

- auditory responses to saccades *J. Neurophysiology* 49, 1230–1253
- 82 Petersen, S.E., Robinson, D.L. and Keys, W. (1985) Pulvinar nuclei of the behaving rhesus monkey: visual responses and their modulation *J. Neurophysiol.* 54, 867–886
- 83 Kastner, S., De Weerd, P., Desimone, R. et al. (1998) Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI *Science* 282, 108–111
- 84 Leeper, R. (1935) A study of a neglected portion of the field of learning – the development of sensory organization *J. Gen. Psychol.* 46, 41–75
- 85 Reynolds, R.I. (1985) The role of object-hypotheses in the organization of fragmented figures *Perception* 14, 49–52
- 86 Gregory, R.L. (1997) *Eye and Brain: The Psychology of Seeing* (5th edn), Princeton University Press
- 87 Carpenter, R.H.S. (1999) A neural mechanism that randomises behavior *J. Conscious. Stud.* 6, 13–22
- 88 Hanes, D.P. and Schall, J.D. (1996) Neural control of voluntary movement initiation *Science* 274, 427–430
- 89 Ellis, S.R. and Stark, L. (1978) Eye movements during the viewing of Necker cubes *Perception* 7, 575–581
- 90 Sabrin, H.W. and Kertesz, A.E. (1980) Microsaccadic eye movements and binocular rivalry *Percept. Psychophys.* 28, 150–154
- 91 Ditchburn, R.W. and Pritchard, R.M. (1960) Binocular vision with two stabilized retinal images *Q. J. Exp. Psychol.* 12, 26–32
- 92 Pritchard, R.M., Heron, W. and Hebb, D.O. (1960) Visual perception approached by the method of stabilized images *Can. J. Psychol.* 14, 67–77
- 93 Blake, R.R., Fox, R. and McIntyre, C. (1971) Stochastic properties of stabilized-image binocular rivalry alternations *J. Exp. Psychol.* 88, 327–332
- 94 Wade, N.J. (1973) Binocular rivalry and binocular fusion of after-images *Vis. Res.* 13, 999–1000
- 95 Britten, K.H., Newsome, W.T., Shadlen, M.N. et al. (1996) A relationship between behavioral choice and the visual responses of neurons in macaque MT *Visual Neurosci.* 13, 87–100
- 96 Celebrini, S. and Newsome, W.T. (1994) Neuronal and psychophysical sensitivity to motion signals in extrastriate area MST of the macaque monkey *J. Neurosci.* 14, 4109–4124
- 97 Thiele, A. and Hoffmann, K.P. (1996) Neuronal activity in MST and STPp, but not MT, changes systematically with stimulus-independent decisions *NeuroReport* 7, 971–976
- 98 Crick, F. and Koch, C. (1995) Are we aware of neural activity in primary visual cortex? *Nature* 375, 121–123
- 99 Crick, F. and Koch, C. (1998) Consciousness and neuroscience *Cereb. Cortex* 8, 97–107
- 100 Wolfe, J.M. (1984) Reversing ocular dominance and suppression in a single flash *Vis. Res.* 24, 471–478
- 101 Sheinberg, D.L. and Logothetis, N.K. (1997) The role of temporal cortical areas in perceptual organization *Proc. Natl. Acad. Sci. U. S. A.* 94, 3408–3413

Mechanisms of selection for the control of hand action

Umberto Castiello

Most attention research has viewed selection as essentially a perceptual problem, with attentional mechanisms required to protect the senses from overload. Although this might indeed be one of several functions that attention serves, the need for selection also arises when one considers the requirement of actions rather than perception. This review examines recent attempts to determine the role played by selective mechanisms in the control of action. Recent studies looking at reach-to-grasp responses to target objects in the presence of distracting objects within a three-dimensional space are discussed. The manner in which motor aspects of the reach-to-grasp response might be influenced by distractors is also highlighted, rather than merely addressing the perceptual consequences of distractors. The studies reviewed here emphasize several factors highlighting the importance of studying selective processes within three-dimensional environments from which attention and action have evolved.

Visual attention is one mechanism that enables us to select relevant objects and spatial locations over less important ones. Visual attention has been the target of extensive research, but despite this large amount of interest our understanding of some aspects of selective behaviour remains unclear. For instance, little is known about the limits governing the brain's ability to process information presented in parallel for the control of action towards three-dimensional (3D) stimuli.

Traditionally, selective attention research in cognitive psychology has been based on very brief presentations of two-dimensional (2D) stimuli (alphanumeric characters) on computer screens or tachistoscopes. This form of testing typically restricts attentional measurement to arbitrary and indirect responses such as key-presses or verbal naming^{1,2}. However, the emergence of more powerful methods for the investigation of these mechanisms within 3D environments

U. Castiello is at the Department of Psychology, The University of Melbourne, 3052, Parkville, Victoria, Australia.

tel: +61 3 93 444303
fax: +61 3 93 476618
e-mail: u.castiello@psych.unimelb.edu.au

has allowed a shift in focus from theoretical discussion to a more integrative approach that considers selection of stimuli for the control of overt action.

Although there is little doubt that perceptions can flow automatically into actions, one possible problem, as highlighted by Neumann, is 'how to avoid the behavioural chaos that would result from an attempt to simultaneously perform all possible actions for which sufficient causes exist' (Ref. 3, p. 374). In other words, if unrestrained, the perception-for-action system would result in chaotic behaviours that are unrelated to behavioural goals. Selective attentional mechanisms would thus serve to specify parameterization for the action towards a particular object and to reject action parameterization for irrelevant objects.

This aspect of the selective integration problem has been defined as 'selection-for-action'⁴. For example, when choosing a piece of fruit from a bowl, many fruits are visible and within the reaching space but only the one that we desire governs the particular pattern and direction of movement. How is the motor output for reaching and grasping that particular fruit selected? Where is the locus of this selection? Do the other fruits, different in size, shape, colour and weight produce interference? Of course the suggestion that selection-for-action is related to an object-level representation is not new, with this notion being incorporated within the concept of an object file⁵. However, the object-file analogy does not specify how motor information is assigned to one, among several, concurrently active object files.

I will focus my discussion on recent studies examining more natural reach-to-grasp tasks⁶ that involve responding to a target, within a 3D space, in the presence of distracting objects^{7–13}.

The role that selective attention plays during the control of an action, such as reaching-to-grasp, suggests that attention needs to access object representations that provide information for the coding of volumetric boundaries, which is necessary for positioning the fingers appropriately on the object. Thus, the frame of reference upon which attention functions might be related to volumetric object representations as well as to the behavioural goal of the task.

Several studies have now shown that selecting a target for grasping in the presence of a distractor object leads to interference effects on movement kinematics. In the following sections, I will review these effects with an emphasis on models that have been proposed to select for action objects that are behaviourally relevant rather than behaviourally non-relevant objects. In particular, I will propose a model of response selection for the reach-to-grasp movements which suggests that selective spatial attention mediates selection for action. This will be compared with an alternative model based on inhibitory mechanisms⁸.

The interaction between spatial attention and response selection

Paradigms in which the reach-to-grasp action is performed at a normal or 'natural' speed have been used extensively by us^{11,12}. A warning signal was given, and, after a variable interval, a movement was initiated on illumination of a target. When the location and identity of the object were known in

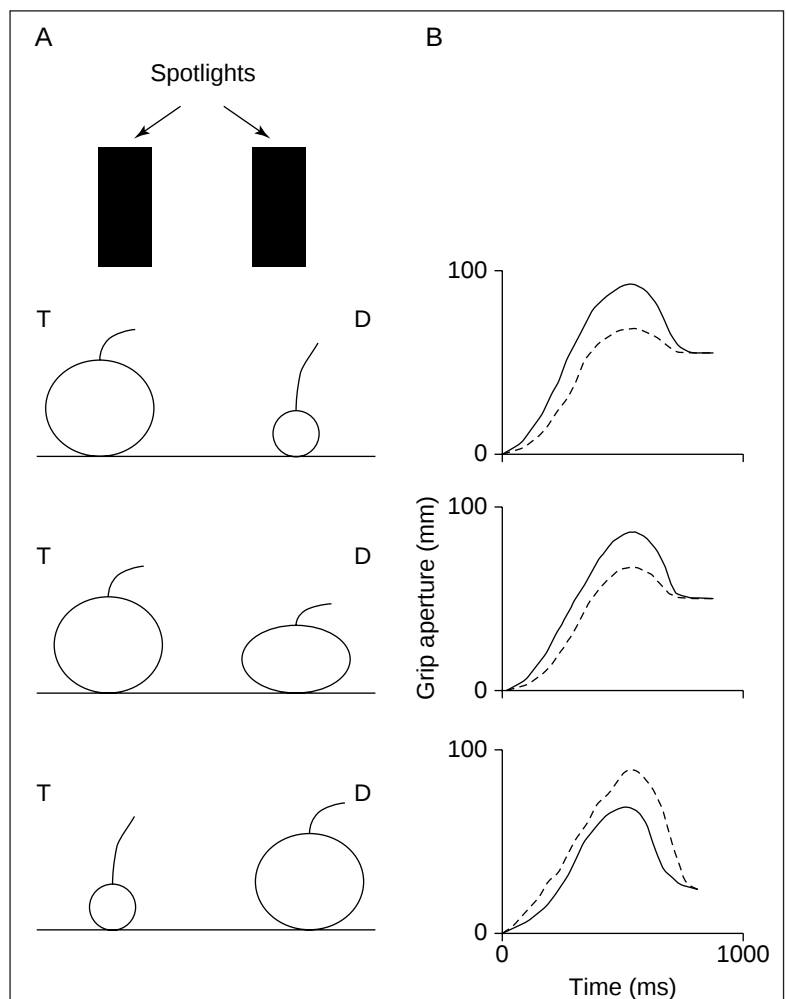


Fig. 1. The dual-task procedure in a grip-aperture task. (A) The dual-task experimental condition, depicted schematically, shows target (T) fruits presented with distractor (D) fruits. The primary task was to reach and grasp the central target fruit while maintaining gaze fixation of this same fruit. The secondary task was to count the number of times that a laterally placed distractor fruit was highlighted, and then report this count at the end of the trial. A warning tone was given and then the subject was required to start movement when the central target fruit was highlighted. In a single target control condition, which allows baseline assessment, the secondary task did not have to be performed. **(B)** The amplitude of peak grip aperture to the target was influenced by the type of distractor. If the central target fruit was an apple (dotted line) than when the cherry was grasped in isolation (solid line). Conversely, the amplitude of peak grip aperture for the grasp of an apple (top) was reduced when the lateral fruit was a mandarin (centre) or a cherry (bottom) compared with when the apple was grasped in isolation. Furthermore, when the subject had to perform the secondary 'counting' task when the primary and the secondary task were executed upon the same object, interference effects were not revealed (not shown). (Data redrawn from Ref. 11.)

advance, irrespective of whether the distractors were presented lateral to the target, midsagittally or close to the hand, no alterations in kinematic parameters were evident^{9,11,12}. In addition, no interference effects were found when the distractor was stationary, as opposed to moving, and did not require a direct computation¹².

A double-task procedure, as shown in Fig. 1, has also been developed¹¹. Participants reach to grasp a target while counting the number of times a spotlight illuminated a distractor object. Under these circumstances the characteristics of the distractor did interfere with the kinematics of the reach-to-grasp movement (Fig. 1). Interference, however, only occurred when attention was directed to a lateral non-target distractor, although eye movements were

Box 1. Effects of attentional impairments on the planning and control of hand movements

Important insights into how the attentional selection of action might operate can usefully be drawn from the study of brain-injured patients. For example, several papers have investigated how hand-path curvature is or is not increased in neglect patients (Refs a–d), and how the presence of a distractor object affects the reaching-to-grasp action towards a target in patients with frontal lobe damage (Ref. e). Results from some of these studies are summarized below.

Chieffi *et al.* investigated the effect of attentional impairments on the planning and control of hand movements in a patient with unilateral neglect (Ref. a). The patient reached and grasped targets in the presence of distractors placed either to the right or left side. Both target and distractor were presented to the same side of the right hand. The patient did not show misreaching, although her hand trajectory deviated abnormally towards the distractor position when the distractor was ipsilateral to the target.

More recently Jackson *et al.* were able to show that the reaches of three neglect patients had a more curved trajectory to visually defined targets compared with when the same targets were defined proprioceptively. These authors therefore argue that abnormal hand paths in neglect result from an impairment in the visual representation of space used to guide reaches. Further, they propose that the curved hand paths reveal exactly how the topography of that representation is distorted in spatial neglect.

Riddoch and colleagues studied reaching-for-grasp responses to a cup in a patient with frontal lobe damage (Ref. e). In one task the patient was instructed to respond with the hand congruent with the location of the cup, irrespective of the position of the handle. It was found that the patient had difficulty in suppressing a response to the 'affordance' of the object (i.e. with the 'wrong' hand), determined by the position of the handle. In a second task, distractor effects were examined. The task now was to respond to the affordance of a central target cup, and a distractor cup (differing in colour) was placed in the reach trajectory. The position of the handle of the distractor cup could be congruent or incongruent with the handle of the target. Interestingly, the patient made errors by sometimes actually reaching to the

distractor rather than the target, but the hand used was always based on the 'affordance' of the target not the distractor. This was the case even though the patient sometimes used a hand incongruent with the affordance of the distractor (e.g. reaching with his right hand to pick up a distractor with a left-side handle, when the target's handle was on the right). Riddoch *et al.* argued that the patient attended to the target and that the grasp response was programmed to that object. However, a distractor in the reach trajectory could also be attended as the action was initiated; thus there was a transference of the grasp activated by the target to the distractor.

These studies support the notion that visual attention serves to control action, such that actions are programmed for attended objects, whether these objects are targets or distractors. Given the attentional bias for the side ipsilateral to the lesion in neglect patients, the evidence of interference effects found for distractors positioned on the ipsilesional side in neglect patients suggests that, when distractors receive more attention, interference effects during the reaching become more evident. Similarly, under conditions of disinhibition, as can occur with frontal-lobe dysfunction, if a distractor is attended it is very difficult to resist the strong motor response elicited by the distractor object.

References

- a Chieffi, S. *et al.* (1993) Study of selective reaching and grasping in a patient with unilateral parietal lesion: dissociated effects of residual spatial neglect *Brain* 116, 1119–1137
- b Jackson, S.R. *et al.* Reaching movements may reveal the distorted topography of spatial representations in neglect *Neuropsychologia* (in press)
- c Milner, A.D. and Harvey, M. (1995) Distortion of size perception in visuospatial neglect *Curr. Biol.* 5, 85–89
- d Karnath, H., Dick, H. and Konczak, J. (1997) Kinematics of goal-directed arm movements in neglect: control of hand in space *Neuropsychologia* 35, 435–444
- e Riddoch, M.J., Humphreys, G.W. and Edwards, M.G. Visual affordances and object selection, in *Attention and Performance XVIII* (Monsell, S. and Driver, J., eds), MIT Press (in press)

precluded. Apparently, the programming of hand movements can be influenced by attended information in the visual field, which is independent of eye movements. Distractor interference during prehension movements can be augmented when the distractor attracts more attention. Support for this latter conclusion can be drawn from the study of brain-injured patients. For example, in considering patients with neglect, who have an attentional bias towards the ipsilesional side, the evidence of interference effects found for distractors positioned on that side suggests that, when distractors receive more attention, interference effects during reaching become more evident (see Box 1).

Using another dual-task paradigm (Fig. 2), the role of overt and covert attention in the manifestation of distractor interference effects was further investigated. In this series of experiments, the target was positioned midsagittally and the distractor was monitored either overtly or covertly. The most consistent finding was that interference effects were evident only when eye movements were fixed on the target and when the distractor was moving. Moreover, interference effects in the grasp, but not in the reaching parameters, were observed only when the distractor was smaller than the target and could potentially become the target by a change in illumination (Fig. 2). This implies that the intrinsic features of a distractor (such as its size), and not simply the extrinsic feature

of location, might elicit competing responses and thus have a selective influence on kinematic parameterization.

These findings all suggest that interference effects are dependent upon a shift in covert attention. Furthermore, with the exception of dual task demands on different objects, the distractor does not influence the computation of the motor program that is related to the target. Put simply, execution of a reach-to-grasp movement is altered when two selection processes refer to different objects. Information gained from the distractor appears to influence the attention-for-motor action pathways. In this view, visual attention serves to control the selection of information for action so that actions are only programmed for attended objects¹⁴. Distractor effects occur on occasions when these items are attended (see Box 1 for neurophysiological evidence consistent with this).

These data on interference effects on grasp responses suggest that attentional coding for boundaries is necessary either for positioning the fingers appropriately on an object, or to access object representations that include volumetric coding. In either case, a 3D object-based representation for action control might be required. Here, the question of what constitutes an object might be taken from the point of view of the attentional system. Certainly it appears that 'objecthood' is not only a matter of perceptual visual

complexity, but also a matter of volumetric coding for the fulfillment of action requirements. Therefore, different objects in the visual field might compete in terms of their structure or dimension as well as in terms of other features such as position, orientation and colour. For example, a projected 2D shape might compete in terms of its size and position in space but not on the basis of its graspable attributes. In this respect, a 3D distractor would certainly be more effective. If this is the case, interference in movement kinematics in, for example, a reach-to-grasp movement, would selectively affect different segments of the action depending on whether the distractor is 2D or 3D.

The distinction between 2D and 3D objects could be an important issue; this differentiation might reflect voluntary 'top-down' determinants of what constitutes an object, including those attributes relevant for action control.

Differential attentional coding for 3D and 2D distractors

The issue of dimensionality relating to graspable attributes of the stimuli has been investigated¹⁵ (Fig. 3). Evidence that dimensionality might be relevant for the coding of relevant and irrelevant information derives from neurophysiological studies. Recently, a group of neurons in the posterior parietal cortex of the monkey has been identified that codes for the 3D structure of objects¹⁶. In particular, the neuronal response varied for different object thicknesses. These surface orientation selective neurons (SOS) were localized in the lateral bank of the caudal part of the inferior parietal sulcus, in the dorsal (spatial) stream of the cortical visual pathway. Thus, in contrast to the idea that object vision is a 'ventral' activity¹⁷, these findings suggest that the dorsal stream might also be involved in the coding of the 3D structure of objects. This hypothesis is consistent with the idea that the dorsal pathway is important for the integration of the perception and action systems¹⁸. The activity of the SOS neurons might be useful for the visual guidance of hand movements, particularly for adjustments of the hand to the surface of an object to be grasped or manipulated.

Shifting covert attention to different faces of a 3D distractor might produce different effects on the kinematics of action to a target, with interference being selectively channelled¹¹. When the distractor is 3D, both the reach and the grasp components are affected; the 3D distractor appears to compete in terms of the grasping action required, as a result of the presence of intrinsic volumetric properties. When the distractor is

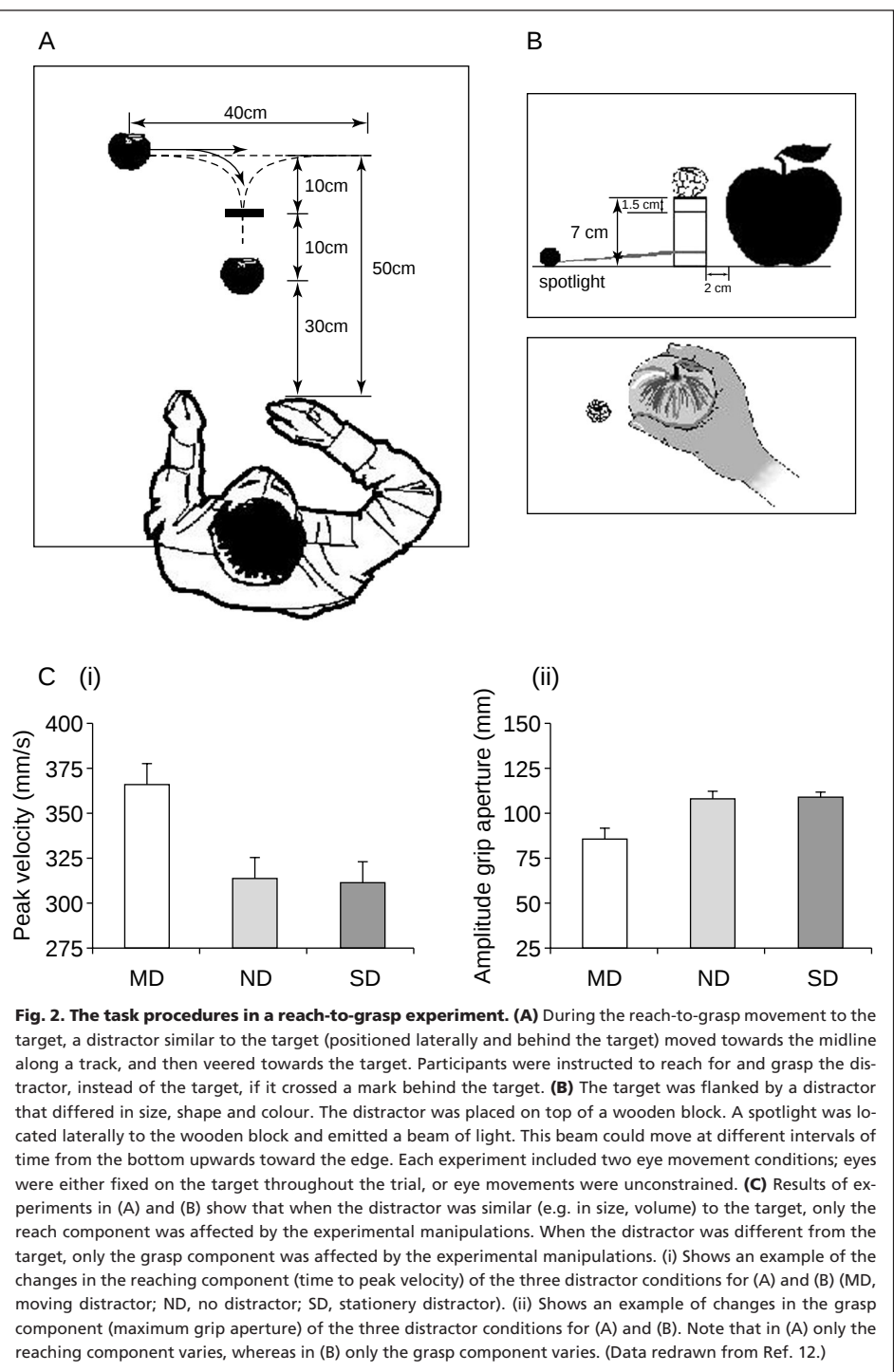
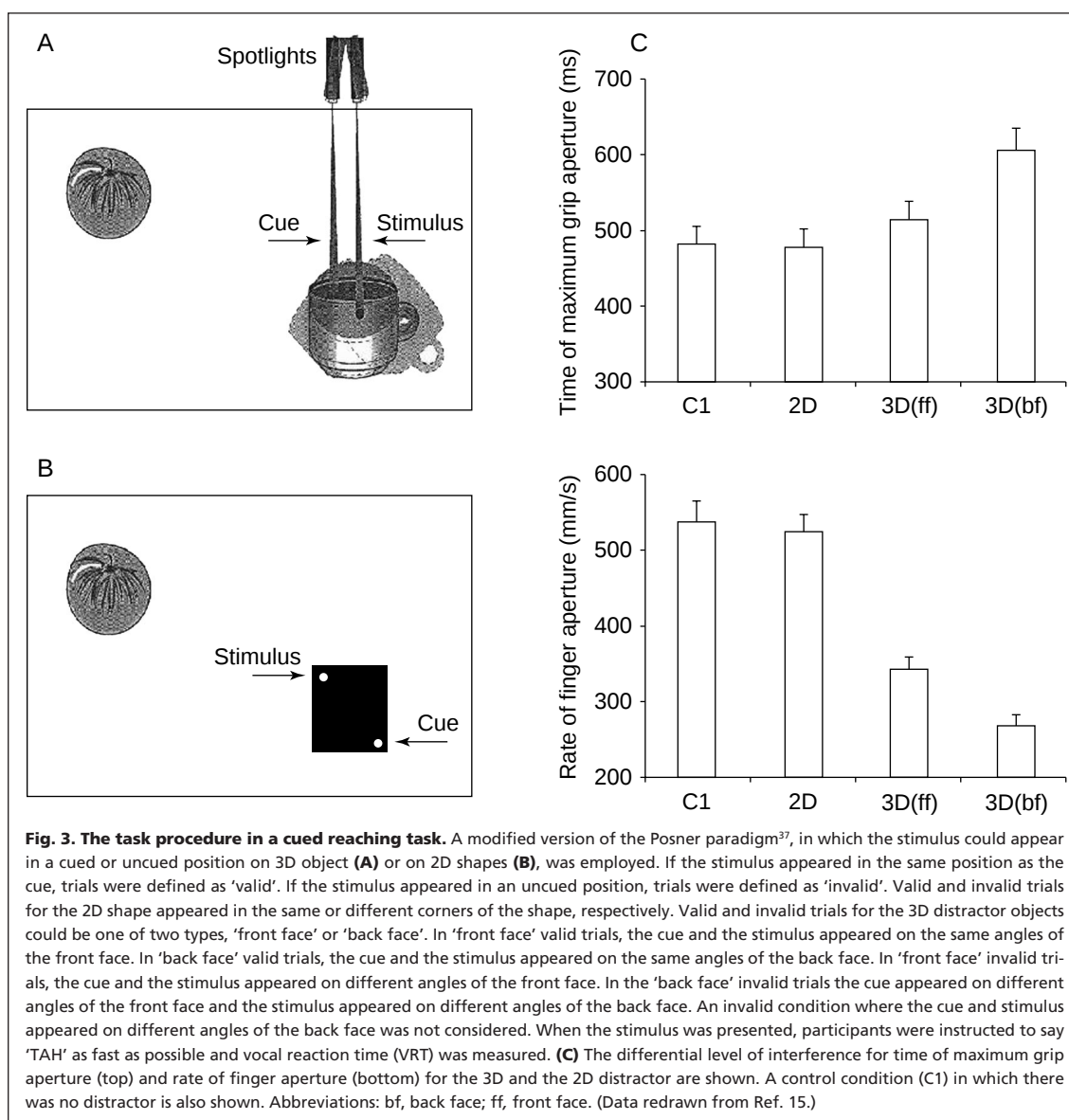


Fig. 2. The task procedures in a reach-to-grasp experiment. (A) During the reach-to-grasp movement to the target, a distractor similar to the target (positioned laterally and behind the target) moved towards the midline along a track, and then veered towards the target. Participants were instructed to reach for and grasp the distractor, instead of the target, if it crossed a mark behind the target. (B) The target was flanked by a distractor that differed in size, shape and colour. The distractor was placed on top of a wooden block. A spotlight was located laterally to the wooden block and emitted a beam of light. This beam could move at different intervals of time from the bottom upwards toward the edge. Each experiment included two eye movement conditions; eyes were either fixed on the target throughout the trial, or eye movements were unconstrained. (C) Results of experiments in (A) and (B) show that when the distractor was similar (e.g. in size, volume) to the target, only the reach component was affected by the experimental manipulations. When the distractor was different from the target, only the grasp component was affected by the experimental manipulations. (i) Shows an example of the changes in the reaching component (time to peak velocity) of the three distractor conditions for (A) and (B) (MD, moving distractor; ND, no distractor; SD, stationary distractor). (ii) Shows an example of changes in the grasp component (maximum grip aperture) of the three distractor conditions for (A) and (B). Note that in (A) only the reaching component varies, whereas in (B) only the grasp component varies. (Data redrawn from Ref. 12.)

a 2D projected shape the reaching component is primarily affected. This 2D shape does not seem to be considered as a graspable object by the perceptual-motor system, or as having functional graspable units; consequently, competition appears to be resolved only at the reaching component level.

A 'task-relevant' hypothesis can thus be proposed and distractors can be expected to interfere only when they share specific task-relevant properties. When grasping is the task, sharing different or similar graspable properties is critical; 2D shapes projected on the table-top do not share these properties. However, when both the 3D target and the 2D distractor are relevant to the task, interference emerges. Thus, the extent of interference on action is a function of whether



distractors compete with the target for computational resources, analysis and control.

Visual attentional selection for action control

Activation of the response to the target (and any distractor, when present) might be enhanced by spatial attention^{11,12}. The role of attention is to modulate the threshold for specific features within the mechanisms relevant for controlling the response process.

As interference effects occur when covert attention is oriented to the distractor, an orienting reaction such as an attentional shift might act as a precursor to selection for action. Attentional shifts towards the distractor might not only select the relevant object characteristics, but also direct such information to the visuomotor channels for any required modification. Attentional shifts might reflect the need for attention to be allocated to the target position before any arm movement is made. Thus, whenever visual attention is allocated to an object, its volumetric and spatial parameters are computed for eventual motor actions such as grasping. When visuospatial mechanisms are directed towards a distractor object, characteristics of that object might

be computed and interfere with those already established for the target object.

Therefore, I propose that covert and overt mechanisms of attention might play a mutual interactive role in the control of action. To some extent covert attention can be seen as a 'navigator' that provides information on the preliminary computations for trajectory formation. This navigator informs, on line, the 'pilot's' overt attention, with cues necessary to achieve a precise and smooth deceleration of the hand on the target¹⁹.

A consequence of this argument is that the direction of attention mediates the conversions between sensory and motor systems²⁰. Whether particular properties belong to the same or different objects is determined by directing attention appropriately. Directing attention towards the signals that are generated in different sensory areas allows binding of different properties for the determination of a specific object¹⁹. It follows that the attentional system must be able to test for, and activate, the sensory-sensory conversions to verify these possible correspondences. Thus, the direction of attention towards the distractor might select the sensory-motor associations that are required for that

object. Interference emerges from competition for computing sensory coordinates for possible conversion to motor output.

Competition might also be sensitive to whether particular attributes of irrelevant objects match those of the relevant goal-directed object. The 3D distractor objects used in the studies mentioned above all required different types of prehension to the target object. Thus, parallel computations for different types of grasp, one for the target and one for the attended distractor, might be at the origin of the changes found for the kinematics of the action directed to the target. This view is supported by neurophysiological and behavioural evidence. With regard to the former, different neural populations subserve different types of grasp or given types of action^{21,22}. In the latter case, the kinematics differ for contrasting types of grasp. For instance, the time course of the manipulation component and its temporal relations with the transport component change according to the type of grasp^{11,23}. Conflicts can emerge when the distractor and target objects require different prehensile patterns, in order to be grasped or manipulated. Neuronal populations, kinematic planning and functional properties for an irrelevant distractor object can interfere with neuronal populations, kinematic planning and functional properties activated by and executed for the target object. In this view, distractors activate their responses without the participants' intention to act (e.g. see Ref. 24). Given this automatic process of converting perceptual input into the action afforded by the distractor objects, different objects in a visual scene can evoke the parallel implementation of actions^{25,26}. If more than one motor pattern is kept active simultaneously, this parallel activation determines mutual interference²⁷.

A model for selection based on inhibition mechanisms

Attention as a mechanism relevant to the representation of peripersonal space, and the idea that a reaching action is defined by the direction and distance between the origin of the hand and the target have been proposed^{7,8,28}. Reaching movements are planned within a hand-centred frame of reference rather than a head- or shoulder-centred frame of reference²⁹. Support for this claim comes from tasks in which the location of the target and the distractor is not known in advance, and hence attention can be assumed to be diffusely distributed across the scene. In such situations, distractors appear to compete for the control of action, interfering with the response to the target. These effects are evident on the spatial path of the hand as it reaches to a target (Fig. 4). The most important result of these studies is that the reach path veers towards, or away from the objects or locations whose representations should supposedly be inhibited by selective attention. In other words, when attention is anchored on the target object, inhibition acts on the representation of a potential distractor¹³: both target and distractor evoke parallel actions, and competition between these simultaneous responses is resolved by inhibition mechanisms⁸.

According to Tipper *et al.*⁸, neurophysiological findings might explain the effects on reaching trajectories. A study investigating neural responses in area 5 of the parietal cortex and the reaching actions subserved by the motor cortex suggests that the direction of movement is represented by a spe-

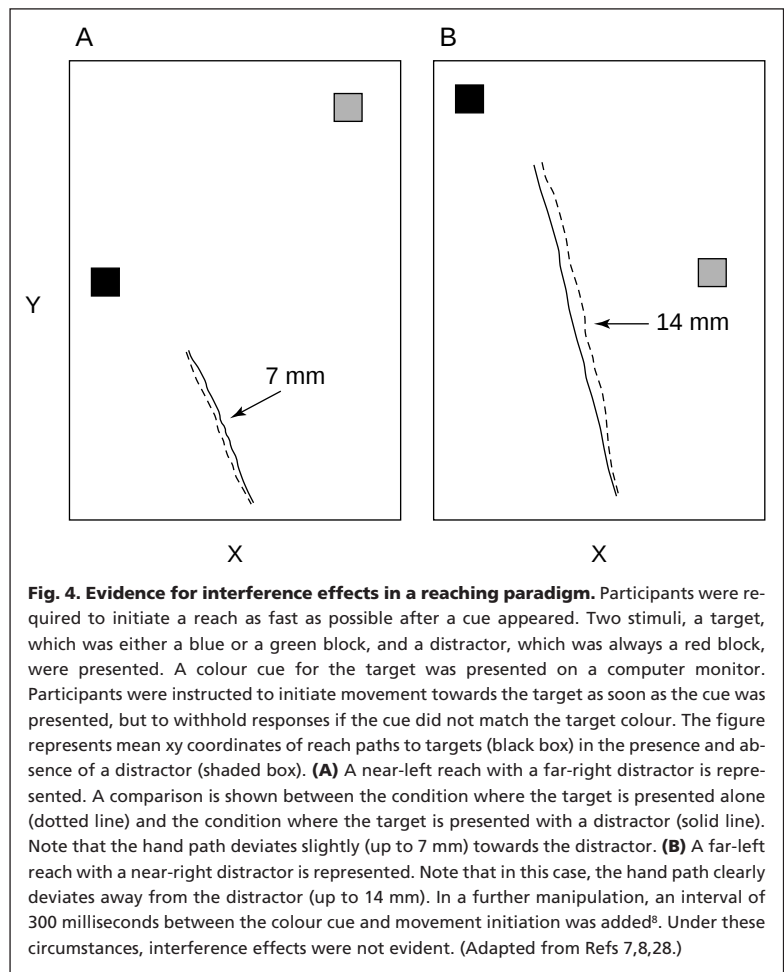


Fig. 4. Evidence for interference effects in a reaching paradigm. Participants were required to initiate a reach as fast as possible after a cue appeared. Two stimuli, a target, which was either a blue or a green block, and a distractor, which was always a red block, were presented. A colour cue for the target was presented on a computer monitor. Participants were instructed to initiate movement towards the target as soon as the cue was presented, but to withhold responses if the cue did not match the target colour. The figure represents mean xy coordinates of reach paths to targets (black box) in the presence and absence of a distractor (shaded box). **(A)** A near-left reach with a far-right distractor is represented. A comparison is shown between the condition where the target is presented alone (dotted line) and the condition where the target is presented with a distractor (solid line). Note that the hand path deviates slightly (up to 7 mm) towards the distractor. **(B)** A far-left reach with a near-right distractor is represented. Note that in this case, the hand path clearly deviates away from the distractor (up to 14 mm). In a further manipulation, an interval of 300 milliseconds between the colour cue and movement initiation was added⁸. Under these circumstances, interference effects were not evident. (Adapted from Refs 7,8,28.)

cific population of neurons³⁰. These neurons respond to varying degrees when movement to a particular direction is programmed. In particular, it is assumed that the direction of a reaching movement is determined by the sum of the single neurons that contribute to the population vector. Cells that do not respond to the direction of the reach, but respond in the opposite way, are inhibited relative to baseline level, a fact that is critical to the proposed adaptation of this model by Tipper *et al.* Thus, when the target is identified, the reach to the distractor is inhibited. The overlap between the neural activation for the target and the distractor determines interference effects.

The neurophysiological explanation is, however, very specific and concentrates only on modelling reaching. Certainly, this is a limiting factor when the action under investigation is reaching-to-grasp, in which the manipulation component is also involved. If neurophysiological speculations are to be made, other anatomical areas where both reaching and grasping neurons are recorded should also be considered. Cortical neurons related to visually guided reaching and grasping have been recorded in the inferior parietal lobe³¹. These neurons can be classified as arm-projection (reaching) and hand-manipulation neurons. Hand-movement neurons have also been shown to be concentrated in a small area within the rostral part of the posterolateral bank of the intraparietal sulcus designated as the anterior intraparietal area²¹. This latter area is connected with area F5 of the ventral premotor cortex in which grasping-with-the-hand neurons have been recorded²⁰.

In experiments where similar objects were used as the target and the distractor^{7,8,28}, it is possible that effects were found only for the reaching component of the movement. By inference, the use of target objects that differ from the distractor object from a functional and intrinsic point would, in principle, produce interference at the level of the grasping component (e.g. on finger trajectories). For example, if the distractor affords a different type of grasp from the target, competition between the two active grasp patterns would also determine interference–inhibition effects at the grasping level^{11,12}. In other words, if the grasp component is represented by a distributed population code, and if these neural populations can overlap for both a target and distractor grasp, then the same model of selection from population codes could apply.

This extrapolation points to the necessity for further research to determine whether, in these reach-to-grasp tasks, there is only a ‘reaching-location-based’ inhibition effect or a ‘grasping-object-based’ inhibition effect, which also depends on the intrinsic features of the distractor.

Finally, it has been suggested by Tresilian³² that changes in trajectory are not caused by selection mechanisms, but rather are a result of the distractor being a 3D obstacle that causes the hand to veer around it. This ‘obstacle avoidance’ account is suggested to be more parsimonious than the model describing inhibitory selection mechanisms acting upon population codes (e.g. Ref. 8). However, in my opinion, this theory is unable to explain large numbers of experimental observations that the population

code account explains easily. For example, the observation that when subjects are fixating at a central location, the reach trajectory is higher when a light-emitting diode is attended at that location cannot be explained by the obstacle avoidance account. Furthermore, the population-coding account³³ is a broad enough theory to explain not only deviations away from a distractor, but also deviations towards them; it also explains not just deviations of the hand, but also deviations of the eyes, which have not had any need to evolve mechanisms to avoid obstacles. Thus, the hand can veer towards a distractor while the saccade simultaneously deviates away from this same distractor. Accounts based purely on obstacle avoidance fail to explain such patterns of behaviour, which emerge quite naturally from population-code models. Other results based on reaction times (RTs) and movement-time data also discredit obstacle avoidance as the most parsimonious explanation. For example, it was shown that RTs are impaired less when the distractor is close to the reach path of the target than when off this path but close to the hand³⁴. Similarly, less distractor interference is exhibited when the distractor contains greater 3D structure, and is hence more of an obstacle than those distractors with little 3D structure³⁵. In summary, although distractors that are obstacles will cause reach path deviations, obstacle avoidance fails to account for all the data on selective reaching.

A final consideration regarding the Tresilian and Tipper models is that in order to compare them it is necessary to assume that it makes theoretical sense to distinguish between ‘obstacles’ and ‘attended objects’. In this regard, it has been maintained that, because external objects must be internally represented when planning actions, the distinction between ‘obstacles’ and ‘attended objects’ is unfounded (S. Jackson, pers. commun.). Describing something as an ‘obstacle’ or as a ‘distractor’ does not explain how we plan and control a hand trajectory past another object when reaching for a target.

Conclusions

The lines of evidence discussed in this review are largely compatible with theories that suggest a predominant role for attention in shaping behaviour by influencing motor output⁴. The suggestion, based on the effects of distractors upon the control of reaching-to-grasp movements, is that the perceptual response to the distractor might be enhanced by the shift of attention. More specifically, grasping interference effects suggest that access to the 3D representation of objects is necessary for action control of grasping. Furthermore, whether visual information can be attended to simultaneously also depends on functional and structural factors of the stimulus, such as affordances and depth structure.

Another point concerns whether inhibition mechanisms are evident not only in temporal measures such as reaction time but also on movement kinematics. This is an interesting issue that deserves further investigation¹³.

The selective action tasks presented in this review are quite different from the majority of the tasks that have been used classically to investigate selective attention. Perception did not evolve to support arbitrary and indirect responses, but rather to orient actions away from or towards objects

Outstanding questions

- How can the ‘ecological’ approach be adapted to allow measurement of the rapid and elusive information-processing system that mediates behaviour?
- Are the mechanisms that guide selection for arbitrary indirect (e.g. key-presses) and overt action responses the same thing? Are they completely unrelated? Do they overlap?
- Selective action is directed towards an object in its entirety. Therefore, the frame of reference upon which attention mechanisms act might also be specific for functional properties of the object. Does visual attention serve to control the selection of information for action (e.g. affordance of the selected object)?
- Can the notion of object-based attention be extended to propose that these mechanisms are influenced by the behavioural goal of the task?
- Although some of the critical factors accounting for the discrepant reach-to-grasp interference findings have been elucidated, others have not. What are the critical factors accounting for the following remaining discrepancies?
 - (i) Interference is reduced or absent when target and distractors are equidistant from the hand and interference is greatest when the distractor is closer to the hand than the target.
 - (ii) When information about the target is given in advance, interference is reduced. In other words, when a distractor’s location and features are known prior to movement initiation, interference effects would not arise because the selective attention, perception and action processes would already have been completed.
 - (iii) Spotlighting the target might give it such an advantage over the distractor, in terms of salience, that the distractor might be rendered ineffective.
 - (iv) Distractor interference might only be apparent in selective reaching when greater emphasis is placed on a highly speeded response, so that the selection of target over distractor has to take place during the reach itself.

within 3D environments. As pointed out by Marr³⁶, attentional processes can be best understood only within the specific environment where organisms evolve, and consequently only within the core of resultant behavioural requirements.

Acknowledgements

This work has been supported by an Australian Research Council grant to Umberto Castiello. I thank Alan Allport, Glyn Humphreys, Stephen Jackson, Steven Tipper and an anonymous referee for their useful comments on previous versions of this manuscript.

References

- 1 Eriksen, B.A. and Eriksen, C.W. (1974) Effects of noise letters upon the identification of a target letter in a non-search task *Percept. Psychophys.* 16, 143–149
- 2 Stroop, J.R. (1935) Studies of interference in serial verbal reactions *J. Exp. Psychol.* 18, 643–662
- 3 Neumann, O. (1987) Beyond capacity: a functional view of attention, in *Perspectives on Attention and Action* (Heuer, H. and Sanders, A.F., eds), pp. 361–394, Erlbaum
- 4 Allport, A. (1987) Selection-for-action: some behavioural and neurophysiological considerations of attention and action, in *Perspectives on perception and action* (Heuer, H. and Sanders, A.F., eds), pp. 395–419, Erlbaum
- 5 Kahneman, D. and Treisman, A.M. (1984) Changing views of attention and automaticity, in *Varieties of Attention* (Parasuraman, R. and Davies, D.R., eds), pp. 29–61, Academic Press
- 6 Jeannerod, M. (1984) The timing of natural prehension movements *J. Motor. Behav.* 16, 235–254
- 7 Howard, L.A. and Tipper, S.P. (1997) Hand deviations away from visual cues: indirect evidence for inhibition *Exp. Brain Res.* 113, 144–152
- 8 Tipper, S.P., Howard, L.A. and Jackson, S.R. (1997) Selective reaching to grasp: evidence for distractor interference effects *Visual Cognit.* 4, 1–38
- 9 Jackson, S.R., Jackson, G.M. and 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
- 10 Chieffii, S. et al. (1993) Study of selective reaching and grasping in a patient with unilateral parietal lesion: dissociated effects of residual spatial neglect *Brain* 116, 1119–1137
- 11 Castiello, U. (1996) Grasping a fruit: selection for action *J. Exp. Psychol. Hum. Percept. Perform.* 22, 582–603
- 12 Bonfiglioli, C. and Castiello, U. (1998) Dissociation of covert and overt spatial attention during prehension movements: selective interference effects *Percept. Psychophys.* 60, 1426–1440
- 13 Tipper, S.P., Howard, L.A. and Houghton, G. (1998) Action-based mechanisms of attention *Philos. Trans. R. Soc. London Ser. B* 353, 1385–1393
- 14 Riddoch, M.J., Humphreys, G.W. and Edwards, M.G. Visual affordances and object selection, in *Attention and Performance XVIII* (Monsell, S. and Driver, J., eds), MIT Press (in press)
- 15 Castiello, U. (1998) Attentional coding for three-dimensional objects and two-dimensional shapes: differential interference effects *Exp. Brain Res.* 123, 289–297
- 16 Shikata, E. et al. (1996) Selectivity of the parietal visual neurones in 3D orientation of surface of stereoscopic stimuli *NeuroReport* 7, 2389–2394
- 17 Ungerleider, L.G. and Mishkin, M. (1982) Two cortical visual systems, in *Analysis of Visual Behavior* (Ingle, D.J., Goodale, M.A. and Mansfield, R.J.W., eds), pp. 549–586, MIT Press
- 18 Goodale, M.A. and Milner, D.A. (1992) Separate visual pathways for perception and action *Trends Neurosci.* 15, 20–25
- 19 Paillard, J. (1982) The contribution of peripheral and central vision to visually guided reaching, in *Analysis of Visual Behavior* (Ingle, D.J., Goodale, M.A. and Mansfield, R.J.W., eds), pp. 549–586, MIT Press
- 20 Stein, J.F. (1992) The representation of egocentric space in the posterior parietal cortex *Behav. Brain Sci.* 15, 691–700
- 21 Rizzolatti, G. et al. (1988) Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements *Exp. Brain Res.* 71, 491–507
- 22 Sakata, H. et al. (1994) The parietal association cortex in depth perception and visual control of hand action *Trends Neurosci.* 20, 350–357
- 23 Gentilucci, M. et al. (1991) Influence of different types of grasping on the transport component of prehension movement *Neuropsychologia* 29, 361–378
- 24 Lhermitte, F. (1983) 'Utilization behaviour', and its relation to lesions of the frontal lobes *Brain* 106, 237–255
- 25 Eriksen, C.W. (1995) The flankers task and response competition: a useful tool for investigating a variety of cognitive problems *Vis. Cog.* 2, 101–118
- 26 Goldberg, M.E. and Segraves, M.A. (1987) Visuospatial and motor attention in the monkey *Neuropsychologia* 25, 107–118
- 27 Duncan, J. (1996) Cooperating brain systems in selective perception and action, in *Attention and Performance XVI* (Inui, T. and McClelland, J.L., eds), pp. 549–578, MIT Press
- 28 Tipper, S.A., Lortie, C. and Baylis, G.C. (1992) Selective reaching: evidence for action centred attention *J. Exp. Psychol. Hum. Percept. Perform.* 18, 891–905
- 29 Soechting, J.F. and Flanders, M. (1989) Sensorimotor representations for pointing to targets in three-dimensional space *J. Neurophysiol.* 62, 582–594
- 30 Georgopoulos, A.P. (1990) Neurophysiology of reaching, in *Attention and Performance XIII* (Jeannerod, M., ed.), pp. 849–859, Erlbaum
- 31 MacKay, W.A. (1992) Properties of reach-related neuronal activity in cortical area 7A *J. Neurophysiol.* 67, 1335–1345
- 32 Tresilian, J.R. (1998) Attention in action or obstruction of movement? A kinematic analysis of avoidance behavior in prehension *Exp. Brain Res.* 120, 352–368
- 33 Tipper, S.P., Howard, L.A. and Houghton, G. Behavioural consequences of selection from neural population codes, in *Attention and Performance XVIII* (Monsell, S. and Driver, J., eds), MIT press (in press)
- 34 Meegan, D.V. and Tipper, S.P. (1998a) Reaching into cluttered visual environments: spatial and temporal influences of distracting objects *Q. J. Exp. Psychol.* 5, 225–249
- 35 Meegan, D.V. and Tipper, S.P. Visual search and target directed action *J. Exp. Psychol. Hum. Percept. Perform.* (in press)
- 36 Marr, D. (1982) *Vision*, W.H. Freeman
- 37 Posner, M.I. (1980) Orienting of attention *Q. J. Exp. Psychol.* 32, 3–25

Coming soon to *Trends in Cognitive Sciences*

- How infants begin to extract words from speech, by P.W. Jusczyk
- Development of theory of mind and executive control, by J. Perner and B. Lang
- Visually timed action: time-out for tau? by J.R. Tresilian
- Embodiment: from fish to fantasy, by A. Clark
- Lessons from children with specific language impairment, by J.B. Tomblin and J. Pandich
- Reply from H. van der Lely