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Natural prehension in trials without haptic feedback but only when calibration is allowed

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Abstract

Reach-to-grasp (prehension) movements are normally accurate, precise and stereotypical in movement pattern. These features disappear when haptic feedback is removed in 'virtual reality' systems or when participants pantomime prehension. [Goodale, M. A., Jakobsen, L. S., Keillor, J. M. (1994). Differences in the visual control of pantomimed and natural grasping movements. *Neuropsychologia*, *32*, 1159–1178] suggested that pantomimed reaches are unnatural in form because the ventral rather than the dorsal stream mediates them. We tested whether calibration can prevent 'unnatural' prehension. Calibration refers to the use of an error (visual and/or kinaesthetic) signal to refine performance. We asked participants to reach-and-grasp in four conditions: (A) baseline; (B) reaching-to-grasp with haptic feedback (visual open-loop prehension to a physical object); (C) no feedback (visual-open-loop prehension to an object that could be seen but not felt); (D) a random mixture of (B) and (C). A 45° mirror was used to display objects without any reduction in visual quality. The normal decrements in performance were observed in condition (C) but not in the identical trials randomly embedded with feedback trials in condition (D). These findings show that participants can produce normal visual-open-loop prehension in the absence of haptic feedback when calibration is allowed. Thus, dorsal stream processing can support pantomimed reaching when calibration is allowed.
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1. Introduction

Reach-to-grasp movements (prehension) constitute one of the most frequent actions performed by humans. Prehension is described in terms of transporting the hand, the 'transport component', and preshaping the fingers, the 'grasp component' (Jeannerod, 1988). The grasp component is sensitive to the size of the object so that a larger grasp aperture is formed for wider objects. The maximum grasp aperture (MGA) is a little wider than the width of the target and occurs later in the movement for larger objects (Jeannerod, 1988; Mon-Williams & Tresilian, 2001; Smeets & Brenner, 1999). In the majority of cases, prehension requires the nervous system to direct hand movements to an object on the basis of visual information. In general, adult humans carry out this action to a very high level of performance—a topic that has received much attention over the last three decades since the pioneering works of Jeannerod (see Jeannerod, 1988).

Goodale et al. (1994) explored the differences between natural reach-to-grasp and pantomimed movements. Goodale et al. found that pantomimed reach-to-grasps were characterised by slower movements (indexed by decreased peak tangential speed and increased duration) and a reduction in maximum grasp aperture. Moreover, Goodale et al. found that pantomimed reach-to-grasps were shorter (i.e. the participants undershot the target location). The explanation provided by Goodale et al. (1994) for their findings rests upon the Milner and Goodale (1995) model. This model suggests that the dorsal stream of visual processing supports skilled action whereas the ventral stream supports conscious visual experience. Goodale et al. (1994) posited that the dorsal (action) stream mediates reaches whereas pantomimed reaches have to rely on a memory representation formed by the ventral (conscious visual experience) stream. Likewise, when participants reach-to-grasp objects in virtual reality (VR) environments without haptic feedback, movements are slow, inaccurate and tend to undershoot target position (Bingham,

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Bradley, Bailey, & Vinner, 2001). One possible explanation for the reduced performance in unnatural prehension tasks is the lack of opportunity for the system to calibrate itself. The term 'calibration' refers to feedback information (obtained through modalities such as vision and kinaesthesis) that provides the system with an error signal that can (and must) be used to refine performance (see Jacobs, Michaels, & Runeson, 2000; Runeson, Juslin, & Olsson, 2000; Stins & Michaels, 1997). Thus, calibration is intrinsic to the acquisition of a motor skill through learning. Recent evidence suggests that such learning continues on a trial-by-trial basis throughout life.

In situations where feedback is removed it is known that the system lacks precision and accuracy (e.g. Bingham & Pagano, 1998; Magne & Coello, 2002; Vindra & Viviani, 1998). Bingham and Pagano (1998) found that reach-to-grasps under restricted field-of-view conditions had a systematic bias (inaccuracy, typically an undershoot) that increased over time (i.e. a growing decrease in precision). Importantly, the tendency to inaccuracy was reduced by the provision of veridical haptic feedback. Magne and Coello (2002) found that reduced cue environments resulted in systematic biases appearing but the provision of a structured visual environment was sufficient to prevent drift. It has been shown that providing participants with distorted haptic feedback causes them to alter their behaviour in a predictable direction (Bingham, Zaal, Robin, & Shull, 2000). These studies show that the system requires and uses feedback (visual and/or haptic) in order to maintain its high levels of performance.

It can be seen that inaccuracy (consistent error) and imprecision (higher variability) in reaching and grasping are predicted when feedback is removed. The slower prehension movements reported by Goodale et al. (1994) and Bingham and Pagano (1998) can be explained by the decreased precision (caused by a lack of feedback information). Loftus, Goodale, Servos, and Mon-Williams (2004a); Loftus, Murphy, McKenna, and Mon-Williams (2004b) showed that removing information causes increased movement duration with decreased peak tangential speed together with a reduction in maximum grasp aperture. Nevertheless, the studies by Bingham and Pagano (1998) and Magne and Coello (2002) suggest that reduced performance in unnatural prehension tasks might not be inevitable if the system has the opportunity to calibrate itself. Thus, one might predict that providing feedback on some trials for the purpose of calibration will allow the system to increase its accuracy and precision and produce faster movement times and normal grasp apertures to objects even when feedback is absent on a particular trial.

We decided to test directly whether providing veridical haptic feedback on 50% of trials would improve performance when reaching-to-grasp objects without feedback. We tested this idea by asking participants to reach-and-grasp in four conditions: (A) normal prehension; (B) grasping with haptic feedback (visual open-loop prehension to a physical object); (C) no feedback (visual-open-loop prehension to an object that could be seen but not felt); (D) a random mixture of (B) and (C). We used a 45° mirror in order to display objects that could be seen but not felt with practically no decrement in the visual information available (apart from the obvious and crucial fact that participants could not see their hand in the vision-open-loop condition).

The study had two aims. It is known that reaches are (i) inaccurate and imprecise over time when feedback is absent and (ii) accurate and precise over time when feedback is available. The first aim was to establish whether intermittent feedback would remove the inaccuracies, have no effect or produce something between the extremes. This is a necessary step in understanding the fundamental processes of calibration. The second aim was to obtain empirical data of applied benefit. VR systems have advantages in prehension research but the unnatural performance obtained with these systems limits their usefulness. If it were possible to produce natural performance by providing intermittent feedback then usefully studying behaviour in distorted visual environments becomes a possibility. Conversely, the data might begin to establish how often feedback needs to be provided within VR. This is important to human factor researchers when considering the design and daily operation of such systems.

2. Method

2.1. Participants

Ten undergraduates at Aberdeen University, ranging in age from 20 to 23 years, participated in the experiment on a voluntary basis. Seven participants were female. All 10 were right-handed, had normal vision and were naïve to the purpose of the study. All of the participants were able to comprehend the instructions and carry out the task without difficulty. None of the participants had any history of neurological or ophthalmological abnormality.

2.2. Apparatus

Participants sat at an L-shaped 'mirror table' (Fig. 1) with their hand resting on a visible start location. The L-shaped surface was plywood and all surfaces except the mirror itself were painted matt black. The table allowed participants to reach comfortably behind the mirror. The mirror allowed us to create the illusion that an object was behind the mirror by using an image of an object physically located in front of the mirror. The mirror was manufactured specially (AC Yule, Tollos Industrial estate, Aberdeen, Scotland) so that it was front surface silvered and had a removable back panel. Removing the back panel allowed the image of the object in front of the mirror to be aligned perfectly with a physically identical object behind the mirror from the perspective of the participant. It also allowed us to measure baseline reach-to-grasps where the hand and the object to be grasped were visible through the mirror surface. Replacing the opaque back surface allowed us to produce an environment in which the visual and physical properties of an object were in perfect agreement but where the reach-to-grasp was visually-open-loop (i.e. only the object was visible with no view of the hand).

Throughout the testing of all participants the room was artificially lit. Participants sat at the table as shown in Fig. 1, with their finger and thumb lightly pinching the start position. Three infrared emitting diodes (IREDs) were placed on the participant's reaching limb (styloid process of the wrist, left edge of the nail of the index finger and right edge of the thumbnail). Positions of the IREDs were recorded by an Optotrak™ movement recording system factory pre-calibrated to a static positional resolution of better than 0.2 mm at 100 Hz (dynamic resolution was not significantly different from this). Data were stored in computer memory for subsequent off-line analyses. The raw X, Y and Z coordinates of each IRED were digitally filtered by a dual pass through a 2nd order Butterworth filter with a cutoff frequency of 20 Hz (equivalent to a 4th order filter with no phase lag and a cutoff of ≈16.5 Hz). Following this operation the tangential speed of the wrist IRED was computed and the onset of the reaching movement was estimated using a standard algorithm (threshold for movement onset and offset was 5 cm/s). Custom analysis routines were used to compute the dependent variables of interest in this study: reach distance and variability, movement time (defined as the time between the wrist starting to move and

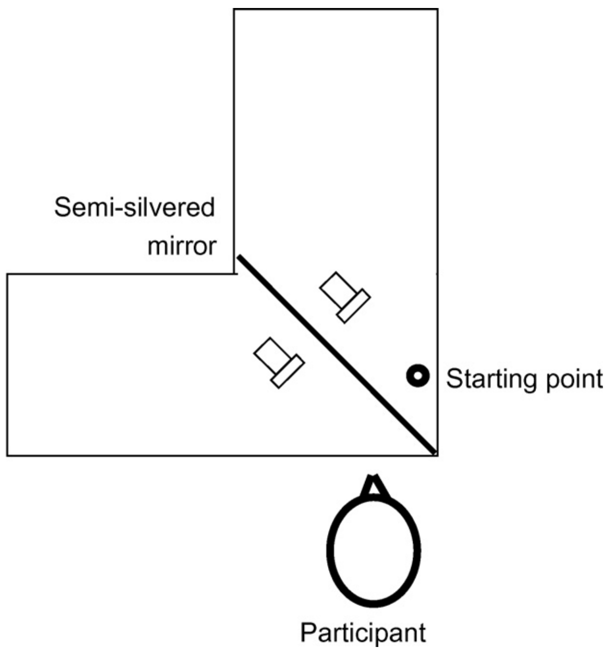

Fig. 1. Schematic of the experimental apparatus. Participants reached behind a semi-silvered mirror to grasp an object they could see in the mirror. In condition (A) the opaque back of the mirror was removed so that participants could see both the object and their hand. In condition (B), the opaque back of the mirror was present and a physical object was placed in exact correspondence with the image of the object seen in the mirror. In condition (C), there was no physical object present behind the mirror. Condition (D) consisted of a random mixture of condition (B) trials and condition (C) trials.

the point at which a stable grasp had been achieved), maximum speed of transport (calculated from the wrist IRED), maximum grip aperture, terminal grasp aperture (the aperture between the digits at the point in time when the changes in grasp configuration were stable) and its variability. Median values for each dependent measure were derived from the 10 experimental trials performed in each condition by each individual participant. These medians formed the basis for further statistical analysis using ANOVA (analysis of variance). On a given trial participants were required to move from the start point to grasp an object between finger and thumb. We asked participants to reach-and-grasp either a large or small object placed either near (17 cm) or far (27 cm) from the hand's starting position. The objects were rectangular in shape and consisted of a 1 cm diameter dowel mounted on a block: the participants were to grasp the dowel by placing their thumb and index finger on the opposite button-like ends, pinching the dowel along its long axis. The dowel projected from each side of the block. The large objects had a width of 8 cm and were 3.2 cm in height. The small objects had a width of 5.2 cm and were 3.2 cm in height. For the experimental conditions other than the baseline condition the participant could not see the object because of the mirror. In those conditions where feedback was provided, objects of identical dimension were placed on the near side of the mirror so that the image of the object created in the mirror was in the exact same position as the object on the far side of the mirror.

2.3. Procedure

All participants were tested in four separate experimental conditions (described below) the order of which was counterbalanced across subjects. Each target position was presented on 10 occasions for each object-distance configuration within a condition. Thus, each condition comprised 40 trials apart from condition (D), which contained 80 trials (so each participant was tested on 200 trials in total). The order of target presentation was randomised within each block and across participants. In all four conditions participants were asked to make quick, accurate and natural reach-to-grasp movements with their right hand, grasping the object by the 'buttons' with their thumb and index finger. The participants were asked to make contact with the objects but not lift them. Participants were informed fully that on some trials no object would be physically present but they should behave in the same manner as when an object was present. Participants were instructed to hold their fingers apart as if they had contacted the dowels when reaching-to-grasp for the objects they could not feel. The reaching-to-grasp hand was not allowed to touch the surface of the table so participants reached the object from above. The participants' vision was occluded while the experimenter placed the objects in their correct positions. Once the experimenter had placed the objects, the participant's vision was restored and after a gap of about 2 s the participant was verbally instructed by the experimenter to reach-and-grasp for the object. The participant remained in position until told by the experimenter to go back to the start position where the participant's vision was again occluded. Data acquisition was initiated approximately half a second before the experimenter's verbal start command and stopped after 3 s, by which time the participant had grasped the object.

There were four conditions in the experiment. Five of the participants were tested on the four conditions in order (A)–(D), while the other five were tested on condition (A) followed by (C) then (B) and finally condition (D). The only object visible within the display (other than the display apparatus) in all conditions was the target object. Condition A, baseline: the participant viewed the target object through the semi-silvered mirror when the mirror back was removed. This condition allowed vision of the hand (visual-closed-loop) and the object to be grasped (haptic feedback) whilst controlling for any optical distortions in the mirror produced in the other conditions (this was to err on the side of safety as no distortions should have been present). Condition B, haptic feedback: the participant viewed the image through the semi-silvered mirror when the mirror back was present. The participant could see the object in the mirror and feel an object (haptic feedback) in perfect correspondence with the visual image when they reached behind the mirror. Participants could not see their hand (visual-open-loop) during the reach-to-grasp movement. Participants were asked to reach-and-grasp the object and remain there until instructed to return to the start. Condition C, no feedback: the participant viewed the image through the semi-silvered mirror when the mirror back was present. The participant could see the object image in the mirror but there was no object on the far side of the mirror (no haptic feedback) and they could not see their hand (vision-open-loop). Thus, there was no feedback information in condition (C) and participants could therefore not calibrate their movements. Participants were asked to reach-and-grasp and remain in position until instructed to return to the start. Condition D, mixed: half of the trials were no-feedback trials and half were feedback. The participant did not know the type of trial in advance. In order to ensure the participants' naivety the experimenter used mimicry by placing blocks before silently removing them, or placing blocks loudly where they were stored when not in use, before silently placing them in the correct positions.

2.4. Variables of interest

The four major variables of interest in the study were the accuracy and precision of reach distance and terminal grip aperture. In order to calculate reach distance we calculated the distance between the three IREDs in their starting position and in their final position (when the wrist had stopped moving and the grasp was stable). The distance travelled by the three IREDs was averaged for each trial. This meant that we had a reach distance for all trials in each condition (how far the participants reached relative to the starting point). The median and standard deviation of these trials was calculated for each participant. The median values were then used to determine the effect of condition on reach distance whilst the standard deviations were used to determine the effect of condition on reach variability. We used median values as these provide a robust indicator of central tendency. We also analysed the mean values and found the same results. In order to calculate the terminal grip aperture we calculated the 3-D resultant distance (i.e. the magnitude of the vector between thumb and index finger regardless of orientation) between the IRED on the index finger and the IRED on the thumb at the time when the grasp formation phase was stable. This provided a terminal grasp aperture for all trials in each condition. The median and standard deviation of these trials was calculated for each participant. The median values were used to determine the effect of condition on terminal grip aperture whilst the standard deviations were used to determine the effect of condition on terminal grip variability.

In addition to the four major variables of interest, we also examined the total movement time, the peak speed and the maximum grip aperture in order to determine whether condition affected these kinematic variables.

3. Results

A three factor, within subject ANOVA was used to analyse the results with Greenhouse-Geisser adjustments to the degrees of freedom and alpha set at 0.05. A separate ANOVA was used for each of the variables. The first level of the ANOVA was condition (A–D with object, D without object), the second was distance (25 or 15 cm) and the third was object width (8 or 5.2 cm).

Fig. 2 shows data from a randomly selected participant in the different trials. It can be seen that the reach distance was accurate and precise in the baseline trials (A). The visually open-loop trials with haptic feedback (B) appear accurate although there is a visible decrement in precision. The no feedback trials (C) appear to be inaccurate (distance underestimated on average) and imprecise. The reaches became increasingly inaccurate (drifted) as reported in previous studies (e.g. Bingham & Pagano, 1998). In contrast the mixed trials (D) appear to have comparable accuracy and precision to the visually open-loop trials (B). The trials in condition (D) where an object was present were indistinguishable by eye from those trials without an object and were not statistically different.

In order to test the pattern of results in a formal manner, repeated measure ANOVA was conducted on the reach distance data. The analysis revealed two reliable interactions. First, an interaction was found between object distance and object width on reach distance ($F_{1,9} = 36.378$, $p < 0.05$) whereby the participants reached further when the object was wider. The over-reach was larger (around 1.5 cm) at the furthest object distance and smaller (around 1 cm) at the closer distance. Secondly (and more interestingly), an interaction was found between condition and distance as illustrated in Fig. 3 ($F_{4,36} = 2.956$, $p < 0.05$). The interesting comparison is between the open-loop, no feedback trials of condition (C) and the mixed open-loop, no feedback trials of condition (D) and how these trials compare to the open-loop, feedback trials of condition (B). In order to compare these conditions we collapsed the data across the two target distances. Planned comparisons showed a reliable difference ($p < 0.05$) between (B) and (C) but not between (B) and the mixed open-loop, no feedback trials of condition (D). Planned comparisons also showed a reliable difference ($p < 0.05$) between (C) and the mixed open-loop, no feedback trials of condition (D). Fig. 3 shows that the no feedback condition (C) resulted in a shorter reach distance and that this effect was greater at the furthest object distance.

A repeated measure ANOVA was also conducted on the reach variability data. A reliable interaction between distance and

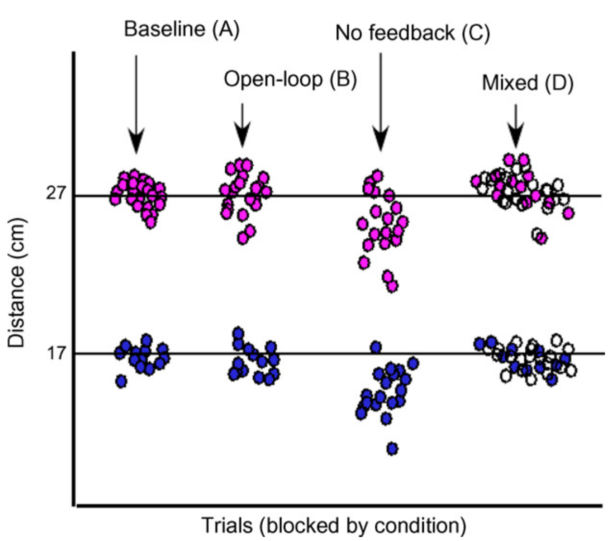

Fig. 2. The data plotted for one of the 10 participants (selected at random). The reach distance (cm) has been plotted for the individual trials and arranged in condition with the different reach distances aligned per condition. The trials have been horizontally separated so that they can be seen (thus, the greater horizontal spread in the mixed block simply reflects that this condition has twice as many trials). Condition (A) illustrates the normal high accuracy and precision present in prehension. Condition (B) shows the normal decrement in precision associated with visual-open-loop reaching. The no feedback trials in condition (C) indicate the loss of accuracy and precision reported previously for 'virtual reaches'. The mixed trials without feedback of condition (D) show a comparable level of accuracy and precision to those recorded in condition (B).

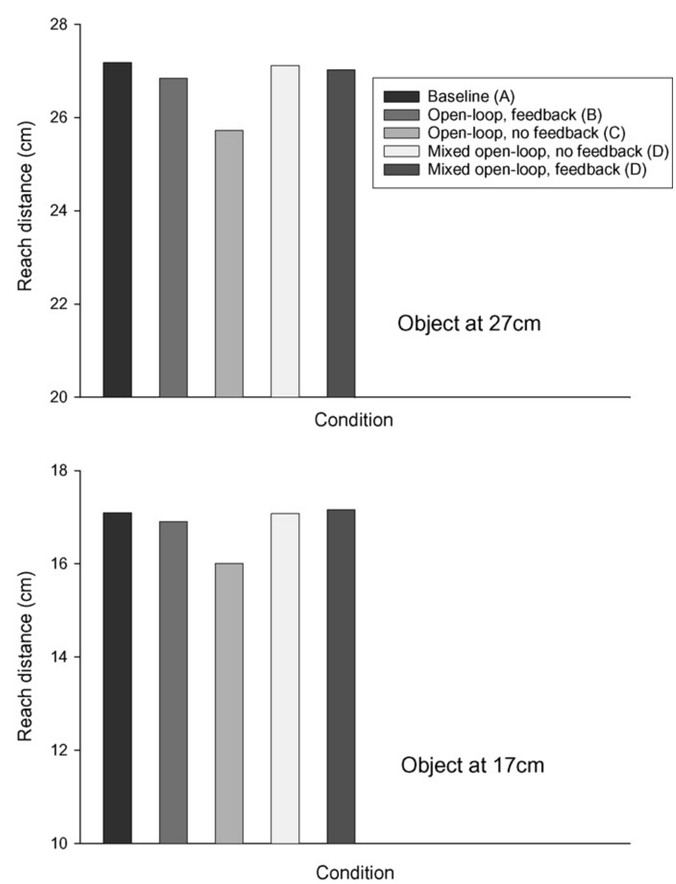

Fig. 3. Upper: the average reach distance (cm) plotted as a function of condition when the object was placed at 27 cm. It can be seen that the no feedback trials are associated with undershooting but the mixed trials without feedback of condition (D) show a comparable level of accuracy to those recorded in condition. (B) lower: the average reach distance (cm) plotted as a function of condition when the object was placed at 17 cm. It can be seen that the no feedback trials are associated with undershooting but the size of this effect is smaller than that found when the target was further. Once more, the mixed trials of condition (D) show a comparable level of accuracy to those recorded in condition (B).

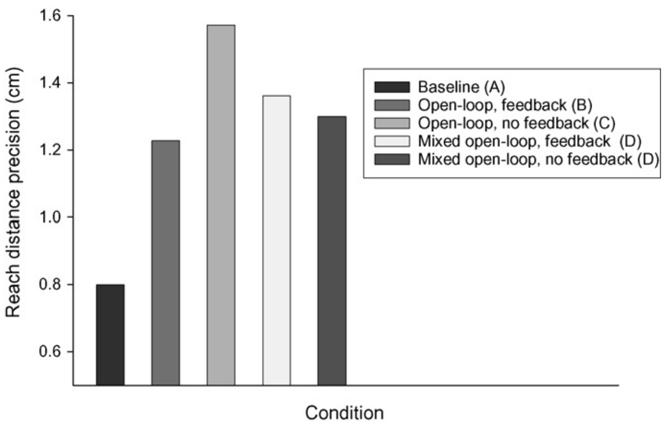

Fig. 4. The average reach distance precision (cm) plotted as a function of condition (we used the standard deviation across trials to index precision). The baseline trials show the highest level of precision with a decrement in precision found with visual-open-loop reaches. It can be seen that the no feedback trials are associated with a loss of precision but the mixed trials without feedback (D) show comparable levels of performance with those recorded in condition (B).

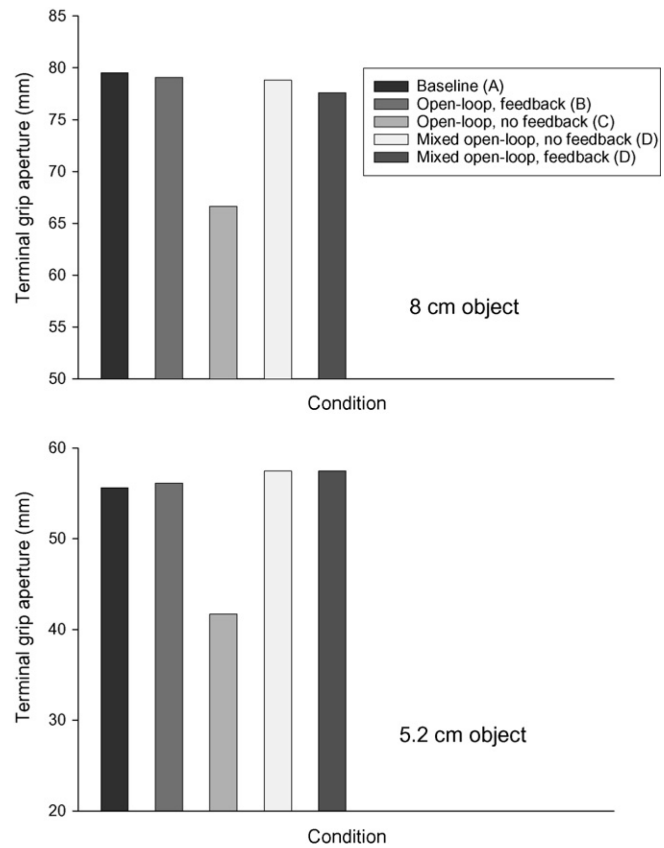

Fig. 5. Upper: the average terminal grip aperture (mm) plotted as a function of condition with the 8 cm object. It can be seen that the no feedback trials are associated with too small a grip aperture but the mixed trials of condition (D) show a comparable grip aperture to those recorded in condition. (B) lower: the average terminal grip aperture (mm) plotted as a function of condition with the 5.2 cm object. It can be seen that the no feedback trials are associated with too small a grip aperture but the mixed trials without feedback of condition (D) show a comparable grip aperture to those recorded in condition (B).

width was found ($F_{1,9} = 6.48$, $p < 0.05$). Participants showed a greater variability (0.22 cm) when reaching for a narrow block at the furthest object distance but this effect was much smaller (0.06 cm) at the closest object distance. The more interesting finding was a statistically reliable main effect of condition ($F_{4,36} = 3.85$, $p < 0.05$) illustrated in Fig. 4. Fig. 4 shows a high degree of precision in the baseline conditions with a decrement in performance in all other conditions. In the no feedback condition there was a notably lower level of precision. The other conditions (visual open-loop and mixed with or without an object) showed a comparable level of performance. The interesting comparison is between the open-loop, no feedback trials of condition (C) and the mixed open-loop, no feedback trials of condition (D) and how these trials compare to the open-loop, feedback trials of condition (B). Planned comparisons showed a reliable difference ($p < 0.05$) between (B) and (C) but not between (B) and the mixed open-loop, no feedback trials of condition (D). Planned comparisons also showed a reliable difference ($p < 0.05$) between (C) and the mixed open-loop, no feedback trials of condition (D).

The terminal grip data were analysed in a similar fashion to the reach data. No reliable interactions were found but a statistically reliable main effect of object width ($F_{1,9} = 323.762$, $p < 0.05$) and condition ($F_{4,36} = 17.729$, $p < 0.05$) was discovered. The effect of object width was due to participants opening their hand wider when the object was larger. Once more, the interesting comparison is between the open-loop, no feedback trials of condition (C) and the mixed open-loop, no feedback trials of condition (D) and how these trials compare to the open-loop, feedback trials of condition (B). Planned comparisons showed a reliable difference ($p < 0.05$) between (B) and (C) but not between (B) and the mixed open-loop, no feedback trials of condition (D). Planned comparisons also showed a reliable difference ($p < 0.05$) between (C) and the mixed open-loop, no feedback trials of condition (D). Fig. 5 shows the effect of condition on terminal grip aperture. It can be seen that terminal grip aperture is comparable across conditions apart from when there was no feedback information available. In this situation the terminal grip aperture was smaller for both the narrow and the wide object. Statistical analysis of the variability of the terminal grip aperture revealed no reliable interactions or main effects for condition, distance or width.

The no feedback data showed longer movement times (see Fig. 6), lower peak speeds and smaller maximum grip apertures than the other conditions. Analysis of the movement time revealed the same reliable effects as reported for reach distance [an interaction between object distance and width ($F_{1,9} = 6.93$, $p < 0.05$) and an interaction between condition and distance ($F_{4,36} = 2.802$, $p < 0.05$)]. Analysis of the peak speed data revealed no reliable interactions but a reliable main effect for reach distance ($F_{1,9} = 133.572$, $p < 0.05$) and a reliable main effect for condition ($F_{4,36} = 4.483$, $p < 0.05$). The maximum grip aperture data showed the same pattern of results as those reported for terminal grip aperture. No reliable interactions were found but a statistically reliable main effect of object width ($F_{1,9} = 232.501$, $p < 0.05$) and condition ($F_{4,36} = 16.371$, $p < 0.05$) was discovered. The findings show that the system was slowing down the movement in the no feedback condition but not in the other visual-open-loop conditions.

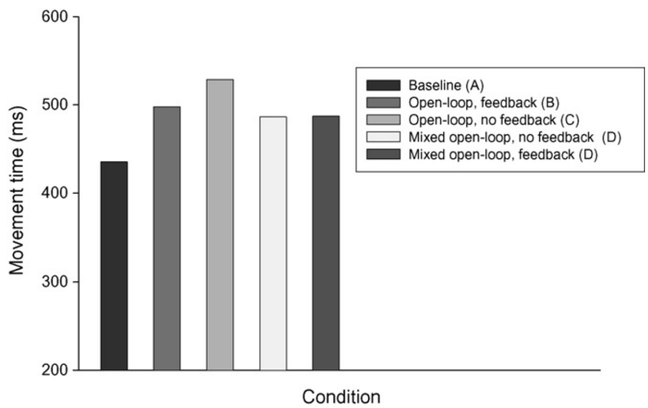

Fig. 6. The average movement time (ms) plotted as a function of condition. The baseline trials show the shortest movement times with a decrease in movement time found with visual-open-loop reaches. It can be seen that the no feedback trials are associated with increased duration but the mixed trials without feedback show comparable levels of performance with those recorded in condition (B).

4. Discussion

Previous research has indicated that movement execution is not naturalistic in situations where calibration is prevented (Bingham & Pagano, 1998; Magne & Coello, 2002). On the basis of this research, one would predict that prehension movements without feedback would be associated with inaccuracy and imprecision. Moreover, it is known that movement time increases when information that supports action is removed (Loftus et al., 2004a,b). The increase in movement time can result in a separate effect of smaller maximum grip apertures (Loftus et al., 2004a,b). Thus one would predict inaccuracy, imprecision, slower movement times and decreased maximum grip aperture in trials where no feedback (visual or haptic) is provided. The results of the present study found exactly that pattern of behaviour when the trials recorded in condition (C) were examined. The question was whether the decrements in performance could be removed if haptic calibration information were provided on 50% of the trials? The results of the study show that unnatural prehension in the absence of feedback is not inevitable if haptic information for calibration is provided on 50% of trials. Thus, the visual-open-loop trials without feedback that occurred in condition (D) were comparable with the visual-open-loop with feedback trials recorded in both condition (D) and the block of visual-open-loop with feedback trials recorded in condition (B). A similar set of results were highlighted to us by an anonymous referee. Opitz, Gegenfurtner, and Bülthoff (1996) reported the same conclusions (in the proceedings of a conference) but used computer generated stereo-projected images to produce objects that did not provide feedback.

The highest levels of performance were found in condition (A) where vision of the hand and the object were available. This is not surprising as from at least the time of Woodworth (1899) the importance of vision for the purpose of on-line control has been known. The visual-open-loop with haptic feedback trials in condition (B) remained relatively accurate but were marked by a loss of precision. This suggests that the nervous system maintained relatively accurate performance but was unable to correct on-line any small errors that occurred in movement execution (owing to the lack of vision of the hand). Loftus et al. (2004a,b) have shown previously that a general slowing down of the movement accompanies a loss of movement precision. The increased movement duration found in the condition (B) trials is consistent with this previous research. Loftus et al. (2004a,b) have suggested that the system slows down the movement in order to increase the opportunity for on-line control and to minimise the potential harm of any collisions resulting from an inaccurate trial. It is of note that the no feedback trials produced a greater reduction in movement speed than the other visual-open-loop trials suggesting that the greater the level of imprecision then the slower the system executes the movement.

The no feedback trials were associated with inaccuracy in distance perception and this inaccuracy was reflected in a systematic undershoot of target position. The undershoot was greater when the object was further which is presumably related to the fact that participants would reach at least a minimum distance. The presence of a systematic undershoot raises the question of why the system should stop short? A number of studies have established that the nervous system is biased towards undershoots in situations of uncertainty such as those that occur in sparse visual conditions (Bingham & Pagano, 1998; Coello & Grealy, 1997; Magne & Coello, 2002; Watt, Bradshaw, & Rushton, 2000). In situations of uncertainty, an initial undershoot may decrease the likelihood of missing or colliding with the target object. A strategic undershoot is then a logical option in situations of uncertainty and is consistent with the idea of a nervous system that seeks to minimise effort and maximise performance.

The no feedback trials were also associated with a decrease in grip aperture. The finding of a decrease in maximum grip aperture can be explained by the increased movement time (see Loftus et al., 2004a,b). It is less clear why the terminal grip aperture should be decreased. Once more, the most plausible explanation is likely to be related to a conservative strategy where the hand goes to some intermediate posture (this would suggest that the grip aperture would be too large when grasping objects of small width without feedback: a testable notion). The reduction in grip aperture may also explain why increased variability was not associated with the terminal grip aperture (the range of possible apertures being decreased by the fact that the hand was always in a relatively closed formation).

In the introduction to this manuscript we highlighted the findings of Goodale et al. (1994) who reported differences between natural reach-to-grasp and pantomimed movements. Goodale et al. (1994) suggested that pantomimed reach-to-grasps are different because a different visual representation is used for such behaviour. The findings reported in this manuscript suggest a parsimonious explanation for the poor performance in pantomimed reach-to-grasps is the absence of haptic calibration information. Our results suggest that dorsal stream processing can support pantomimed reaching when calibration is allowed. Thus, the neurophysiological system supporting skilled action, dorsal versus ventral stream visual processing, requires calibration and when calibration is allowed supports normal and pantomimed reaching. The implication is that reaches in virtual reality can be normal.

An anonymous reviewer has pointed out that the trials in condition (C) not only lack feedback but are also accompanied by the knowledge that a physical object will not be contacted. In condition (D) the participant is unaware on any individual trial whether an object will be present or not. Thus, the natural prehension might be produced by a strategy based on the assumption that an object is present. It is difficult to separate the effects of feedback from the knowledge that an object might be present and thus we cannot rule out this possibility. Nevertheless, it is our opinion that the alterations in behaviour are driven by the presence of feedback rather than a shift in cognitive strategy. It is difficult to see why participants should adopt a strategy that results in inaccuracy and imprecision when they know an object is not physically present. Bingham et al. (2000) have shown that the system uses feedback information to calibrate behaviour and it seems reasonable to suppose that removing information that the system is known to use will produce decrements in performance.

In summary, our findings suggest that participants can produce normal visual-open-loop prehension without haptic feedback when calibration is allowed. It remains to be established whether a smaller percentage of feedback trials would continue to allow the system to calibrate itself. These results are important because they provide a powerful means of exploring the information used for supporting skilled prehension. Virtual reality systems can be used to perturb the visual array in order to measure the effect on naturalistic behaviour as long as the system has been provided with the opportunity to calibrate itself. The results also have important ramifications for the design and use of virtual reality displays: the opportunity to calibrate movements is required within virtual reality.

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