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Action-based mechanisms of attention

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Actions, which have effects in the external world, must be spatiotopically represented in the brain. The brain is capable of representing space in many different forms (e.g. retinotopic-, environment-, head- or shoulder-centred), but we maintain that actions are represented in action-centred space, meaning that, at the cellular level, the direction of movement is defined by the activity of cells. In reaching, for example, object location is defined as the direction and distance between the origin of the hand and the target. Most importantly, we argue that more than one task-relevant action can be evoked at any moment in time. Therefore, highly efficient selection processes that accurately link vision and action have had to evolve. Research is reviewed which supports the notion of action-based inhibitory mechanisms that select the target from competing distractors.

Keywords: attention; inhibition; response competition; action-based frames; population vectors

1. INTRODUCTION

It is apparent that vision and action systems evolved together to enable successful interactions with the environment, and that highly efficient vision–action systems have evolved in humans (see, for example, Gibson 1979). There is now abundant evidence that visual processes can flow automatically into actions, such that the latter can be evoked with little or no conscious intention to act (see, for example, Simon 1969; Bridgeman *et al.* 1979; Reason 1979; Duncan-Johnson & Koppell 1981; Norman 1981; Lhermitte 1983; Coles *et al.* 1985; Weiskrantz 1986; Goldberg & Segraves 1987; Gratton *et al.* 1988; Miller & Hackley 1992).

One of the drawbacks to such efficient vision–action systems is that, unrestrained, they would result in chaotic behaviour that is unrelated to behavioural goals. Under conditions of disinhibition, such as can occur with damage to the frontal lobes of the brain, the great propensity to respond to stimuli is released (see, for example, Lhermitte 1983). That is, the most dominant perceptual input captures action, and this varies haphazardly over time. Clearly, therefore, to exercise free choice and control it is essential that organisms have the capacity to resist the strongest response of the moment (Diamond 1990). Paradoxically, the best definition of voluntary action is those actions that can be suppressed.

Of course, one of the most striking features of the actual behaviour of higher mammals is its selectivity. Such selective behaviour is achieved because the many actions that are evoked by visual inputs are not released (and as we discuss here, it is also unlikely that all visual inputs in extremely complex environments are simultaneously processed to a point that they evoke action). Consider an apparently trivial task such as picking up a glass of beer from a table containing several other glasses, for example (see Tipper *et al.* 1992). How does the hand consistently reach one particular glass, given that each of the other glasses evokes a similar action? Extremely efficient mechanisms to achieve goals such as these have had to evolve. These selection mechanisms have been associated with the subjective phenomenon of attention, in which the mind selects from a multitude of available perceptual inputs, one for deeper contemplation and action (James 1890).

In psychologists' attempts to understand attention disparate issues have been addressed, such as the way in which attention can be moved from one spatial location to another to facilitate or inhibit perceptual processes (see, for example, Posner 1980), or how it searches complex environments for target objects (see, for example, Treisman & Gelade 1980). Our concern in this paper is with another specific issue: the medium of attention. That is, within which kinds of internal representation do selection processes occur (see Tipper & Weaver 1998)?

The experimental measures described here provide insights into both the medium of attention, and the mechanisms by which selection is achieved. There are three kinds of dependent measure that are taken. First, the interference effects caused by the presence of a distracting to-be-ignored object can be used to infer the kinds of internal representation achieved by the ignored object, and the medium or frame of reference within which selection takes place. The second measure of negative priming also enables us to infer the frame of reference of selection, and in addition, reveals which of a distractor's representations are associated with inhibition during selection. The third measure arises from ideas based on distributed neural representations for reaching behaviours. That is, ignored objects should influence the path of the hand as it reaches to a target.

There is increasing evidence that, depending on the behavioural goals of an organism, mechanisms of attention have access to different frames of reference. For example, when the task requires a saccade to a specific locus, inhibition is associated with a retinotopic frame of reference

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(Abrams & Pratt 1998). When the task requires detection of stimulus onset, the frame of reference in which inhibitory selection mechanisms are observed is environment-based (see, for example, Posner & Cohen 1984). When mobile objects are encountered, object-based frames are active, and inhibition can move with the object (Tipper *et al.* 1990, 1991, 1994).

The research to be reviewed here demonstrates that when the behavioural goal is to reach for an object, the frame of reference in which the objects are represented and on which selective inhibition mechanisms act, is hand-centred. This means that the location of an object is specified at the neuronal level in respect of the current location of the hand, and the movement required to apprehend the object from that location. The findings are incompatible with other frames of reference that might theoretically determine reaching behaviour, such as retinotopic-, environment-, head-, or shoulder-centred frames. Rather, it appears that within the constraints of a particular behavioural goal (e.g. picking up a glass) the actions which different objects evoke (afford) can automatically be encoded in parallel, and that competition and selection take place between these action-based representations.

2. INTERFERENCE EFFECTS

Figure 1 represents the stimuli used by Tipper and co-workers (1992). Participants were required to reach from the start location and depress the key adjacent to the red target light. The critical variable manipulated in this experiment was the location of interfering irrelevant yellow distractor lights. By examining the pattern of interference and negative priming produced by distractors it was possible to infer which internal representations guide selective behaviour in this task.

Although targets could appear in any location, we only discuss data for reaches to the middle row. When the starting position of the reaching hand was at the front of the display adjacent to the participant's hand (figure 1*a*) distractors in the front row produced significantly greater interference (23 ms) than those in the back row (4 ms). However, when the starting position of the hand was at the back of the board, the pattern of interference was completely reversed. Now distractors at the back of the board (near the participant's hand) produced greater interference (26 ms) than those at the front (2 ms) (figure 1*b*).

These results confirm that stimuli which are irrelevant to the participants' behaviour are automatically encoded in terms of the actions they evoke in a hand-centred frame of reference. The data cannot be explained in terms of visual frames of reference, such as retinal (Eriksen & Eriksen 1974) or viewer-centred frames (Downing & Pinker 1985), because visual input was held constant by maintaining fixation at the centre of the display. Similarly, the distractor interference effects cannot be explained in terms of other body-centred frames, such as head-centred (Andersen & Zipser 1988) or shoulder-centred (Soechting & Flanders 1989), because these body parts remained in essentially the same loci relative to the display whether the hand was at the front or the back of the board.

We therefore interpret our data in terms of a hand-centred race model. Reaches to near objects are initiated faster than to far objects. This advantage for more proximate movements has previously been demonstrated by Fitts & Peterson (1964), Glencross (1973) and Rosenbaum (1980) in adult subjects, and in infants who prefer to reach for the closer of two objects which subtend the same visual angle (Bower 1972). Faster responses are interpreted as reflecting quicker processing of the stimulus and its associated response.

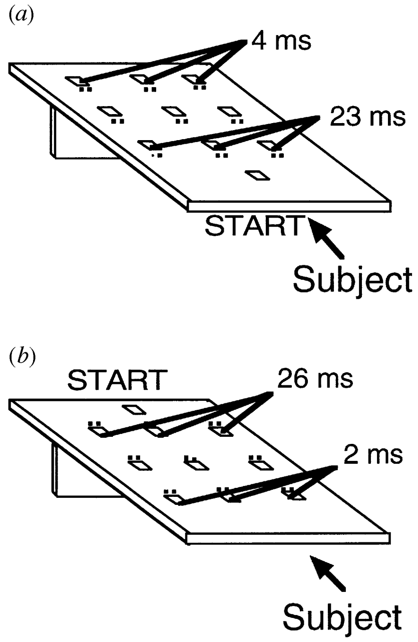

Figure 1. Stimulus board with keys, each accompanied by two light-emitting diodes (LEDs), used by Tipper *et al.* (1992). (*a*) Shows the start key close to the participant, (*b*) shows the start key far from the participant. (Not drawn to scale.)

The mechanisms that enable action to be directed to one object in the presence of other objects which evoke competing responses have been extensively debated. Our account suggests that there are dual mechanisms of attention (see, for example, Houghton & Tipper 1994). That is, as well as excitatory processes directed towards the target, there are also inhibitory processes directed towards the distractor. Houghton & Tipper (1994; Houghton *et al.* 1996) have argued that the inhibition mechanism is reactive, responding to the relative activation level of the distractor. In the present reaching tasks distractors close to the hand have greater levels of activation than those far from the hand, which is the reason for their greater interference with responses to the target. Hence, in this experiment, distractors closer to the responding hand than the target would be expected to cause high levels of interference because they win the race for the control of action, and so are harder to ignore, requiring greater levels of inhibition than distractors further from the hand than the target.

3. NEGATIVE PRIMING EFFECTS

Negative priming effects are thought to be one means by which the aforementioned inhibitory processes can be observed (see, for example, Neill 1977; Tipper 1985). The logic of the procedure is as follows: if the internal representations of a distractor are associated with inhibition during selection of the target, then processing of subsequent stimuli that gain access to or retrieve the same

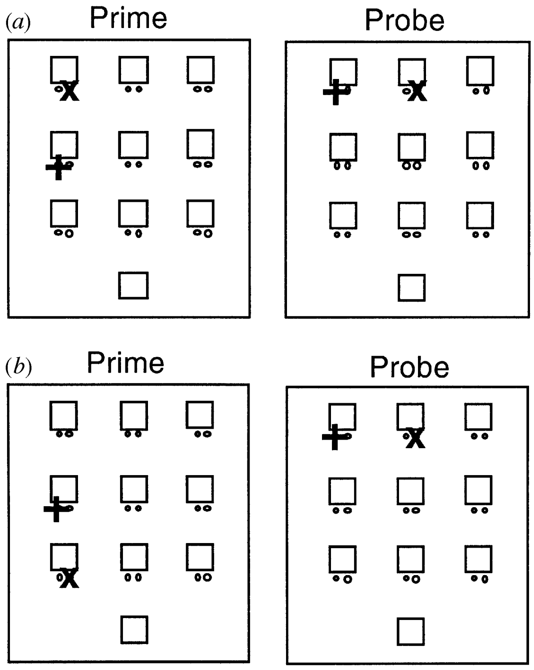

Figure 2. Negative priming procedure. Trials consist of prime and probe displays, each incorporating a red target (+) and yellow distractor (x). In the example, identical sequences of reach are shown (left, centre row in prime, and left, back row in probe). In (*a*) the ignored-repetition trials, however, the probe target is in the same location as the prime distractor, whereas in (*b*) the control trials it is not.

representations will be impaired. For example, if a picture of a dog is ignored while the participant attends to a picture of a table, processing the picture of the dog shortly afterwards will be impaired if the prior inhibitory processing is retrieved. In line with Houghton & Tipper (1994), inhibition reacts to the distractors' levels of excitation. Thus, distractors near to the responding hand will be associated with greater levels of inhibition, and hence negative priming will be greater for near than for far items.

The anticipated pattern of data was confirmed in a series of experiments by using a stimulus board similar to that shown in figure 1, and examples of the prime-probe sequence of trials are shown in figure 2. In the prime display of each trial, participants reached for a key adjacent to a red target light-emitting diode (LED), in the presence of a yellow distractor LED which they ignored. On the immediately subsequent probe display, participants again reached for the red target and ignored the yellow distractor. Comparisons were drawn between the time taken to reach for targets in probe displays which were in the same location as the prime distractor, and those in which the probe target was in a completely different location from any items in the prime display (see Tipper *et al.* 1992). Response time was longer in the former than the latter condition, which is the negative priming effect. Importantly, negative priming was greater for distractors closer to the responding hand (32 ms against 15 ms when the hand was at the front of the board, and 22 ms against 12 ms when the hand was at the back of the board).

Therefore the negative priming effects confirm the interference effects. The distractors compete and are inhibited in a hand-centred frame. All other frames (for example, retinal-, viewer-, head- and shoulder-centred) were held constant whether the hand was at the front or back of the board. Hence these frames cannot account for the dramatic changes in interference and negative priming that occur with different starting positions of the hand.

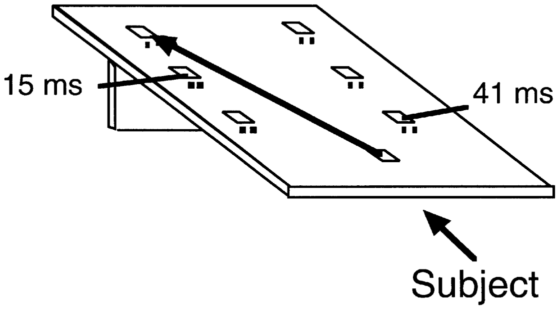

Figure 3. Interference effects of a distractor on the hand path (15 ms) and of one close to the start point of the hand (41 ms) in reaches to the far-left target.

4. FURTHER EVIDENCE FOR HAND-CENTRED FRAMES

As discussed, distractors between the responding hand and target object produce most interference effects and require substantial levels of inhibition for successful action. There are two possible reasons why such results are observed. First, it could be that interference is caused because the distractor is in the reach path as the hand moves towards the target. Hence the problem is one of preventing action being captured by the distractor as the hand approaches and passes it (Tipper *et al.* 1992; Pratt & Abrams 1994). Alternatively, the proximity of the distractor to the action path may not be the main source of the interference effects. Rather, all the effects could be determined simply by the initial distance between the distractor and the responding hand. The closer the distractor to the hand, the greater the interference effects produced by it when reaching for a more distant target. As discussed, the action-based model described predicts that the distance between object and hand is the main factor determining the size of the interference effects produced by the object.

Experiments by Meegan & Tipper (1998*a*) have investigated this issue in displays similar to that of figure 3. Consider reaching for the far-left target. If interference is caused because the distractor is close to the path the hand takes to the target, then particular patterns of interference are predicted. For example, a distractor adjacent to the target on the reach path (middle row, left side) should produce greater interference than a distractor that is close to the starting position of the hand, but not on the reach path (near-right key). This is because the former distractor is spatially close to the target, and the hand passes closer as it approaches the target. In contrast, the hand never approaches the distractor at the near-right location, and in fact it moves away from this key throughout most of the reach.

However, if distractor interference effects are caused by the initial spatial proximity of the distractor to the responding hand, then the opposite pattern of interference effects are predicted. That is, the near-right distractor is closer to the start point of the hand than the distractor on the reach path, and hence the near-right distractor should interfere most. Across a range of similar contrasts, the data clearly supported the distance hypothesis (see figure 3) (near-right distractor: 41 ms interference; middle-left distractor: 15 ms interference). Thus, interference effects were greater when the initial locus of the distractor was close to the responding hand, and this was little affected by whether or not the distractor was within the response path towards the target. Furthermore, these results cannot be accounted for by spotlight models which involve a spatiotopic map. This is because the distractor on the reach path is much closer to the far-left target than is the near-right distractor. The extensive literature demonstrating that distractors closer to the target interfere more than distant distractors (see, for example, Eriksen & Eriksen 1974; Eriksen & Schultz 1979) predicts results opposite to those obtained here.

In the experiments described here, although eye, trunk, head and shoulder position could largely be controlled, the focus of covert attention could not. Therefore one explanation of the observed results could be that because the target location could not be known in advance, participants did not attend to the visual display. Rather, as the task required participants to move their hands from the start point to the target, covert visual attention was focused on the reaching hand. If this were the case, the patterns of distractor interference effects that were obtained could have been produced because distractors close to the hand were also close to the focus of covert attention, and they therefore received preferential processing. To dissociate explanations based on the focus of visual attention from those based on action-centred frames, a task was required which held constant the locus of the hand–attention, while varying the nature of the action.

A considerable body of evidence has shown that the time taken to prepare a motor programme is a direct reflection of the complexity of the action to be produced, both in simple (see Keele 1981, for review) and choice (see Klapp 1978, for review) reaction time tasks (see also Henry & Rogers (1960) and Sternberg *et al.* (1978), for other 'response complexity' effects). Therefore Meegan & Tipper (1998*b*) varied the ease with which an action could be evoked by a stimulus while holding its spatial location constant.

In figure 4 the near-right stimulus location is of most importance. In figure 4*a* this location is equivalent to that used in the first series of studies. Participants can efficiently reach out and depress the target key. Because the location of this stimulus is near and ipsilateral to the responding right hand, actions are fast. Therefore, when this stimulus is ignored it produces substantial interference because the processing associated with it tends to win the race against the other stimuli, which are processed more slowly. Because inhibition is reactive to the level of activation (Houghton & Tipper 1994), high levels of inhibition are associated with this stimulus, as observed via negative priming effects.

In figure 4*b* the near-right stimulus now includes a transparent occluding surface. The visual information available concerning the critical key and stimulus lights is equivalent in figure 4*a*,*b*: the actions required, however, are very different. In figure 4*b* participants have to reach around the occluding surface to depress the key. This action is substantially more complex and takes significantly longer to complete. Therefore, according to an action-based race model, in competition with the other stimuli, the occluded stimulus should now lose the race for the control of action, and hence interference from it, and inhibition associated with it, should be markedly reduced.

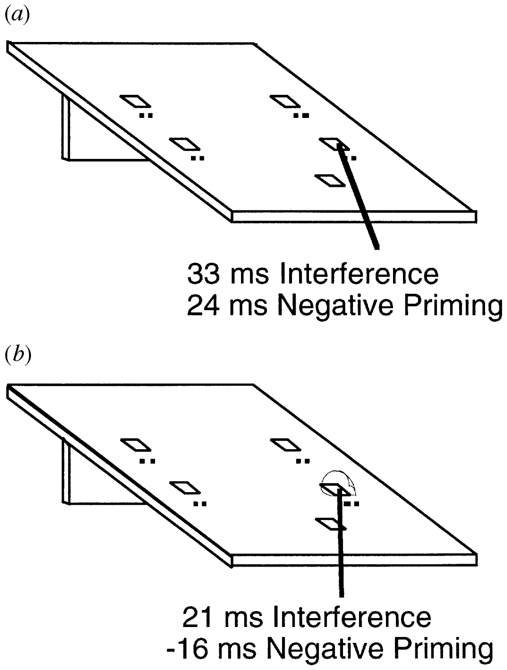

Figure 4. Stimulus board with four target–distractor keys. Mean interference from, and negative priming effects at the near-right location are shown. In (*b*), when the near-right key is occluded, there is less interference, and priming becomes facilitatory.

In contrast, the alternative account explains distractor interference effects in terms of the locus of covert attention, which may be directed towards the responding hand at the start of experimental trials. In this experiment, of course, the hand always starts from the same location. Therefore, the spatial spotlight account predicts that there should be no change in the pattern or size of distractor interference and negative priming effects.

The results clearly support the action-centred account, in which stimuli are encoded in terms of the actions they evoke, not in terms of visuospatial frames. Thus, when the action towards the near-right distractor can be rapidly programmed (figure 4*a*), interference (33 ms) and negative priming (24 ms) effects associated with this stimulus are large. In contrast, when the action to this same location in space is made more complex (figure 4*b*), interference declines (21 ms), and most interestingly, negative priming is not observed. In fact, a small facilitatory priming effect is produced (−16 ms). It is difficult to interpret this facilitation with the spatial spotlight account. However, in action-centred terms, it could be argued that the occluded stimulus does not require any inhibition as a distractor in the prime display, and therefore the residual activation leads to a repetition priming effect.

5. INVESTIGATIONS OF REACH KINEMATICS

So far our investigations of selective reaching behaviour have relied entirely on temporal measures. Either the total response time from target onset to response completion has been reported; or this has been subdivided into reaction time (RT) to begin the movement, and movement time to complete the action. Of course reaching behaviour is played out throughout space as well as time, and hence our more recent work has begun to investigate the kinematic properties of the hand as it moves through 3D space. Consideration of the physiological processes known to mediate reaching behaviour motivates our search for other means of investigating selective reaching.

Georgopoulos (1990), Kalaska (1988), and Kalaska *et al.* (1983) have investigated neural responses associated with reaching behaviour in area 5 of the parietal cortex and in the motor cortex. They observed distributed neural activity in which a particular reach is represented by the activity of a population of cells. Each individual neuron's level of activity is broadly tuned to various reach directions, which are centred on its particular preferred direction of reach, in which highest activity is evoked. Accordingly a given cell will contribute, to a greater or lesser extent, to reaching movements in various directions. The direction of the reach is determined by the sum of the single cell contributions to the population vector.

To try to understand and predict attentional effects on reach kinematics in more detail we have been developing a computational model which aims to integrate our previous modelling work on the strategic use of inhibition in attention (Houghton & Tipper 1994) with such current ideas concerning the nature of the representations controlling reaching actions. In doing so, we also hope to give more substance to the idea of 'action-centred' attentional processes.

In the model, representations guiding reaching are: (i) hand-centred, in that directions of objects are represented dynamically with respect to the (moving) hand; and (ii) action-centred, in that, direction of reach (for example, away against towards the body) affects the salience of objects (Tipper *et al.* 1992). The model represents, in parallel, the directions of two objects with respect to the current hand position. Direction is coded by the distributed activity of a population of cells, as discussed already in this paper. This can be computed from the differences in position of the hand and object with respect to some other frame of reference, for example, the body. Hand movement direction is derived from the resultant of the direction cell population vector. As the simulated hand moves, the position of objects with respect to it changes, and the directional representation changes moment by moment. The amplitude of the cell responses is also affected by the distance of an object from the hand.

We suggest that when attention is fixed on a target object, inhibition acts on the representation of a potential distractor, but in a way that is dependent on the action (Tipper *et al.* 1992). In particular, objects lying ahead in the direction of movement, and in the space between the current hand position and the target (i.e. closer to the hand) can produce strong interfering activation in the direction cell population. In the model, if this interfering activation is not suppressed the hand path will deviate significantly in the direction of the distractor, and in the extreme the reach may even be 'captured' by the distractor. This may, in fact, reflect one source of the 'slips of action' which have been investigated in other realms (see, for example, Reason 1979). Objects beyond the attended target produce less interfering activation, and path deviations of the reach are less significant, even without distractor suppression. Combined with the use of the distributed population vector to determine reach direction, this has interesting consequences, depending on the relative locations of target and distractor and direction of movement.

Figure 5*a* shows the magnitude of activation in cells tuned to make an action at a particular angle; across the cells, this forms a distributed representation of a reach to a target near to the hand on the left of the participant's midline. However, we have argued that at least two reaches can be encoded at the same time, and figure 5*b* shows the distributed representation in the same population of cells for a reach to a distractor further from the hand on the right. Because of the distributed nature of these representations, it is likely that some activated cells are common to both the target and distractor representations (cells 10–14 in this example). The overall population of neural activity for the target and distractor is shown in figure 5*c*. In the absence of any inhibitory mechanisms acting on this distributed representation, the reach, as shown by the resultant of the population vector (signified by the arrow), would pass between the two objects.

Although such behaviour has been observed in eye movement systems when two stimuli have been presented (centre of gravity effects: Findlay 1982), they are not typically observed in reaching behaviour. Therefore, we propose that inhibitory mechanisms, centred on the population vector of the distractor, suppress neural activity. At the present time it is not known how the selection dimension of colour (select red, ignore yellow), which is encoded in the ventral stream (V4) is integrated with the parietal–frontal system mediating reaching.

It can be seen in figure 5*d* that as a result of the inhibitory selection processes, the population vector has shifted slightly to the right, towards the distractor, as compared with reaches in which the target is presented alone (figure 5*a*). Under other circumstances, it is possible for inhibition to result in a shift away from the distractor. Recall that inhibition is reactive to the relative activation level between target and distractor. That is, the greater the activation of the distractor representation, the greater is the inhibition feeding back on to it. When the distractor is less salient than the target (for example, it is further away from the reaching hand), less inhibition will feedback on to it, and hence reach path will deviate towards the distractor, as in the present example. However, this model also predicts that distractors that are more salient than the target will receive greater reactive inhibition, and in extreme cases this will result in paths deviating away from the distractor. This latter situation is shown in figure 6*a*,*d*, where the target is in the far-left and the distractor is in the near-right loci. (Note that in figures 5 and 6 we have represented stimulus salience by the level of neural activity. That is, objects near to the hand are represented by more intense firing than those far from the hand. This increased intensity may result from an increased rate of firing, or from increased numbers of cells firing synchronously. At this point, however, there is little experimental evidence that proximity to the hand affects the intensity of neural firing.)

The idea that different stimuli are represented by overlapping neural populations, and that the distribution of neural activity can be effected by inhibition or fatigue, has

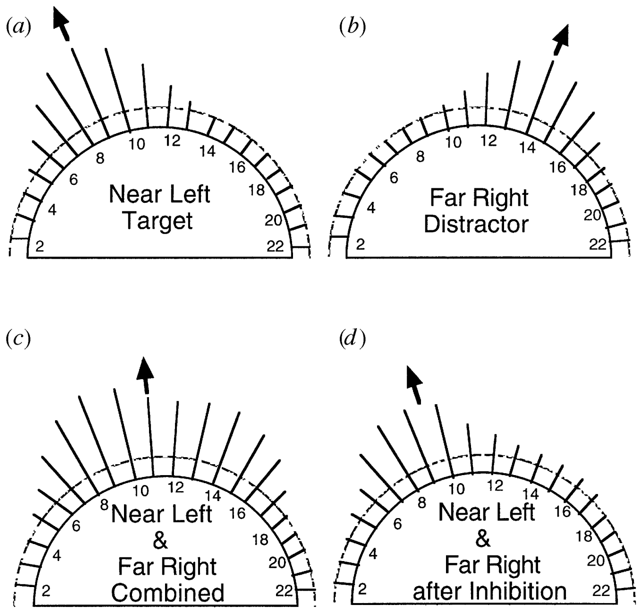

Figure 5. Simulation of neural activity representing a reach to a near-left target and far-right distractor (Tipper *et al.* 1997). The length of each line represents the level of cell activity. The dotted semi-circle represents baseline activity levels. The arrow in each panel represents the mean of the distribution, which is the resultant reach direction. Activation is normally distributed with s.d. = 1.35. $M=9$ and the maximum activity level is set at 5 for the near-left reach (*a*). $M=14$ and the maximum activity level is set at 4 for the far-right reach (*b*). (*c*) Shows the combined activation when these two reaches are simultaneously activated, $M=11.03$. The distribution shown in (*d*) represents the near-left target after inhibition of the far-right non-target, $M=9.41$. Inhibition is normally distributed, centred on the direction of the distractor (i.e. cell 14), and s.d. = 2.00. The extent of inhibition is determined by the relative level of activation between target and distractor, expressed as a percentage of 78% (at which level path is not affected). Thus, to create the activation levels shown in *d*, the maximum inhibition is 62.4% (4–5 of 78%) which is applied to the distribution in *c*. The mean of the resultant distribution has shifted rightward, slightly towards the far-right non-target.

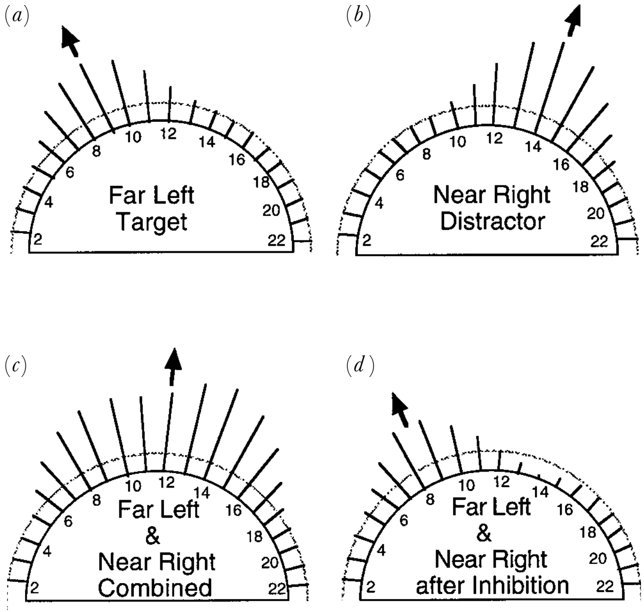

Figure 6. Simulation of neural activity representing a reach to a far-left target and near-right distractor (Tipper *et al.* 1997). The figure shows the activity of the same cells as figure 5 under these different conditions. (*a*) Shows activation levels associated with the far-left target, with maximum activity set at 4, $M=9$. (*b*) Shows activation levels associated with the near-right reach, and maximum activity is set at 5, $M=14$. (*c*) Shows the combined activity of cells involved in both reaches, in which the activity of cells involved in both reaches (cells 8 to 15) has been summed, $M=11.97$. (*d*) Represents reach direction after inhibition of the distractor, $M=8.66$. For the far-left target with a near-right non-target, the maximum level of inhibition is 97.5% (5–4 of 78%), and reduces the activity of cells 13 to 17 below baseline levels. The mean of the distribution remaining above baseline has shifted to the left, away from the near-right distractor.

been previously demonstrated in vision. For example, consider the tilt after-effect shown in figure 7. Perception of lines of a particular orientation (for example, vertical) is believed to be determined by a population of cells (figure 7*a*). When adapting to a second orientation (figure 7*b*) many of the same cells are activated, and after extensive viewing these cells become fatigued. Hence when viewing the vertical stimulus again (figure 7*c*), the underlying population of cells has a different distribution as compared with that of initial viewing (figure 7*a*), and hence the lines in this stimulus are actually perceived as being tilted to the left.

Experiments by Tipper and co-workers (1997) have analysed reach paths to test these ideas. In line with the mentioned reactive inhibition model, the reach path does deviate when a distractor is present, as compared with trials in which the target is presented alone. This deviation can be towards or away from the distractor. For example, when reaching for a near-left target the hand veers towards a far-right distractor (figure 8*a*) as predicted by the neural activity shown in figure 5 (at the midpoint, the distance between the reach paths was 7 mm ($p<0.05$)). In contrast, when reaching towards a far-left target while ignoring a near-right distractor, the hand veers away from the distractor (figure 8*b*: distance between the reach paths at their midpoint = 14 mm ($p<0.05$)). This supports the notion represented in figure 6, that more salient distractors receive proportionally greater inhibitory feedback.

Finally, a serious concern in the interpretation of such path effects is that they could be produced by distractors being encoded as obstacles. Specifically, hand deviations away from distractors may not reflect inhibitory mechanisms so much as the avoidance of a collision between the reaching hand and the distractor. Various control experiments were undertaken in our original research (Tipper *et al.* 1997) which eliminated obstacle collisions as the sole explanation of our path deviation effects.

6. INHIBITION OF RETURN (IOR) EFFECTS

More recently, we have begun to investigate other inhibitory attention mechanisms by analysing the reach path. To successfully search an environment it is critical that attention is not immediately returned to previously examined loci. One means by which movement of attention to novel loci may be achieved is by inhibition of previously

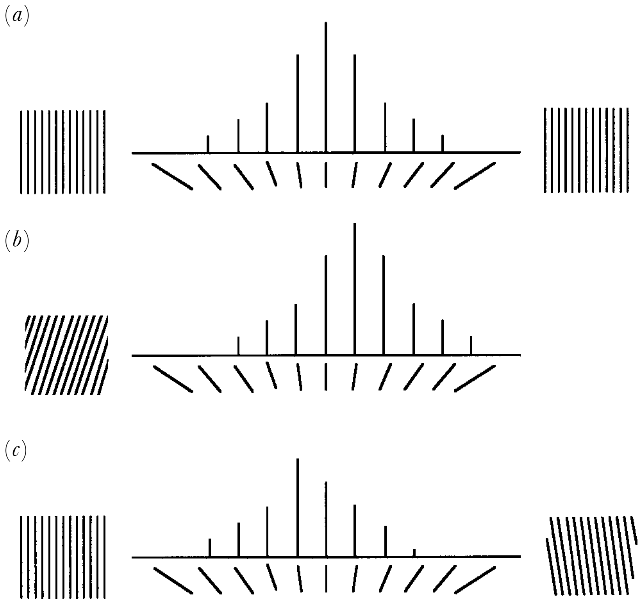

Figure 7. Explanation of the tilt after-effect. The stimuli are shown on the left, cellular distributions are in the middle, and resultant perceptions are shown on the right. In (*a*), vertical lines are perceived correctly in accordance with the pattern of activation over the relevant cells. (*b*) Shows the cell activation levels at the beginning of adaptation. When the vertical lines are subsequently viewed (*c*), the fatigued cells can no longer respond as in *a*, and until they recover, the lines are perceived as being tilted in the opposite direction to those of the previous stimulus.

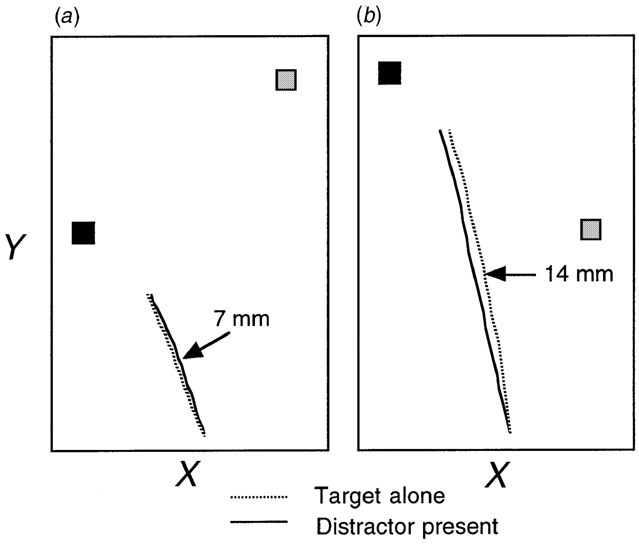

Figure 8. Mean *xy* coordinates of reach paths to targets (black boxes) in the presence and absence of a distractor (shaded boxes). (*a*) Shows a near-left reach with a far-right distractor. Compared with the target alone condition (dotted line) the hand path deviates slightly towards the distractor. (*b*) Shows a far-left reach with a near-right distractor, and in this case, the hand path clearly deviates away from the distractor.

attended loci. Posner & Cohen (1984) demonstrated inhibition of the return of attention (IOR) in the following simple procedure. Initially a peripheral cue was briefly flashed on a computer screen. Participants were informed that this cue was irrelevant and to be ignored. Nevertheless, responses to a subsequent target were affected by cue location: responses to targets at the same location as the cue were slower than responses to those at new locations. It was hypothesized that the sudden onset of the cue triggered automatic exogenous orienting of attention to the cued location, which was then inhibited as attention was withdrawn. Processing of targets subsequently appearing at the cued location was impaired because attention was inhibited from returning to that recently attended place.

We examined such IOR in a reaching task by using two measures. The first was the traditional RT measure. Consider figure 9*a*, which represents the to-be-ignored red cue. This cue, which is presented in all trials, and equally often in all locations, does not predict the locus of the subsequent target. It was predicted that detection of the green target 500 ms after the cue would be slower when the target was in the cued location (figure 9*b*) than in an uncued location (figure 9*c*). What is novel in this work was that IOR could also be observed in the path of the reaching hand when responding in uncued trials. For example, in figure 9*c* the reach is directed towards the far-left target after cueing of the near-right location. If the cue and subsequent target activate populations of cells in motor systems, as described already in this paper, then any residual activity in the network associated with the

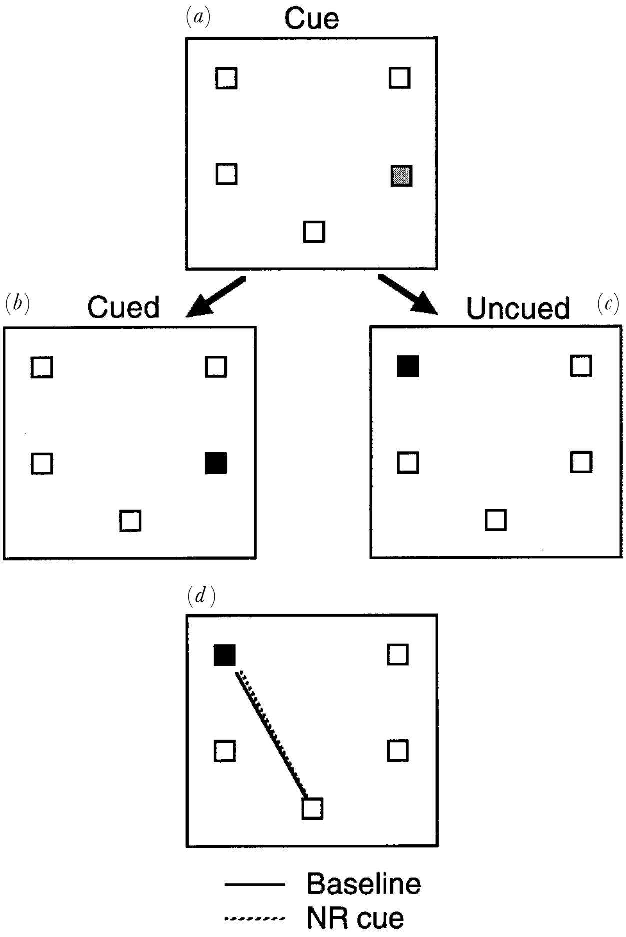

Figure 9. IOR procedure. A cue (near-right in (*a*)) is followed by a target appearing in the cued (*b*) or uncued location (far-left in (*c*)). IOR is seen in the delayed response to a cued location. It is predicted that inhibition might also be seen in path deviations during uncued reaches (*d*).

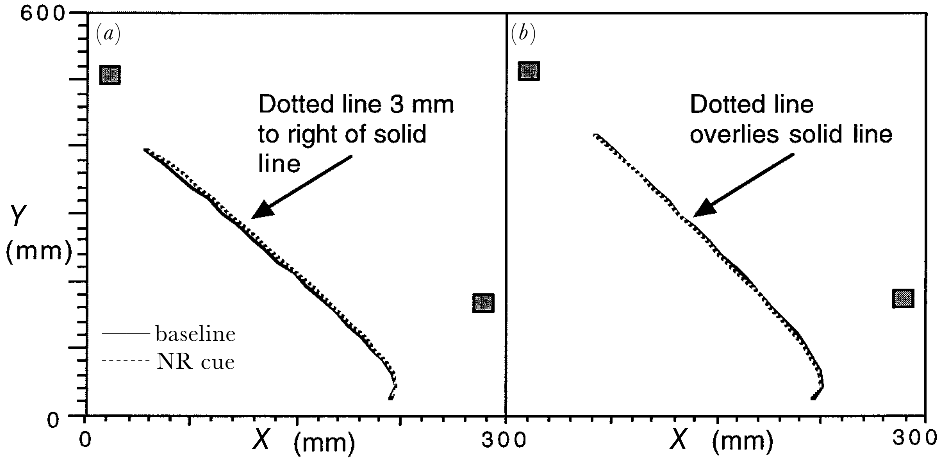

Figure 10. Hand path and RT effects in an IOR experiment for reaches to a far-left target. (*a*) Shows a small deviation in hand path towards the near-right cue (cue presented in 100% of trials); (*b*) (cue presented in 80% of trials) shows no deviation for the same reach, although the RT effect remains comparable (47 ms in *a* against 50 ms in *b*).

cue would affect the reach path to the uncued target (figure 9*d*).

Potentially, three forms of reach path can be produced, depending on the level of reactive inhibition. In each case it is assumed that the cue evokes a hand-centred representation, meaning that reaching actions are evoked and have to be suppressed. If the amount of reactive inhibition is low, then there may be residual activation in the cell population associated with the cue which may bias the population vector that controls the target reach towards the cued location. This is similar to the ideas described in figure 5. In contrast, if the amount of inhibition of the neural population activated by the cue is high, then the hand may veer away from the cued location, similar to figure 6. Finally, the level of inhibition may be such that no changes in hand path are observed compared with baseline. In fact, as can be seen in figure 10*a*, there is a tendency for the hand to veer very slightly towards the cued location, suggestive of a low level of inhibition.

We suspect that reach path reveals hand-centred internal representations; whereas the traditional RT measure accesses visual frames of reference, whether they be retinotopic-, location-, or object-based. One reason for supposing the RT and path measures arise from different representations is that they appear to be dissociable. For example, the proportion of trials with and without cues affects path, but not RT. Figure 10 shows the results of an experiment in which the proportion of trials in which a cue was presented was manipulated. In figure 10*a*, a cue preceded the target on 100% of trials, producing an IOR effect in an RT of 47 ms, and a small significant deviation in hand path towards the cue (3 mm at the midpoint). Figure 10*b* shows results from the same conditions when no cue was presented on 20% of the trials in the experiment. The RT measure is little affected, being 50 ms, but in sharp contrast, there is no significant effect on the path (1.2 mm).

It is likely that in the IOR procedure, when a cue precedes targets in 100% of trials, little stimulus processing is required, because participants can simply respond to the second (target) event. However, if no cue appears in 20% of trials, participants must process stimulus colour (by which cue and target are discriminated) if they are to perform the task correctly. In this latter version of the task, cues are processed more thoroughly than in the first version, and according to the reactive inhibition model, will require greater inhibitory feedback. In this experiment, that amount of inhibition was enough to obscure the path deviation effect towards the cue which is otherwise apparent (figure 10) but was not enough to make the path deviate away from the cue. However, the IOR effect in RT remains at the same level in both versions of the task, which we therefore assume arises from a frame of reference in which stimulus selection is unaffected by the probability of a cue.

7. CONCLUSION

We have argued for a view of visuomotor processes in which information flows continuously into action-based representations. These representations are highly flexible, being determined by the behavioural goals of the task. In the current work they have been hand-centred frames, but in a task where a foot response was required, as when kicking a ball for example, the frame of reference would shift to this body part. It is important to note that we are not proposing that extremely large numbers of objects can all activate their associated responses in parallel independent of task context. Rather, a small number of task relevant objects, such as glasses of beer when about to reach for one's own glass, are able to evoke actions independent of the individual's intention to reach for a specific glass. A corollary of such efficient visuomotor processes, is that highly effective selection mechanisms have evolved, to prevent what would otherwise be chaotic behaviour, driven by the dominant action representation of the moment. Our research suggests that an important component of this selection system is an inhibitory mechanism acting on the competing hand-centred representations of the distractor object.

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