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Attention to Action [and Discussion]

R. E. Passingham, D. Weinberger and M. Petrides

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Attention to action

R. E. PASSINGHAM

Department of Experimental Psychology, University of Oxford, South Parks Road, Oxford OX1 3UD, U.K.

SUMMARY

The paper considers the question of why subjects are poor at performing two tasks simultaneously if both require attention. It is shown using positron emission tomography (PET) that during new learning of a motor sequence task the prefrontal and anterior cingulate cortex are extensively activated, but that they are no longer activated when a motor sequence has been practiced for an hour until it is automatic. It is also shown that early in motor learning there is interference if subjects are required to generate verbs at the same time, but that the interference is much less if they are required to do this late in motor learning. The prefrontal and anterior cingulate cortex are activated during verb generation. It is therefore suggested that the interference occurs centrally, and that it occurs in either prefrontal or anterior cingulate cortex.

1. INTRODUCTION

We distinguish between those actions to which we attend and those to which we do not. For example, we do not attend to our breathing because we did not learn to breathe and it comes 'naturally'. We do not attend to riding a bicycle because, though we learnt to ride, it has become 'second nature'

2. NEW LEARNING AND AUTOMATIC PERFORMANCE

This paper reports studies in which positron emission tomography (PET) has been used to study the changes that occur in the brain when a motor task is learned and then practiced until it has become automatic. The task was to learn a sequence of finger movements, eight moves long. The task is described by Jenkins *et al.* (1994). The subjects learned by trial and error. An example of a sequence is fingers 1, 3, 4, 3, 1, 4, 2, 3. A pacing tone sounded every 3 seconds and when the subjects heard the tone they pressed one of four keys. If they correctly identified the first keypress in the sequence, they were rewarded by a high-pitched tone; on the next trial they tried to identify the next press in the sequence. If they were wrong they heard a low-pitched tone, and at the next pacing tone they tried another key by pressing with a different finger. The end of the sequence was identified by three short high-pitched tones. The subjects then returned to the beginning, and continued to perform the task in the same fashion.

Regional cerebral blood flow (RCBF) was measured using $H_2{}^{15}O$. The subjects were scanned while they learned new sequences (NEW) and while they performed a prelearned sequence (PRE) which they had learned before scanning and had practiced for one hour. They were also scanned during a baseline condition (BASE) in which they heard the pacing tones and the auditory feedback but made no movements.

We have carried out two studies using this task, one by Jenkins *et al.* (1994) and a more recent one by Jueptner *et al.* (1996) using a more sensitive scanner. In both studies the dorsal prefrontal cortex (areas 9, 46, 10) was extensively activated during new learning (NEW v PRE, figure 1), but was not significantly activated above baseline levels when the subjects performed the prelearned task (PRE v BASE, figure 2). The same pattern was found for the anterior cingulate, Brodmann's area 32.

We have also scanned subjects while they learned a verbal version of this task (Jenkins *et al.*, in preparation). As for the finger sequence, there were four elements. The difference was that these were the words

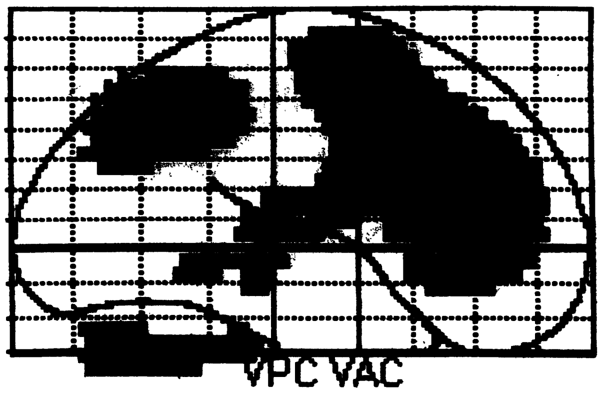

Figure 1. Saggital view of the brain showing activation in black for new motor learning compared with performance of the prelearned task (NEW v PRE). In this and the other figures the brain is shown as if it were transparent, showing activation on the lateral surface of both hemispheres as well as in subcortical nuclei. Data from Jueptner *et al.* (1996).

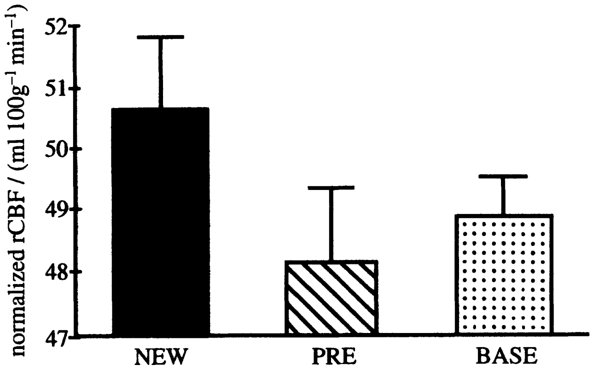

Figure 2. Histograms showing regional cerebral blood flow in right dorsal prefrontal cortex (area 9/46) for new learning (NEW), performance of the prelearned task (PRE) and the baseline condition (BASE). Regional cerebral blood flow for the peak coordinate ($x = 38$, $y = 24$, $z = 28$). Data from Jueptner *et al.* (1996*a*).

'the', 'with', 'how' and 'of'. Again, the subjects learned by trial and error. However, instead of moving one of four fingers on each trial, the subjects said one of the four words. As before, auditory cues told the subject whether the response was correct at that point in the sequence. The subjects were scanned while they learned new sequences (NEW) and also while they performed a sequence that they had learned and practised for one hour before scanning (PRE).

Again there was extensive activation of the prefrontal cortex (areas 9, 46, 10, 45, 47) during new learning (NEW v PRE, figure 3). As for the finger sequence, the prefrontal cortex was no longer activated above resting levels when the subjects performed the overlearned verbal sequence (PRE v BASE, figure 4). The pattern for the anterior cingulate area 32 was the same: it was activated during new learning (NEW v BASE) but not during automatic performance (PRE v BASE).

Raichle *et al.* (1994) have studied the learning of another verbal task. The task was verb generation: for each noun that was presented, the subject was required to produce a verb that was semantically related. The subjects were scanned while they produced verbs to a series of nouns. They were also scanned later after they had been repeatedly presented with the same nouns and their responses had become stereotyped. On the first trial of the task there was extensive activation of the left prefrontal cortex and the anterior cingulate cortex. However, these areas were no longer activated when the subjects had practised the task.

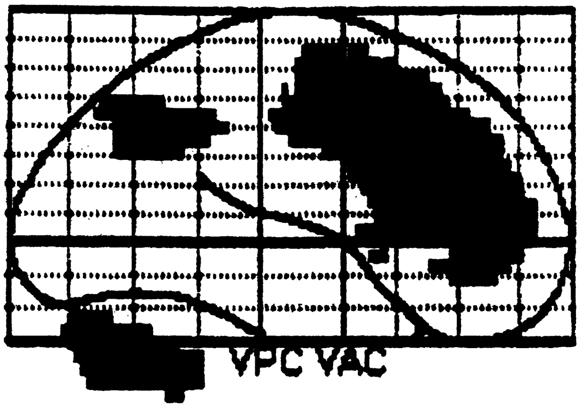

Figure 3. Saggital view of the brain showing activation in black for new verbal learning compared with performance of the prelearned task (NEW v PRE). Data from Jenkins *et al.* (in preparation).

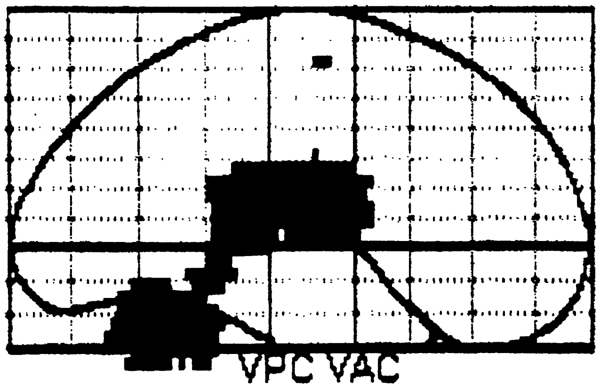

Figure 4. Saggital view of the brain showing activation in black for performance of the prelearned verbal sequence (PRE v BASE). Data from Jenkins *et al.* (in preparation).

These studies of verbal and motor learning suggest that the prefrontal and anterior cingulate area 32 are engaged when subjects must concentrate on solving new problems but not when attention is no longer required because the task has become automatic. Frith *et al.* (1991) also distinguish between routine and non-routine performance. They showed that the prefrontal and anterior cingulate cortex were activated when the subjects had to perform non-routine tasks in which they generated either words or movements at will, but that the same areas were not activated when subjects said the same words on every trial or moved their fingers as indicated by the experimenter.

3. DUAL TASK PERFORMANCE

The standard method for demonstrating that a task is automatic is to investigate whether it can be performed with minimal interference at the same time as another task. We therefore tested other subjects using a dual task paradigm. We taught 20 subjects a finger sequence outside the scanner; as before the sequence was 8 moves long (Watkins *et al.* unpublished data). They were trained in the same way as for the prelearned task in the imaging studies, except that they were required to make a movement every 2.5 seconds instead of every 3 seconds. On the first trial they learned the sequence by trial and error until they could perform the sequence in one run without error. They were then tested for a further 12 trials, each trial lasting for 90 seconds.

On trial 3 and trial 12 the subjects were required to perform a verbal task at the same time as the motor sequence. Every 2.5 seconds a word was presented on a computer monitor at the same time as the pacing tone. Ten subjects were required to repeat the word (noun repetition). The other ten subjects were required to produce a verb that was semantically appropriate

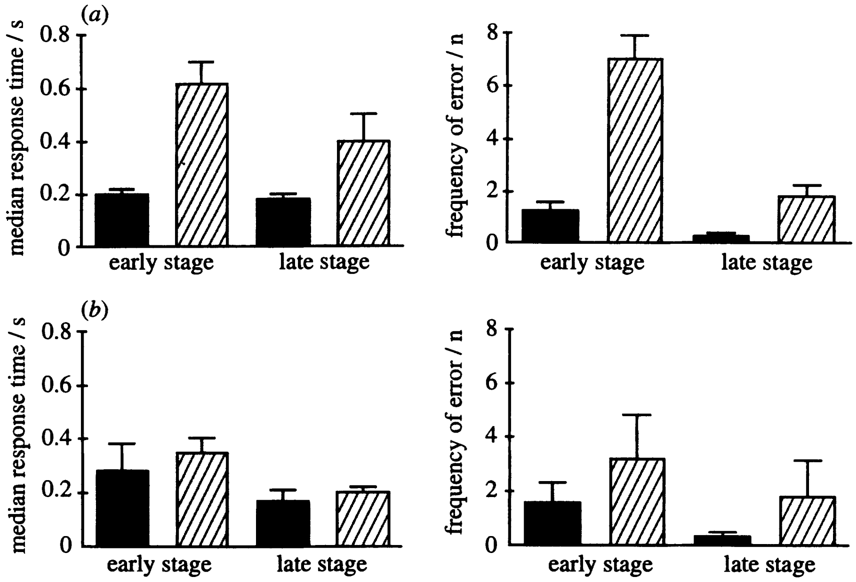

Figure 5. Response times and errors on the motor sequence task. The data are shown during (*a*) performance of verb generation, and (*b*) performance of noun repetition. Single task denated by solid bars; dual task denoted by hatched bars.

for the noun (verb generation). These two tasks were chosen deliberately because it is known that the prefrontal cortex is activated in one (verb generation) but not in the other (noun repetition) (Petersen *et al.* 1988; Raichle *et al.* 1994).

Figure 5 shows the response times and the errors on the motor learning task for trials 3 (early stage) and 12 (late stage). For comparison, the times and errors are shown for the neighbouring trials in which the subjects only performed the motor task, that is for trials 2+4 (early stage), and for trials 11+13 (late stage). There was more interference when the subjects generated verbs than when they repeated nouns. Furthermore, there was a significant interaction between type of performance (dual task or not) and trial (early v late): for response times [$F(1,9) = 8.04$, $p = 0.02$] and for errors [$F(1,9) = 9.01$, $p = 0.015$]. The decline in interference between trials 3 and 12 was greater when subjects performed the verb generation task than it was when they performed the noun repetition task.

4. CENTRAL INTERFERENCE

These results prompt the question as to the stage in processing at which the interference occurs in the brain. Interference could occur if both tasks engaged the same perceptual or motor systems, or if they engaged common associative areas. Each possibility will be discussed in turn.

On the perceptual side, motor sequence learning engages the sensory and associative areas of the parietal lobe (Jenkins *et al.* 1994), whereas viewing words and generating words engage the striate and ventral prestriate areas and the ventral temporal lobe (Petersen *et al.* 1988; Raichle *et al.* 1994). On the motor side, the learning of finger sequences engages the lateral premotor cortex and the hand area of motor cortex (Jenkins *et al.* 1994), whereas producing words engages the frontal operculum and the face area of motor cortex (Petersen *et al.* 1988; Raichle *et al.* 1994).

We also found much less interference when subjects learned the motor sequence at the same time as repeating nouns. Yet the same perceptual and motor areas are engaged when subjects repeat nouns they read as when they generate verbs in response to nouns that they read. The supplementary motor area is also activated both in noun repetition (Petersen *et al.* 1988) and verb generation (Wise *et al.* 1991).

It appears, therefore, that there is interference centrally. The data for verb generation and noun repetition suggest that it occurs in the frontal lobe. The term 'frontal' is used rather than the more restrictive term 'prefrontal' because the frontal lobe includes the anterior cingulate cortex. When verb generation is compared with noun repetition, there is additional activation in the prefrontal and anterior cingulate cortex (Petersen *et al.* 1988; Raichle *et al.* 1994). The hypothesis is that when subjects are learning the motor sequence task on trial 3, there is still some activation of the frontal areas, and that interference occurs because the verb generation task also makes demands on these frontal areas. On trial 12 these areas are no longer activated during the motor sequence task, and thus they can be fully engaged by the task of generating verbs.

On this hypothesis, the reason why there is less interference with noun repetition is that this task does not engage the prefrontal and anterior cingulate cortex. Noun repetition is an overlearned skill which can be performed without attention. As mentioned earlier, we have taught subjects a verbal sequence and compared new learning (NEW) with performance of an overlearned sequence (PRE) (Jenkins *et al.* 1996). During new learning both Broca's area and the supplementary speech area were strongly activated, but neither area was engaged when the sequence had become automatic. When the sequence had been overlearned, there was extensive activation in the cerebellum and basal ganglia, but the motor output was limited to the insula and operculum at the base of the motor cortex (figure 4). Raichle *et al.* (1994) also found that when subjects generated verbs to a list they had practiced, there was activation in the sylvian-insular cortex. This area was similarly activated in noun repetition.

5. ATTENTION TO ACTION

There is a relation between these findings concerning the brain and the subjective report that early in learning subjects must pay attention to the motor sequences but need not do so when the task has been practiced for many trials. Shallice (1982) has previously argued that the prefrontal cortex acts as a 'supervisory attentional system' that influences the selection of action when subjects perform tasks that are non-routine. It should therefore be possible to show that the prefrontal and anterior cingulate cortex are activated when the subjects must pay attention to the task in hand.

In a recent study we have compared performance of a prelearned motor sequence with and without attention (Jueptner *et al.* 1996). In one condition the subject performed a prelearned motor sequence (PRE) which has been practiced for one hour before scanning. In the other condition the subjects performed the same sequence, but they were asked to attend to what they were doing (ATT). Specifically they were asked to think about the next movement. When these conditions were compared (ATT v PRE) the only areas that were activated were the left dorsal prefrontal cortex (9, 46, figure 6*a*) and the right anterior cingulate cortex (areas 32, 24, figure 6*b*).

A distinction should be drawn between attention to action and attention to locations in the external world. There is activation in the parietal lobe when subjects are required to attend to spatial locations (Posner & Petersen 1990; Corbetta *et al.* 1993) or to aspects of complex stimuli (Haxby *et al.* 1994). However, in the present study, while the dorsal prefrontal cortex was activated when subjects were required to attend to their actions (ATT v PRE), the parietal cortex was not.

The term 'attention to action' is not precise. There are many operations which may require attention. In new learning of motor sequences the subjects must generate new moves, monitor the outcomes and mentally rehearse the sequence. The dorsal prefrontal cortex is engaged when subjects must generate numbers, and monitor their responses, while remembering the ones that they have produced (Petrides *et al.* 1993). The sequence is also 'supraspan' and Grasby *et al.* (1993, 1994) have shown that the prefrontal cortex is activated when subjects must remember lists that are supraspan.

During performance of the prelearned task with attention (ATT) the subjects did not have to make new decisions, monitor the outcomes or mentally rehearse the sequence. When a comparison was made of new learning with the attention condition (NEW v ATT), there was more activation of the dorsal prefrontal and anterior cingulate cortex (32) during new learning than in performance of the prelearned task with attention (Jueptner *et al.* 1996, figure 2). Any one or all of these processes may account for the extensive activation of the prefrontal cortex in new learning. The results do not indicate which of these processes cannot be performed without interference in the dual task paradigm.

During new learning of the motor sequences one of the operations that the subjects must perform is the generation of new responses. It has been shown in other studies that the dorsal prefrontal cortex is activated when subjects must decide of their own accord which movements to make (Deiber *et al.* 1991; Frith *et al.* 1991). We have also scanned subjects while they made decisions as to when to move their forefinger (Jahanshahi *et al.* 1995). In one condition the subjects themselves decided when to move the finger (SELF) and in the comparison condition they moved their finger when they heard a tone that functioned as an external trigger stimulus (EXT). The anterior cingulate cortex (areas 32, 24) was activated in both conditions (SELF v BASE, EXT v BASE) but the dorsal prefrontal cortex was only activated in the self-paced task (SELF v BASE). Furthermore, the dorsal prefrontal cortex was the only area that was differentially activated when the two conditions were directly

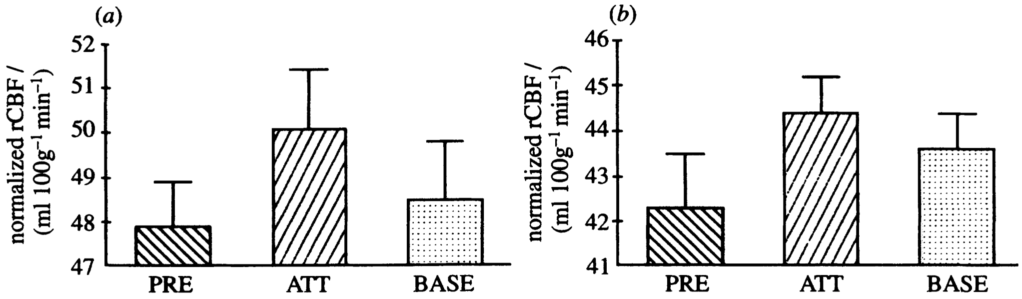

Figure 6. Histograms showing regional cerebral blood flow in new learning of the motor task (NEW), performance of the prelearned task (PRE) and performance of the prelearned sequence with attention (ATT). Data from Jueptner *et al.* (1996*a*).
(*a*) Left dorsal prefrontal cortex (area 9/46) ($x = -34$, $y = 20$, $z = 32$)
(*b*) Right anterior cingulate cortex (area 32/24) ($x = 18$, $y = 10$, $z = 28$)

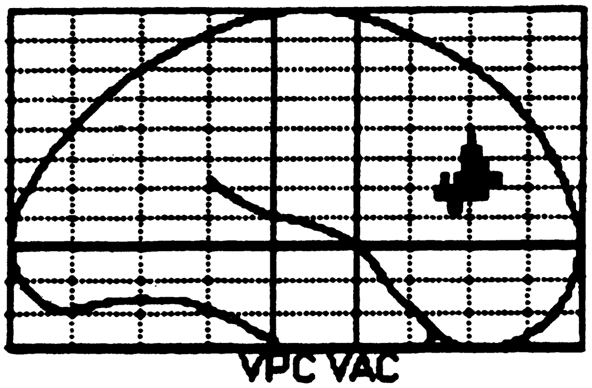

Figure 7. Saggital view of the brain showing activation in black for performance of the self-paced task (SELF) compared with performance of the externally paced task (EXT). Data from Jahanshahi *et al.* (1995).

compared (SELF V EXT, figure 7). This result implicates the dorsal prefrontal cortex in the process of making decisions concerning action.

Verb generation also requires subjects to make decisions. The subjects must produce a verb that is appropriate, but they themselves decide which of many possible verbs to produce. Frith *et al.* (1991) have also studied verbal fluency tasks in which the subjects are required to produce words that begin with particular letters. Again the subjects have a choice of which words to produce. Frith *et al.* (1991) showed that the prefrontal cortex and anterior cingulate cortex were activated when subjects performed the verbal fluency task.

Motor sequence learning and verb generation are alike in that before the subject responds there are no external prompts to specify which responses should be selected. In this sense they involve 'willed action' (Frith *et al.* 1991). They are also alike in that the subjects must reflect on and manipulate possible responses in the head (Frith & Grasby 1995).

Baddeley (1996) has also shown that there is considerable interference if subjects are required to generate a random sequence of key responses at the same time as producing a novel sequence of number and letters such as K-5-L-6-M-7. Interference on the motor task was measured by the decrease in randomness in the sequence of key responses. The subjects were also slow to produce the verbal sequence when required to perform both tasks at the same time. Baddeley argues that both tasks place a heavy load on the 'central executive' of working memory.

6. PREFRONTAL CORTEX AND ANTERIOR CINGULATE

It is not clear whether interference occurs in prefrontal cortex, the anterior cingulate cortex or both.

(*a*) *Prefrontal cortex*

When subjects learn a finger sequence, there is activation in the dorsal prefrontal cortex (areas 9 and 46). However, Petersen *et al.* (1998) and Raichle *et al.* (1994) report that when subjects generate verbs there is a peak of activation in the ventral prefrontal cortex (area 45). Frith & Grasby (1995) have compared the peaks for activation reported in the literature for verbal and motor tasks, and they conclude that for verbal tasks there are peaks of activation in ventral prefrontal cortex whereas for motor tasks the peaks lie in the dorsal prefrontal cortex.

There are also differences in the laterality of the activation for verb generation and motor sequence learning. When subjects generate verbs the activation is restricted to the left prefrontal cortex (Petersen *et al.* 1988; Raichle *et al.* 1994). When subjects learn the finger sequence, there is activation in both the left and right prefrontal cortex, but the activation is more extensive on the right (Jenkins *et al.* 1994; Jueptner *et al.* 1996).

It could therefore be argued that verbal and motor tasks are processed in parallel systems within the prefrontal cortex. However, there is clear overlap between the systems.

First, Petersen *et al.* (1988) report that, as well as a peak in the ventral prefrontal cortex for verb generation, there is also a peak more dorsally. It lies within the conservative coordinates given by Rajkowksa & Goldman-Rakic (1995) for area 46. Furthermore, Raichle *et al.* (1994) present a figure (figure 4) showing the extent of the activation in lateral prefrontal cortex during verb generation, and it is clear that the activation overlaps with that found for motor -sequence learning (see Jenkins *et al.* 1994, figure 5). Second, Buckner *et al.* (1995) report that there is activation of the left frontal pole (area 10) during verb generation. Again, this activation overlaps with the activation seen during motor sequence learning (see Jenkins *et al.* 1994, figure 5).

(*b*) *Anterior cingulate cortex*

There is also extensive activation in the anterior cingulate cortex (area 32) when subjects generate verbs (Petersen *et al.* 1988; Raichle *et al.* 1994) or learn motor sequences (Jenkins *et al.* 1994; Jueptner *et al.* 1996). Frith & Grasby (1995) review the evidence that this area is activated when subjects must select between responses whether the tasks are verbal or motor.

Posner & Petersen (1990) have argued that the anterior cingulate cortex is especially activated when subjects must attend to the selection of responses. They base their argument on the claim that the activation of the anterior cingulate cortex increases as the number of targets to be detected increases. Frith & Grasby (1995) have reviewed attempts to distinguish between the functions of the anterior cingulate and prefrontal cortex. There is, as yet, no clear demonstration of a task that activates the anterior cingulate cortex without also activating the prefrontal cortex. For example, Pardo *et al.* (1990) claimed that only the anterior cingulate cortex was activated when subjects performed the Stroop task, but it has been shown more recently that the frontal polar cortex is also activated during this task (Carter *et al.* 1995).

(*c*) *Scanning during dual task performance*

One way to resolve the issue would be to scan subjects while they try to perform verb generation and learn motor sequences at the same time. We have not done this. However, Shallice *et al.* (1994) and Fletcher *et al.* (1995) have scanned subjects while they encoded verbal information at the same time as performing a motor task. When the motor task was easy, there was activation in the left prefrontal cortex during encoding of words. When the motor task was difficult, the prefrontal cortex was no longer significantly activated. However, there was an increase in the activation of the anterior cingulate cortex.

Unfortunately, this study does not decide the issue. The design of the experiment did not permit an assessment of the activation induced by the distractor task alone. It is true that Fletcher *et al.* (1995) report a comparison between the activation induced by the difficult compared with the easy motor task. However, this comparison does not show which areas were activated during performance of the more difficult motor task compared with a rest condition.

There is another issue that would be clarified by scanning subjects while they performed verb generation and motor sequences at the same time. Figure 5 shows that even on trial 12 there was some interference as measured by the effect of verb generation on the response times for the motor task. One explanation would be that during dual task performance either the dorsal prefrontal or the anterior cingulate cortex were to some extent reactivated during performance of the motor sequence because the subjects were not confident of performing the motor sequence task without attention. D'Esposito *et al.* (1995) reported activation of these areas when subjects were faced with a dual task paradigm, even though these areas were not activated when the subjects performed either task alone. By scanning verb generation and the performance of the motor sequence on trial 12 it would be possible to see if there was more activation of the dorsal prefrontal or anterior cingulate cortex when the motor sequence was performed with verb generation than occurred without. The prediction would be that this would no longer happen if the motor sequence was overtrained for many more trials.

7. CONCLUSIONS

It has been claimed that interference may occur between two tasks if both tasks engage the prefrontal and anterior cingulate cortex. The advantage of this claim is that, if it is correct, there is an objective way of deciding whether a motor task is 'routine' or not. Shaffer (1975) has argued that the notion of automated performance begs the question of what is attention. It is proposed here that the more routine a task, the less the prefrontal and anterior cingulate cortex will be activated.

It is important to note that this is not a claim that this is the only stage of processing at which interference can occur. For example, it is known that there is interference with verbal memory if subjects are required to say 'la la la' either aloud or in their head at the same time as remembering the words (Baddeley 1986). Paulesu *et al.* (1993) have shown that when subjects remember letters, there is activation in left perisylvian areas: these include the superior temporal cortex, the inferior parietal cortex, Broca's area and the neighbouring ventral premotor cortex. In a recent experiment Paulesu *et al.* (1996) have found that one of these areas, the ventral premotor cortex, is activated when subjects repeat 'la la la' aloud or in their head. This result is consistent with the claim that interference can occur if two tasks engage a common area.

The claim made in the present paper concerns the interference that occurs when subjects must attend to the selection of more than one action at the same time. The claim is a version of the hypothesis that attentional selection occurs 'late' rather than 'early' (Allport 1991). The assumption is that the system is built to produce coherent action, and that it is adaptive to concentrate on one task at a time. Just as the animal scans the visual environment in a serial fashion, so it may pay to deal with problems concerning action in series. Serial processing at a late stage may be a design advantage, not a limitation.

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Discussion

D. WEINBERGER (*Clinical Brain Disorders Branch, National Institute of Mental Health, Neuroscience Center at St. Elizabeths, 2700 Martin Luther King Jr Avenue, SE, Washington D.C. 20032*). In both monkeys and humans there is a body of literature that argues that when you learn a novel complex motor sequence there is an increased cortical area that subserves that activity whilst there is another body of literature, similar to your own, which suggests the exact opposite. I would be interested in your perspective on this inconsistency.

R. E. PASSINGHAM. There is no inconsistency. We have compared the first run of new learning with automatic performance and we report more activity in many cortical and subcortical areas during new learning. Others have compared several runs of new learning and they report increases in certain areas over these runs. Our data suggest that if scans were to be taken for many more runs, many of these increases would be reversed. We are now using fMRI to scan subjects while they learn and perform the same sequence until it becomes automatic, and our preliminary data support this claim.

M. PETRIDES (*Montreal Neurological Institute, 3801 University Street, McGill University, Montreal, Quebec, Canada, H3A 2B4*). We too have performed an experiment in which the subjects were scanned after they had learned a highly automated sequence and , in agreement with your findings, prefrontal cortex became activated only when the subjects were asked to perform it explicitly. However, in contrast to your findings, the activated area was ventrolateral rather than dorsolateral prefrontal cortex. As this task does not require any obvious manipulation of the material in memory and therefore the explicit and implicit tasks should be equated in terms of monitoring requirements, then in accordance with the hypothesis that I am proposing, such a task would be predicted to activate ventrolateral frontal cortex rather than dorsolateral prefrontal cortex. One possible explanation for the discrepancy in the site of prefrontal activation observed may lie in how well the control task matched the experimental task. Were the monitoring requirements of your two tasks well matched but the retrieval requirements different? In our study, we attempted to equate the monitoring components of the two tasks, which would be predicted to activate dorsolateral prefrontal cortex, in order to see ventrolateral activation. Would you like to comment on this?

R. E. PASSINGHAM. Our data are consistent with your view that the dorsal prefrontal cortex is concerned with the manipulation of information in working memory. As you comment, we found activation in dorsolateral prefrontal cortex during new learning. Our sequences were supraspan, and the subjects needed to evolve strategies for learning the sequence.