Exp Brain Res (2000) 134:268–273
DOI 10.1007/s002210000479

RESEARCH NOTE

M. Mon-Williams · R.D. McIntosh

A test between two hypotheses and a possible third way for the control of prehension

Received: 28 October 1999 / Accepted: 10 May 2000 / Published online: 29 July 2000

Abstract We used an obstacle avoidance task to test two opposing accounts of how the nervous system controls prehension. The visuomotor account supposes that the system independently controls the grip formation and transport phase of prehensile movements. In contrast, the digit channel hypothesis suggests that the system controls the thumb and finger more or less independently. Our data strongly favoured the traditional visuomotor channel hypothesis and demonstrated that the time taken to grasp an object in the presence of obstacles was well predicted by a Fitts' law relationship. We suggest a "third-way" hypothesis in order to retain the advantages of the digit channel hypothesis within the visuomotor framework. The third-way hypothesis suggests that the nervous system selects a single digit to transport to the object. We speculate that the actual digit selected might depend upon attention and the nature of the prehension task. This hypothesis is able to account for most of the empirical findings unearthed by researchers investigating the control of prehension.

Key words Prehension · Precision grip · Motor programming · Visual cues · Obstacle avoidance · Human

Introduction

We may be within a megaparsec (where a megaparsec is 3.1×10^{24} cm) of calculating the distance to neighbouring galaxies (Paczynski 1999), but we are a long way from understanding basic human behaviour. Imagine reaching out to pick up a wine glass – an everyday task for a majority of Europeans. The task depends upon the nervous system accurately gauging the distance of the wine glass from the body, judging the properties of the glass (e.g. size, weight) and generating the appropriate motor commands in response to this information. We are still many megaparsecs from understanding how the system solves these various problems. Our lack of understanding can be illustrated by the controversy that exists with regard to just one aspect of that task – namely, what commands does the nervous system send to the hand to ensure that the digits travel the correct distance and open wide enough to grasp the wine glass? Two different hypotheses have been proposed to account for the nature of the commands. The first (traditional) hypothesis postulates that the visuomotor transformations related to reaching and grasping are controlled independently (i.e. a separate transport and grip formation component exist). This hypothesis is known as the visuomotor channel hypothesis and was originally proposed by Jeannerod (1988). An alternative model suggests that separate visuomotor channels exist for the finger and the thumb. This hypothesis was proposed by Smeets and Brenner (1999), and we will refer to it as the digit channel hypothesis. In the digit channel hypothesis, Smeets and Brenner (1999) abandon grip as a variable within grasping. Instead, they regard grasping as simply moving the fingers and thumb to positions on the surface of an object of interest. One important feature of Smeets and Brenner's model is that the digits approach surfaces perpendicularly. This feature has empirical support (Smeets and Brenner 1995), and this constraint allows Smeets and Brenner (1999) to generate realistic digit trajectories for grasping movements. These authors (Smeets and Brenner 1999) provided an extensive review of extant studies on reaching and grasping to show that their model can account for observed human prehensile behaviour.

Smeets and Brenner (1999) have highlighted various advantages that the digit channel hypothesis holds over the visuomotor channel hypothesis. First, since they claim that both the finger and thumb are transported, it avoids the problem of deciding which anatomical part of the hand is controlled in the transport phase (an inherent difficulty with the visuomotor channel hypothesis). Second,

M. Mon-Williams (✉) · R.D. McIntosh
School of Psychology, University of St Andrews, St Andrews, Fife KY16 9JU, Scotland
e-mail: mon@st-andrews.ac.uk
Tel.: +44-1334-462074
Fax: +44-1334-463042

the account allows the movement of the digits to be modelled using existing accounts of motor control such as the minimum-jerk model. Third, the model takes account of the contact points on an object when describing grip formation. Although the digit channel hypothesis has advantages over the visuomotor channel hypothesis, it remains an empirical question as to which hypothesis best captures the nature of prehension. Clearly, describing the opening and closing of the grasp aperture in terms of the movement of the two digits is a mere tautology. Smeets and Brenner (1999) are not providing a tautology, however, but are suggesting a different underlying neural organisation to that traditionally envisaged. Differentiating between the two hypotheses is thus difficult unless we can gain an insight into the underlying organisation of the system. One possible way of testing the two hypotheses is to manipulate the manner in which a prehensile movement can be carried out and then to observe the effect of that manipulation on a known feature of the system's organisation. Arguably, Paul Fitts (1954) has provided the only lawful account of the system's behaviour, and thus the best approach to testing the two hypotheses might be usefully centred around Fitts' law. It should be noted that Fitts' law was developed to account for simple aiming movements and not prehension movements per se. Nonetheless, numerous studies have shown that Fitts' law generalises to movement other than simple arm movements (Langolf et al. 1976). Fitts' law describes the speed-accuracy trade-off in aiming tasks as follows:

$$MT = a + b \log_2(2A/W) \qquad (1)$$

where MT is movement time, *a* and *b* are constants that depend upon the individual and the task, *A* is the movement amplitude and *W* is the target width. $\log_2 (2A/W)$ is referred to as the index of difficulty (ID). Once more, imagine reaching out to pick up a wine glass, but this time picture it located between a bottle of Claret on the right and a glass of water on the left. It is clear that the system must now take into account the obstacles present when grasping the wine glass and modify its commands accordingly. The manner in which the commands are modified will be different depending upon whether the system is controlling two digits or two components of the prehensile movement.

We tested the two hypotheses by exploring the extent to which the different hypotheses could account for the time taken to grasp a target object located next to an obstacle. According to the visuomotor channel hypothesis, the nervous system is trying to match the distance between the digits with the size of the target ("target grip aperture" in Fig. 1). The size of the target grip aperture is dictated by the gap between the two obstacles (under the assumption that the system is trying to ensure that the inter-digit distance is smaller than the gap between the obstacles and larger than the object). The visuomotor channel hypothesis thus predicts that MTs will be governed by the width of the "grip aperture" (i.e. the distance between the two obstacles). In contrast, the digit channel hypothesis suggests that MT should be predicted by the width of the aperture for the thumb and the width of the aperture for the index finger. In this situation, the Fitts' law relationship becomes more complicated. Fitts' law states that MT may be predicted from ID using Eq. 1 (with particular values of *a* and *b*) for a particular person performing a particular aiming task. It does not state that changing the aiming task (or the conditions under which it is executed) will allow Eq. 1 to predict MT from ID with the same values of *a* and *b*. Indeed, it is known that the values of *a* and *b* can vary from task to task and are consequently rather sensitive to task parameters. In general, therefore, Fitts' law can be written:

$$MT = A(T) + B(T)ID \qquad (2)$$

where *A* and *B* are functions of the task context (T), taking particular constant values (*a* and *b*) for particular task conditions. In bi-digit aiming, the task context is determined by the IDs of the two targets and so, for the thumb, Eq. 2 becomes:

$$MT_i = A_i(ID_R, ID_L) + B_i(ID_R, ID_L)ID_i \qquad (3)$$

where i=R or L (R and L indicate the thumb and index finger, respectively). Equation 3 implies that the MT of one digit can depend both upon the ID of its own target and on what the other digit is doing. As it stands, Eq. 3 is an empirical relationship which can be considered a general but completely unconstrained version of Fitts' law that, in principle, allows MT to be almost any function of the IDs. In order to make Eq. 3 into a meaningful expression of Fitts' law, additional simplifications and constraints are needed. Ultimately such constraints must come from fitting models of the form of Eq. 3 to the experimental data. The simplest form of Eq. 3 that can usefully be considered arises from the following set of simplifying assumptions: (1) The influence of a constant task for one digit on the other digit is independent of the other digit's task. This means that A_L and B_L would depend only upon ID_R, and A_R and B_R only on ID_L; (2) B_i is constant (b_i); (3) A_R and A_L are linear functions with constant coefficients: $A_R(ID_L)=c_R+m_R ID_L$; (4) the constants b_i and m_i are equal. If these assumptions are in place, then Eq. 3 reduces to the simplest form possible, which is consistent with the finding of synchronous movements of the two digits:

$$MT_i = c_i + d_i\,(ID_L + ID_R)/2 \qquad (4)$$

which is a Fitts' law relation stating that the MT of the index finger is a linear function of the mean index of difficulty of the thumb and the index finger's target, $(ID_L+ID_R)/2$. If the two digits move synchronously ($MT_R=MT_L$), then c_i and d_i are the same for both thumb and index finger. A previous experiment (see Wann et al. 1998 for a discussion of the data currently submitted for publication) has established that bimanual MTs are well described by a Fitts' law relationship involving the mean ID of the two targets if the attentional demands of the task are constant (i.e. MTs were predicted by Eq. 4). In the current experiment, the index of difficulty of the thumb's "tar-

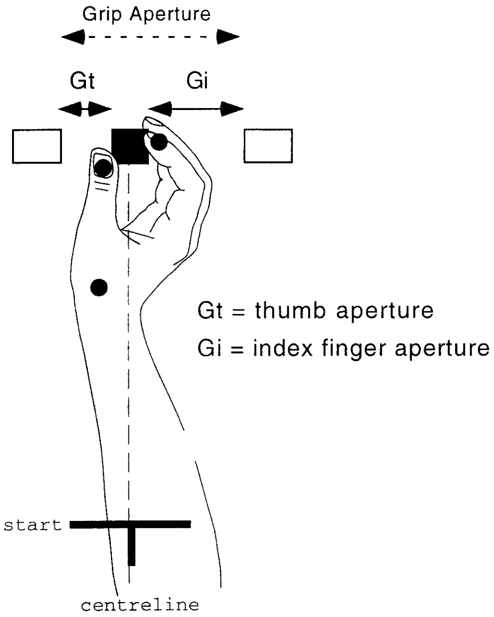

Fig. 1. Schematic of the experimental configuration. The hand belongs to James Tresilian and was drawn by Anna Plooy from a captured video image. In the posture shown, the distance from the tip of the index finger to the styloid process of the wrist is approximately 15 cm. Participants reached to an object (*solid black square*) placed on the midline. Obstacles (*hollow rectangles*) were placed on the right and the left of the target. According to the visuomotor channel hypothesis, task difficulty should be dictated by the distance reached and the total distance between the inner edges of the two obstacles (the "grip aperture"). According to the digit channel hypothesis, the task difficulty should be dictated by the distance reached and the width of the gap for the thumb (thumb aperture) together with the width of the gap for the finger (index finger aperture). See text for details

get aperture" was held constant and thus the attentional demands were constant for this digit. The digit channel hypothesis then predicts that the MT should be predicted by the meanID of the two targets (the target aperture for the thumb and the target aperture for the index finger).

Materials and methods

Six people (four men, two women) participated in this study voluntarily. All were members of the School of Psychology at the University of St Andrews and had normal or corrected-to-normal vision. The age range was 21–28 years and all subjects were naive to the aims of the experiment. The experimental task was to reach forward and grasp a target object using a precision grip. An obstructing object was placed on each side of the target object (see Fig. 1). Target and obstructing objects were arranged on a smooth, flat, white table surface. The target object was a rectangular (6 cm height × 3 cm width × 2 cm depth) block of plastic painted green. The obstacles were unpainted grey plastic blocks, 20 cm height × 3 cm width × 1 cm depth. Positions of three small infra-red-emitting diodes (IREDs) placed on the participant's reaching limb were recorded by an Optotrak movement recording system. The Optotrak camera system was positioned approximately 2 m from the experimental workspace at a height 1.5 m above the table surface. The system was factory-precalibrated to a static positional resolution of better than 0.2 mm (dynamic resolution at speeds characteristic of human arm movements in reaching to grasp tasks was not significantly different from this). The three-dimensional (3D) coordinates of the IREDs were referenced to a coordinate system defined by three IREDs. With this set-up, the 3D coordinates of IREDs within the workspace could be measured to within ±0.5 mm of their positions as measured with a ruler. Three IREDs were attached to participants' right arms at the wrist (styloid process of radius), distal phalanx of the index finger and of the thumb as indicated in Fig. 1. Positions of the IREDs were recorded at a sampling rate of 100 Hz.

Participants reached for the target object which was placed either 20 cm or 30 cm from the start position along the centreline, which was approximately along the participant's midline (Fig. 1). The hand was initially positioned with the wrist in a relaxed neutral posture (neither flexed nor extended), with the fingers flexed and the thumb and index finger touching. The hand was positioned such that the point at which the thumb and index finger pads met was above the start point defined as the junction of the T in Fig. 1. Reaches were made under eight obstacle conditions. The gap between the object and the obstacle on the side of the index finger varied in each condition. The gaps were 2.1 cm, 3.7 cm, 5.6 cm and 7.7 cm when the object was at 30 cm, and were 2 cm, 2.75 cm, 3.6 cm and 4.5 cm when the object was at 20 cm. The gap between the object and the obstacle on the side of the thumb was maintained at a constant index of difficulty (the gap was approximately 4 cm at 30 cm and 3 cm at 20 cm). The gap sizes were chosen simply to provide a range of indices of difficulty that would allow differentiation between the two hypotheses. We ensured that the thumb gap had a fixed index of difficulty, in order to ensure that the attentional demands for this digit remained constant over the trials. It will be noted that this arrangement results in asymmetric positions for obstacles on either side of the target. It has been established previously that equally spaced flanking objects produce much less effect when located on the side contralateral to the reaching limb, i.e. when the flanking object is ipsilateral to the fingers and contralateral to the thumb (Jackson et al. 1995). Our stimulus configuration thus provided us with a good test between the two different hypotheses. We avoided having a no obstacle condition, as it is not possible to calculate an index of difficulty for such a condition.

Ten reach trials in each of the eight obstacle conditions were presented in a randomised order (80 trials in total). Participants were instructed to reach out and grasp the target, pick it up and the replace it on the table, in the presence of the obstacles. They were instructed to grasp the target object on the lateral surfaces. Participants were allowed a small number of practice trials with the obstacles randomly placed in one of the eight possible positions. Participants were instructed to reach as quickly but as accurately as possible. The participants were explicitly told to avoid touching the obstacle. In the event, no participant touched the obstacle during the practice period. Following the practice period, the participant performed the blocks of experimental trials. Any trial during which a participant touched an obstacle was considered void and immediately re-run; in the event this occurred only infrequently. Participants were cued to start by one of the experimenters with the verbal signal "Go". Data acquisition was initiated approximately simultaneously with the experimenter's verbal start command. Data were recorded for a period of 1.5 s, which was always sufficient to capture the whole movement to object contact. 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 10 Hz. Following this procedure, the tangential speed of the IREDs was computed and from this the onset and offset of the reaching estimate was estimated using a standard algorithm (see Jakobson and Goodale 1991 for details). We also inspected six other kinematic variables in order to ensure that the prehensile movements were "normal": (1) peak velocity, (2) peak acceleration, (3) time to peak velocity, (4) time to peak acceleration, (5) time spent decelerating (the time to peak velocity subtracted from the MT), (6) normalised time spent decelerating (deceleration time divided by the MT). We could make no a priori quantitative predictions regarding the effect of obstacles on these parameters (Fitts' law only describes MT), and thus the dependent measure was MT.

Results

Table 1 provides the kinematic variables recorded during the experiment. It can be seen that the participants showed normal reaching and grasping responses. Figure 2 shows the predicted pattern of results for the two hypotheses. The left-hand column shows the predicted results if the visuomotor channel hypothesis is correct when MT is plotted against the ID calculated from the visuomotor channel hypothesis (Fig. 2a) and when MT is plotted against the ID calculated from the digit channel hypothesis (Fig. 2b). The right-hand column shows the predicted results if the digit channel hypothesis is correct when MT is plotted against the ID calculated from the visuomotor channel hypothesis (Fig. 2c) and when MT is plotted against the ID calculated from the digit channel hypothesis (Fig. 2d). Plotting the MT against the incorrect ID produces distinct patterns in the relationship between ID and MT – these patterns thus serve as useful qualitative features for discriminating between the two hypotheses.

Table 1 Summary of the seven kinematic variables with SDs across participants

	Mean	SD
Movement time (ms)	526.120	171.220
Deceleration time (ms)	318.179	116.980
Normalised deceleration time (%)	59.290	0.030
Peak acceleration (cm/s^2)	55.040	25.670
Peak velocity (mm/s)	991.869	185.794
Time to peak acceleration (ms)	299.997	103.441
Time to peak velocity (ms)	207.941	54.537

Figure 3 shows the actual MTs plotted against the ID calculated from the visuomotor channel hypothesis, and the ID calculated from the digit channel hypothesis. It should be noted that the MTs of the thumb and index finger were synchronous so that the movement of the two

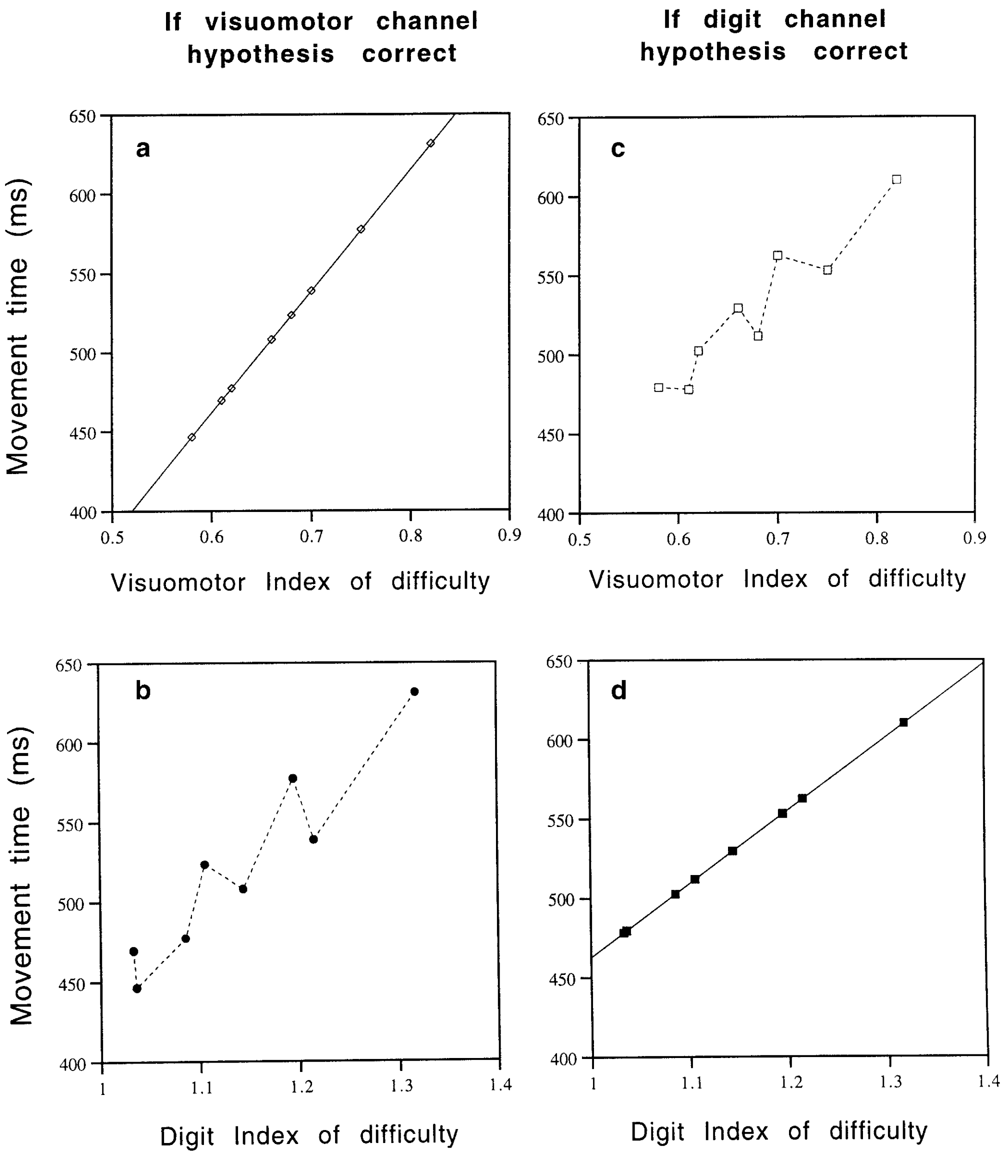

Fig. 2a–d Schematic qualitative behaviour of movement time as a function of index of difficulty predicted by the visuomotor channel hypothesis (*right-hand column*) and the digit channel hypothesis (*left-hand column*). **a** and **c** show the movement time data plotted as a function of the index of difficulty predicted by the visuomotor channel hypothesis. **b** and **d** show the movement time data plotted as a function of the index of difficulty predicted by the digit channel hypothesis. It will be noted that plotting movement times against the incorrect indices of difficulty causes a distinctive pattern of results. These patterns thus serve as useful qualitative features for differentiating between the two hypotheses. See text for details

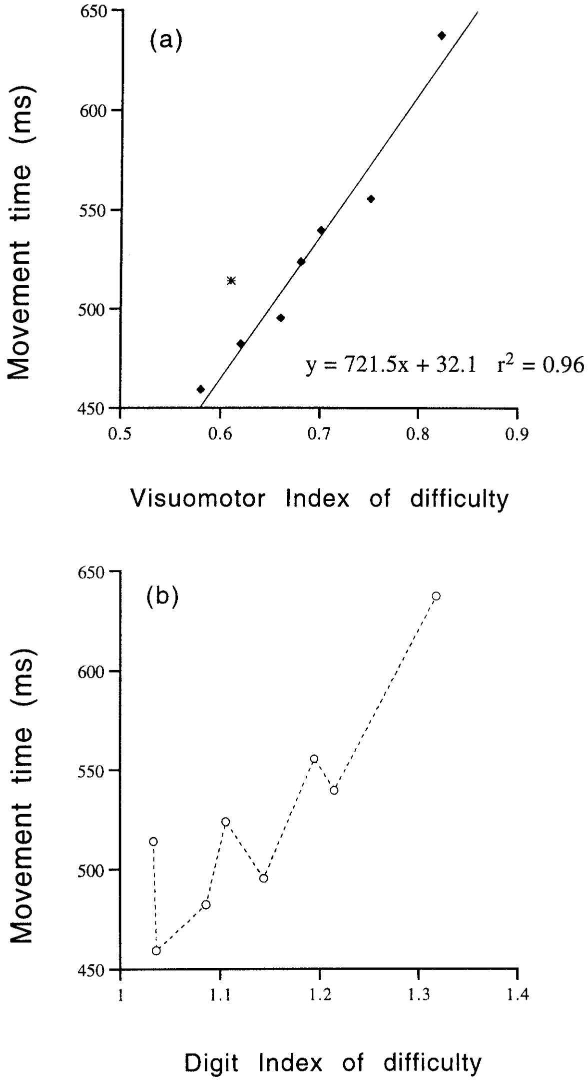

Fig. 3a,b Actual movement times (mean across six participants) plotted as a function of the index of difficulty predicted by the visuomotor channel hypothesis (**a**) and the index of difficulty predicted by the digit channel hypothesis (**b**). The point marked as an asterisk in **a** was not included in the linear regression analysis (least-squares fits to the data) shown on the graph. The movement time for this experimental configuration was 45 ms slower than that predicted by the linear fit. The slower movement time can be accounted for by the presence of a ceiling effect (see text for details). It should be noted that the presence of a ceiling effect for this configuration does not alter the conclusions. Compare **a** and **b** with the left- and right-hand columns of Fig. 2. It is clear that there is excellent qualitative agreement between Fig. 2a and b and **a** and **b**, respectively. The results thus favour the visuomotor channel hypothesis over the digit channel hypothesis

digits began and finished together. It is clear that the empirical data correspond to the left-hand column of Fig. 2 when Fig. 2a and Fig. 2b are compared with Fig. 3a and Fig. 3b, respectively. The data plotted in Fig. 2a were well described by a linear fit apart from one point that indicated a MT that was 45 ms slower than that predicted from the linear fit (this point was excluded from the fit shown in Fig. 3). This point corresponds to the condition in which the index finger's obstacle was furthest away and the object was at 30 cm. The slower time can be explained by the presence of a ceiling effect, where the distance to be reached and the presence of an obstacle on the side of the thumb place constraints on the speed of the movement regardless of the distance away of the obstacle on the side of the index finger. It should be noted that this ceiling effect does not affect the conclusions in any way – in fact, the MT predicted from the linear fit in Fig. 3a would improve the quantitative similarity between Fig. 3b and Fig. 2b. Nonetheless, the qualitative similarity between Fig. 3b and Fig. 2b is particularly striking, with the empirical data closely following the predicted pattern of results. The results thus strongly support the visuomotor channel hypothesis over the digit channel hypothesis.

Discussion

Our results are highly suggestive: the empirical data strongly support the visuomotor channel hypothesis. The MT for reaching out and grasping the object was well predicted by the total width of the aperture between the two obstacles. In contrast, the mean ID of the target aperture for the finger and thumb did not predict MT. It should be noted that the ID for the thumb was held constant; it follows that the MT could not be predicted from a consideration of the ID of the target aperture for the thumb, finger or the mean ID. Notably this is not true for bimanual tasks where the limb movements are well described by a Fitts' law relationship involving the mean ID of the two targets (see Wann et al. 1998 for a discussion of the data currently submitted for publication).

In the Introduction we highlighted various advantages that the digit channel hypothesis holds over the visuomotor channel account. Our findings raise the question of whether the empirical data must force us to “abandon the baby together with the somewhat dirty bathwater”? We suggest that this may not be necessary and would like to propose an alternative hypothesis that retains many of the digit channel features within the visuomotor channel framework. We will call the alternative account the “third-way” hypothesis. According to the digit channel hypothesis, both the thumb and the index finger are being transported when carrying out a precision grip. Let us suppose, however, that the nervous system is concerned with transporting just one digit to the object and that the actual digit selected depends upon the task in hand. For example, imagine reaching for the wine glass with the bottle of Claret on the thumb side but nothing on the other side of the glass. In this situation it is likely that the gap between the glass and the bottle will be foveated. We suggest that the system would then programme a movement to transport the thumb to the foveated location. Alternatively, the bottle might be located on the index finger side of the glass and this gap is then fixated. In this case the system might choose to programme a transport trajectory for the index finger. Note that in both of these situations the visuomotor channel controlling the grasp aperture formation will ensure that the distance between the digits is sufficient for grasping the object whilst avoiding any obstacles within the workspace. If an obstacle is located on either side of the wine glass then the system can chose to fixate either gap (perhaps selecting the smallest) and move the appropriate digit to the gap (it is likely that the system will also slow the whole movement down; Tresilian 1998). This organisation need not depend upon moving to the point of fixation – the system might chose to move the selected digit to a non-fixated point – although there are clear advantages to moving to a point of foveation. Wing and colleagues (Wing and Fraser 1983; Wing et al. 1986) have previously suggested that it is the tip of the thumb that is transported, but Smeets and Brenner (1999) have pointed out that there is equal evidence for the system transporting the tip of the index finger. Clearly, the third-way hypothesis suggests why some evidence points towards transport of the thumb whilst other evidence suggest that it is the index finger that is transported. It is possible, of course, that individuals have a strong bias towards using one digit or another – our hypothesis merely says that it is one or the other. Smeets and Brenner (1999) have highlighted the advantages of ensuring that the approach path is perpendicular to an object's surface when grasping. The third-way hypothesis is consistent with their insight into the nature of the approach trajectories generated by the system. The third-way hypothesis also retains one of the very attractive features of the digit channel hypothesis: namely, it allows transport movements to be modelled using the minimum-jerk criterion (or any other control theory for pointing movements). Note that the anatomical dependency between the thumb and the index finger ensures that any movement programmed for the transport of one digit will produce a similar but slightly different movement profile for the other digit. It follows that ensuring an optimally smooth movement for one digit will produce a reasonably smooth movement of the other. This observation accounts for the success achieved by Smeets and Brenner (1999) when modelling the movement of the two digits using the minimum-jerk model but explains why there are asymmetries in the velocity profiles of the two digits (their model cannot account for these asymmetries). It should be noted that the experimental results reported within the current manuscript provide no evidence for the third-way hypothesis; the hypothesis is an a posteriori account that retains some of the attractive features from two opposing accounts of prehensile organisation.

In summary, the empirical data favour the visuomotor channel hypothesis over the digit channel hypothesis. Nonetheless, it is possible to retain many of the very attractive features of the digit channel hypothesis within an alternative account that we have christened the third-way hypothesis. According to this hypothesis, the system transports either the tip of the thumb or the tip of the index finger with the grip formation being controlled relatively independently. We envisage that the system programmes a movement between the effector and the point of attention (generally the point of fixation) on an object. We are currently testing this model in order to discover whether it provides an elegant account of how prehensile movements are controlled or whether it should be consigned to galaxies many megaparsecs from here.

Acknowledgements We are grateful to James Tresilian for his insights into Fitts' law and to Yves Rossetti for reminding us that there is often a third way.

References

Fitts PM (1954) The information capacity of the human motor system in controlling the amplitude of movement. J Exp Psychol 47:381–391

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

Jackson SR, Jackson GM, Rosicky J (1995) Are non-relevant objects represented in working memory? The effect of non-target objects on reach and grasp kinematics. Exp Brain Res 102: 519–530

Jeannerod M (1988) The neural and behavioural organization of goal-directed movements. Oxford University Press, Oxford

Langolf GD, Chaffin DB, Foulke JA (1976) An investigation of Fitts' law using a wide range of movement amplitudes. J Mot Behav 8:113–128

Paczynski B (1999) The devil is in the distance. Nature 401:331–332

Smeets JBJ, Brenner E (1995) Perception and action are based on the same visual information: distinction between position and velocity. J Exp Psychol Hum Percept Perform 21:19–31

Smeets JBJ, Brenner E (1999) A new view on grasping. Mot Control 3:237–271

Tresilian JR (1998) Attention in action or obstruction of movement? A kinematic analysis of avoidance behavior in prehension Exp Brain Res 120:352–368

Wann JP, Mon-Williams M, Carson RG (1998) Assessing manual control in children with coordination difficulties. In: Connolly K (ed) The psychobiology of the hand. Cambridge University Press, Cambridge, pp 213–229

Wing AM, Fraser C (1983) The contribution of the thumb to reaching movements. Q J Exp Psychol 35:297–309

Wing AM, Turton A, Fraser C (1986) Grasp size and accuracy of approach in reaching. J Mot Behav 18:245–260