vis Sci*. 2007;48:1139-1148.
25. Marotta JJ, Goodale MA. The role of familiar size in the control of grasping. *J Cog Neurosci*. 2000;13:8-17.

26. Knill DC, Kersten D. Visuomotor sensitivity to visual information about surface orientation. *J Neurophysiol.* 2004;91;1350-1366.
27. Gardner PL, Mon-Williams M. Vertical gaze angle: absolute height-in-scene information for the programming of prehension. *Exp Brain Res.* 2001;136;379-3785.
28. Oldfield RC The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologica.* 1971;9;97-112
29. Hall C. The relationship between clinical stereotests. *Ophthalmic. Physiol. Opt.* 1982;90;91-95.
30. Fawcett SL, Birch EE. Validity of the Titmus and Randot circles tasks in children with known binocular vision disorders. *JAAPOS.* 2003;7;333-338.
31. Lang J. Anomalous retinal correspondence update. *Graefes Arch Clin Exp Ophthalmol.* 1988;226;137-140.
32. Davis AR, Sloper JJ, Neveu MM, Hogg CR, Morgan MJ, Holder GE. Electrophysiological and psychophysical differences between early- and late-onset strabismic amblyopia. *Invest Ophthalmol Vis Sci.* 2003;44;610-617.
33. Rabbetts RB. Bennett & Rabbett's clinical visual optics. London, Butterworth Heinemann. 3<sup>rd</sup> edition, 1998.
34. Rogers BJ, Cagenello R. Disparity curvature and the perception of three-dimensional surfaces. *Nature.* 1989;339:135-137.
35. Johnston EB. Systematic distortions of shape from stereopsis. *Vision Res.* 1991;31:1351-1360.
36. Jones RK, Lee DN. Why two eyes are better than one: the two views of binocular vision. *J Exp Psychol Hum Percept Perform.* 1981;7:30-40.
37. Thompson AM, Nawrot M. Abnormal depth perception from motion parallax in amblyopic observers. *Vision Res.* 1999;39:1407-1413.
38. Nawrot M, Frankl M, Joyce L. Concordant eye movement and motion parallax asymmetries in esotropia. *Vision Res.* 2008;48:799-808.
39. Schlicht EJ, Schrater PR. Effects of visual uncertainty on grasping movements. *Exp Brain Res.* 2007;182:47-57.
40. Morgan MJ, Castet E. Stereoscopic depth perception at high velocities. *Nature.* 1995;378:380-383.
41. Greenwald HS, Knill DC, Saunders JA. Integrating visual cues for motor control: a matter of time. *Vision Res.* 2005;45;1975-1989.

42. Johansson RS, Westling G. Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip. *Exp Brain Res.* 1988;71:59-71.
43. Weir PL, MacKenzie CL, Martenuik RG, Cargoe SL, Frazer MB. The effects of object weight on the kinematics of prehension. *J Motor Behav.* 1991;23:192-204.
44. Wing AM, Fraser C. The contribution of the thumb to reaching movements. *Q J Exp Psychol.* 1983;35A:297-309.
45. Melmoth DR, Grant S. Vision of the thumb as the guide to prehension. *Perception Supplement.* 2005;34:243.
46. Lenoir M, Musch E, La Grange N. Ecological relevance of stereopsis in one-handed ball-catching. *Percept Motor Skills.* 1999;89:495-508.
47. Mazyn LI, Lenoir M, Montagne G, Savelsbergh GJ The contribution of stereo vision to one-handed catching. *Exp Brain Res.* 2004;157:383-390.

## Figure Legends

**Figure 1.** Contrast sensitivity functions obtained under binocular (Both), dominant (DOM) eye and non-dominant (N-D) eye viewing conditions in individuals with (A) normal, (B) coarse (subject CS9), and (C) negative (subject SN6) stereo acuity. Upper panels, foveal vision ( $0^\circ$  eccentricity); lower panels, peripheral vision ( $10^\circ$  eccentricity).

**Figure 2.** Movement profiles obtained from subjects with normal, coarse and negative stereo vision on equivalent binocular trials (involving the smaller object, at the same far location). The cue to move occurred at time 0 ms, with movement onset starting ~400-500 ms later. (A) Velocity profiles: the moments of peak deceleration in the reach and of initial contact with the object are indicated by the open and filled circles, respectively. Times in contact with the object prior to lifting it were extended in the two stereo-deficient adults, with the stereo negative subject showing a prolonged (~200 ms) ‘plateau’ (arrowed), representing an adjustment or ‘error’ during the period of grip application. (B) Grip profiles: grip sizes at initial object contact (filled circles) were somewhat larger in the two stereo-deficient adults, and were followed by adjustments or ‘errors’ in the digit positions (arrowed) while the object was being secured prior to lifting it. (Note: the very early ‘peak’

in two of the profiles occurring as the movements began was associated with release of the start button).

**Figure 3.** Average number of total (A) reaching and (B) grasping errors occurring on all binocular trials in subjects with normal, coarse and negative stereo vision. Asterisks indicate significant increases compared to normal binocular vision (\*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ). Error bars, SEM.

**Figure 4.** Average grip application times in contact with the small and large objects as a function of binocular (filled squares) and dominant (DOM) eye (open circles) viewing condition for subjects with normal, coarse and negative stereo vision. Error bars, SEM.

**Figure 5.** Correlations between the mean durations of the terminal low velocity phase (LVP) of the reach and the grip application time (GAT) with best crossed stereoacuity thresholds for binocular (■) and dominant eye (o) movements in long-term stereo-deficient adults.

**Figure 6.** Average number of total (A) reaching and (B) grasping errors occurring under normal binocular (Plano lens), Low Plus and High Plus lens conditions. Asterisks indicate significant increases compared to normal binocular vision (\*\*,  $p < 0.01$ ). Error bars, SEM.

**Table 1: Details of the Stereo-deficient Subjects**

Subject	Sex, Age	logMAR Visual Acuity			Binocularity, stereopsis and motor fusion					Observations
		BO	DOM	N-D	Bagolini	Xed SA	BaseOut	BaseIn		
					W-T	TNO				
CS1	F, 23	-0.08	-0.04	0.0	Passed	100	480	25	10	Aniso, L meridional
CS2	M, 21	-0.2	-0.2	0.02	Passed	100	240	35	14	Aniso, R myopia
CS3	M, 25	-0.1	-0.08	-0.08	L Intermittent	200	120	16	10	Strab, L SOT
CS4	M, 21	-0.3	-0.3	-0.26	R Intermittent	140	240	14	10	Strab, R SOT microtropia
CS5	F, 35	-0.04	-0.08	0.18	Passed	140	240	25	14	S + A, R microtropia + meridional
CS6	M, 24	-0.12	-0.08	0.06	L Partial	200	200	35	14	S+A, L XOT + myopia
CS7	F, 19	-0.18	-0.04	0.04	Passed	400	480	20	12	Idiopathic
CS8	F, 20	-0.16	-0.14	-0.02	Passed	800	1700	45	16	Idiopathic
CS9	F, 19	-0.1	-0.1	0.2	Passed	3000	1700	45	25	Aniso, L hypermetropia, R myopia
CS10	F, 21	0.02	0.06	0.24	L Intermittent	3000	Failed	14	12	S + A, L SOT + meridional
SN1	M, 21	-0.24	-0.22	0.06	L Partial	Failed	25	6	Aniso, L hypermetropia	
SN2	F, 21	0.08	0.18	0.08	R Intermittent	Failed	20	10	S+A, R SOT + hypermetropia	
SN3	F, 33	0.04	0.06	0.22	L Partial	Failed	18	16	Strab, early SOT, now XOT	
SN4	M, 19	-0.06	0.0	0.0	R Partial	Failed	16	8	S+A, R SOT + hypermetropia	
SN5	F, 21	-0.18	-0.14	-0.06	L Partial	Failed	16	6	Strab, L XOT	
SN6	M, 33	0.0	0.0	0.0	L Intermittent	Failed	14	8	Strab, L SOT	
SN7	M, 36	-0.22	-0.16	0.2	L Intermittent	Failed	14	6	Strab, L SOT	
SN8	M, 24	-0.16	-0.14	0.24	R Total	Failed	12	4	Strab, early R SOT, now XOT	
SN9	F, 30	0.04	0.04	0.2	L, R Total	Failed	0	0	Strab, Alternator	
SN10	M, 34	-0.04	-0.04	-0.04	L, R Total	Failed	0	0	S+A, Alternator + L myopia	

Key: Subjects classed as having Coarse Stereopsis (CS) passed the Wirt-Titmus (W-T) stereotest; Stereo Negative (SN) subjects failed this and the TNO test. Binocular (BO), dominant (DOM) eye and non-dominant (N-D) eye visual acuities are given in logMAR notation. Bagolini (striated glasses test): Passed, the subject perceived two lines in a persistent cross; Intermittent, one line faded in and out; Partial, the central part of one line was continuously suppressed; Total, only one line was perceived; L, left R, right was the affected eye in these situations: Xed SA, the best crossed stereoacuity threshold (in arc secs) recorded on each test: motor fusion values represent the initial break-point (in prism dioptres) to Base Out and Base In challenges. Observations refer to each subject's current status, with indications as to the cause of their stereo losses: Aniso, anisometropia; Strab, strabismus; S+A, strabismus and anisometropia; SOT, esotropia; XOT, exotropia; Idiopathic, two CS cases had elevated stereo thresholds without detectable cause or history of pre-disposing (amblyogenic) factors, but were considered genuine as they also performed rather poorly on an alternative 'real-world' (two-pencil) test<sup>29,31</sup> of binocular stereopsis. We further note that two SN cases (SN2, SN7) reported perceiving depth when viewing 3D movies, indicating that they had stereopsis for low spatial/high temporal frequencies beyond the range examinable with our routine clinical tests.

**Table 2. Definition of dependent kinematic and error measures**

<u>Parameter</u>	<u>Definition</u>
<u>General kinematics</u>	
Movement Onset time	Reaction time between the cue to move and initiation of the reach (defined as the moment when the wrist velocity first exceed 50mm/s)
Movement Duration	Execution time from the onset to the end-point of the movement (defined as the moment when the target object was displaced by $\geq 10$ mm)
<u>Reach kinematics</u>	
Peak Velocity	Maximum wrist velocity (before object contact)
Time to Peak Deceleration	Time from movement onset to peak wrist deceleration (before object contact)
Low Velocity Phase	Time spent in the final approach to the object, between peak deceleration and initial object contact (defined as displacement of the target by $\geq 1$ mm)
Reach-Grasp Coordination	Time between initial object contact and the end of the reach (minimum wrist velocity after peak deceleration)
<u>Grasp kinematics</u>	
Time to Peak Grip	Time from movement onset to maximum grip aperture (at hand pre-shaping)
Peak Grip Aperture*	Maximum aperture between thumb and finger (before object contact)
Distance of Peak Grip	Distance of the mean digit positions from the centre of the target at peak grip
Grip Closure Time	Time from maximum grip aperture to initial object contact
Grip Size at Contact*	Aperture between the thumb and finger at initial object contact
Grip Application Time	Time applying the grip while in contact with the object prior to lifting it
<u>Movement courses</u>	
% Low Velocity Phase	Time in the final approach as a percentage of the movement's duration
% Grip Closure Time	Time spent closing the grip as a percentage of the movement's duration
% Grip Application Time	Time spent applying the grip as a percentage of the movement's duration
<u>Movement errors</u>	
Reach: Velocity corrections	Extra movements or plateaus in the velocity profile during the final approach
Reach: Spatial path adjustments	Changes in the hand path just prior to object contact in the trajectory profile
Grasp: Grip closure adjustments	Extra openings or changes in digit positions just prior to object contact in the grip profile
Grasp: Wide initial contacts	Inaccurate grip sizes at initial contact that were $>2$ times the diameter of the smaller object or $>1.5$ times the diameter of the larger object
Grasp: Grip application adjustments	Additional movements in the velocity profile <i>or</i> changes in the hand path <i>or</i> extra opening of the digits occurring between object contact and lifting
Grasp: Prolonged contacts	Long 'tails' in the grip profile during object manipulation lasting $>150$ msec

\*For comparability with our earlier work<sup>24</sup>, these measures of the grasp width were corrected for differences in hand size and digit thickness between participants, by calculating the average distance between the thumb and finger markers while each subject grasped the start button (diameter = 30 mm) on each trial and subtracting this value (minus 30 mm) from all their grip aperture data.

**Table 3. Mean ( $\pm$  SD) binocular & monocular prehension performance in normal & stereo-deficient adults**

<u>Dependent Measure</u>	<u>BINOCULAR</u>			<u>DOM EYE</u>			<u>Normal vs. SD Binocular</u> <u>F(2,37) statistic</u>
	<u>Normal</u>	<u>Coarse</u>	<u>Negative</u>	<u>Normal</u>	<u>Coarse</u>	<u>Negative</u>	
<u>Planning &amp; Execution</u>							
Movement Onset Time (ms)	483 $\pm$ 103*	494 $\pm$ 77	466 $\pm$ 68	506 $\pm$ 111	504 $\pm$ 88	469 $\pm$ 61	0.5, $p=0.6$ (ns)
Movement Duration (ms)	788 $\pm$ 133***	884 $\pm$ 102***	867 $\pm$ 82*	885 $\pm$ 155	984 $\pm$ 195	893 $\pm$ 89	3.6, $p=0.04$
<u>Reach Parameters</u>							
Peak Velocity (mm/s)	767 $\pm$ 155***	683 $\pm$ 131	701 $\pm$ 62	739 $\pm$ 160	669 $\pm$ 144	693 $\pm$ 55	1.7, $p=0.2$ (ns)
Time to Peak Deceleration (ms)	441 $\pm$ 75	476 $\pm$ 86	463 $\pm$ 56	438 $\pm$ 82	508 $\pm$ 91	471 $\pm$ 48	2.3, $p=0.1$ (ns)
Low Velocity Phase (ms)	230 $\pm$ 87***	262 $\pm$ 93***	258 $\pm$ 64	295 $\pm$ 99	307 $\pm$ 81	259 $\pm$ 78	0.6, $p=0.5$ (ns)
Reach-Grasp Coordination (ms)	32 $\pm$ 14***	40 $\pm$ 22***	52 $\pm$ 17**	62 $\pm$ 24	65 $\pm$ 27	67 $\pm$ 21	4.7, $p=0.015$
% Low Velocity Phase	28 $\pm$ 8***	29 $\pm$ 9*	30 $\pm$ 6	33 $\pm$ 8	31 $\pm$ 5	29 $\pm$ 6	0.1, $p=0.9$ (ns)
Total Reach Errors	3.7 $\pm$ 3.1***	3.8 $\pm$ 3.7**	6.7 $\pm$ 4.8	10.1 $\pm$ 6.1	8.7 $\pm$ 5.4	9.2 $\pm$ 6.4	3.6, $p=0.039$
<u>Grasp Parameters</u>							
Time to Peak Grip (ms)	453 $\pm$ 91	521 $\pm$ 127	477 $\pm$ 42	467 $\pm$ 95	561 $\pm$ 127	490 $\pm$ 42	4.6, $p=0.017$
Peak Grip Aperture (mm)	79 $\pm$ 11***	76 $\pm$ 9***	78 $\pm$ 6	84 $\pm$ 12	80 $\pm$ 10	80 $\pm$ 7	0.4, $p=0.7$ (ns)
Distance of Peak Grip (mm)	68 $\pm$ 18***	55 $\pm$ 12***	64 $\pm$ 15	76 $\pm$ 18	62 $\pm$ 10	66 $\pm$ 13	3.5, $p=0.042$
Grip Closure Time (ms)	218 $\pm$ 61***	217 $\pm$ 51***	244 $\pm$ 51	267 $\pm$ 77	253 $\pm$ 47	240 $\pm$ 59	0.8, $p=0.4$ (ns)
Grip Size at Contact (mm)	43 $\pm$ 3***	44 $\pm$ 4**	45 $\pm$ 4**	46 $\pm$ 3	46 $\pm$ 3	47 $\pm$ 3	1.4, $p=0.2$ (ns)
Grip Application Time (ms)	116 $\pm$ 26***	146 $\pm$ 43***	146 $\pm$ 29*	152 $\pm$ 39	170 $\pm$ 53	163 $\pm$ 27	4.5, $p=0.018$
% Grip ClosureTime	28 $\pm$ 6***	24 $\pm$ 6**	28 $\pm$ 4	30 $\pm$ 7	26 $\pm$ 5	27 $\pm$ 5	2.0, $p=0.2$ (ns)
% Grip ApplicationTime	15 $\pm$ 2***	17 $\pm$ 2	17 $\pm$ 2	17 $\pm$ 3	17 $\pm$ 3	18 $\pm$ 2	3.5, $p=0.04$
Total Grasp Errors	8.4 $\pm$ 4.2***	17.9 $\pm$ 7.4***	19.6 $\pm$ 12.3**	20.5 $\pm$ 10.3	27.8 $\pm$ 8.4	25.1 $\pm$ 12.4	10.7, $p<0.001$

Key: Asterisks denote significant within subject-group differences in binocular *versus* dominant (DOM) eye performance: \* $p<0.05$ ; \*\* $p<0.01$ ; \*\*\* $p\leq 0.001$ . The right-most column shows the results of the univariate ANOVA comparing the binocular performance of the subjects with Normal, Coarse and Negative stereoacuity (see text for results of post hoc comparisons)

Figure 1:

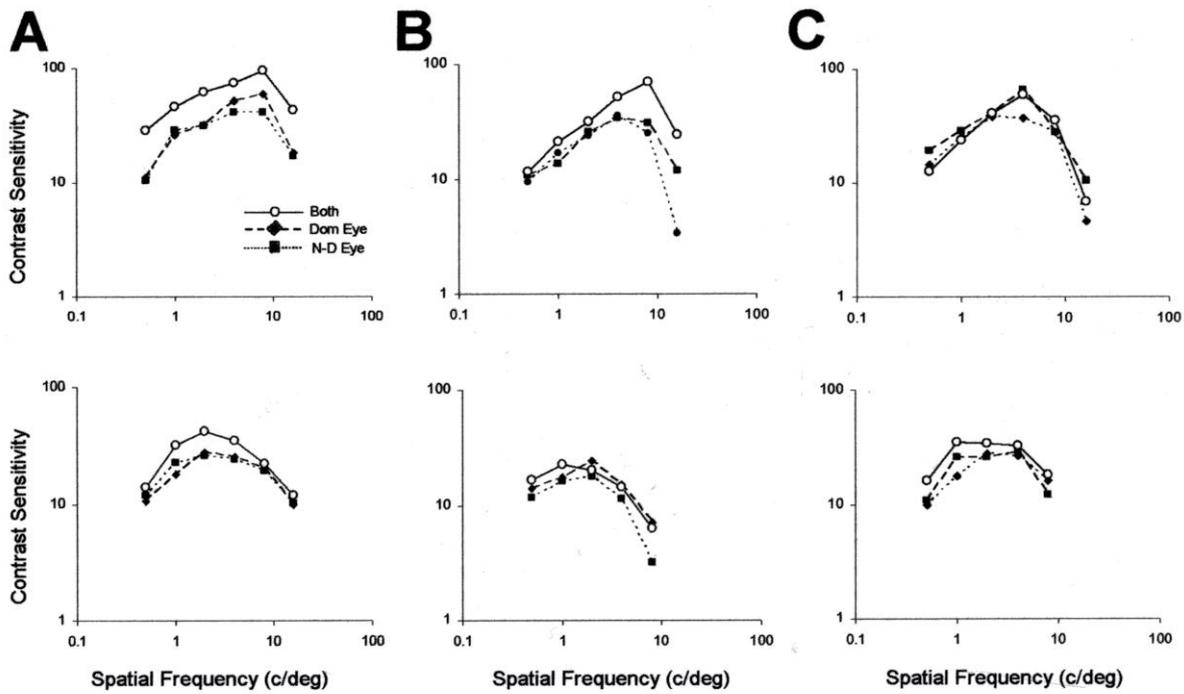


Figure 2:

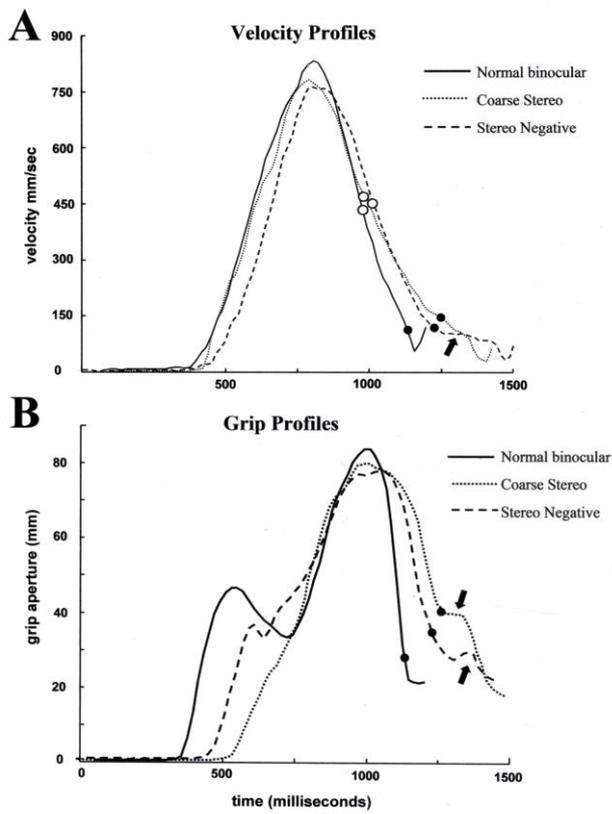


Figure 3:

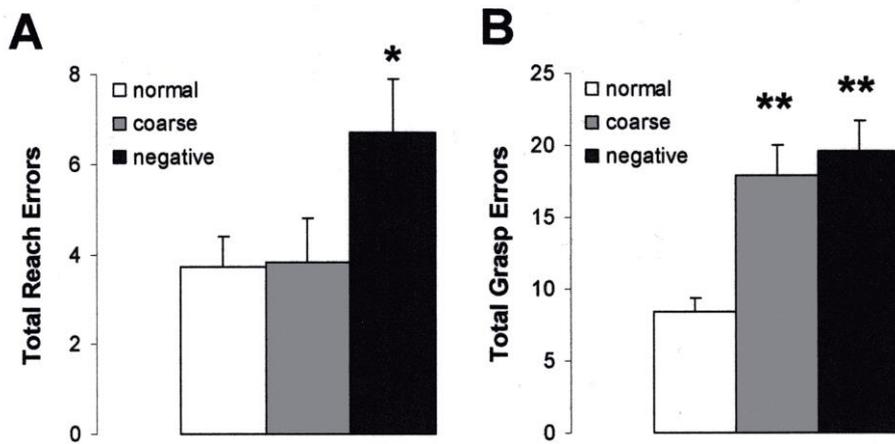


Figure 4:

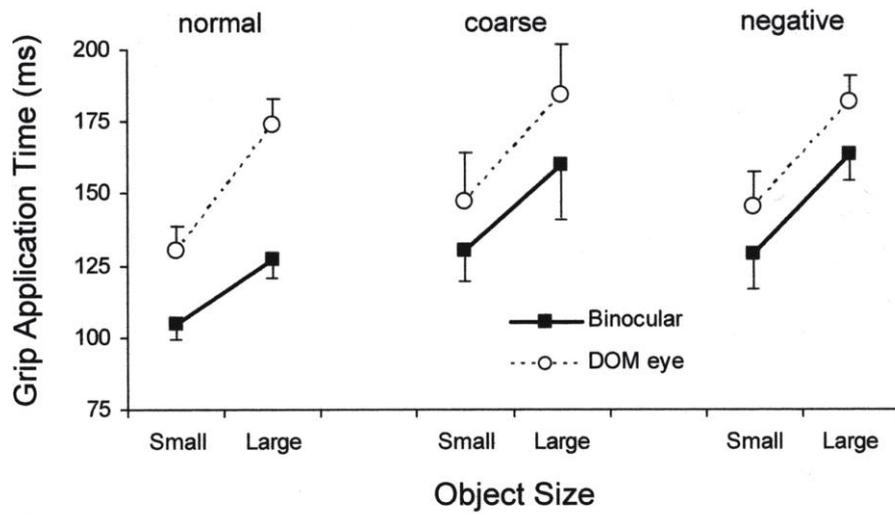


Figure 5:

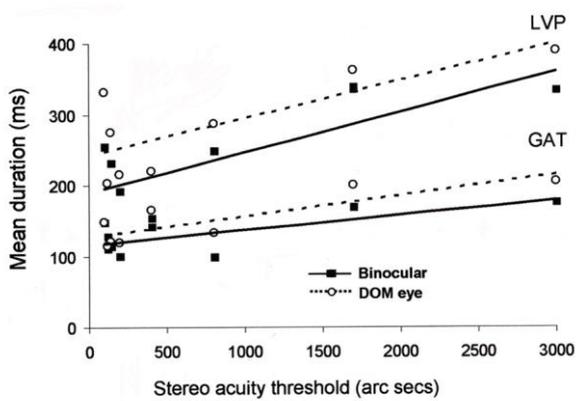


Figure 6:

