Perceptual versus motoric attention: An fMRI investigation of the speed-accuracy tradeoff in decision-making

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Abstract

Selectively attending to either the sensory qualities of a stimulus or the response required by a task can influence the speed and accuracy of performance. Prior fMRI studies have identified medial and lateral prefrontal regions to play a critical role in accommodating speed instructions; however, no neural regions that accommodate improvements in accuracy have been identified. Here event-related fMRI was used to investigate *when* brain regions respond to speed-accuracy tradeoff manipulations and whether there are distinct brain regions for achieving greater accuracy *or* greater speed. First, visual-attention regions had greater activation when emphasizing accuracy rather than speed. Secondly, the pre-supplementary motor area increased activation during response preparation when emphasizing speed over accuracy. Lastly, the lentiform nucleus increased activation just prior to the execution of a response when emphasizing speed. Trading speed for accuracy may involve shifting the balance of neural activation between systems that prepare for action and those involved with visuo-spatial attention.

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Introduction

Performance of even the simplest tasks can require several cognitive processes such as stimulus perception, stimulus identification, attention, memory, decision-making, and response preparation, among others (see Bogacz, Wagenmakers, Forstmann, & Nieuwenhuis, 2009; Pachella, 1974; Sternberg, 1969). How these processes modulate information processing to meet specific task demands has been a main theme of experimental psychology for well over a century. It is generally accepted that one can control how long perceptual and motor processes are implemented (e.g., Lange, 1888/2009). The term 'speed-accuracy tradeoff' (SAT) has been introduced to describe the trading relationship between the speed and accuracy of our decisions. The SAT remains one of the most replicable findings in experimental psychology. An SAT occurs when fast decisions are made at the expense of accuracy, and accurate decisions are made at the expense of speed (e.g., Carrasco & McElree, 2001; Forstmann et al., 2008; Ivanoff, Branning, & Marois, 2008; Ruthruff, 1996; van Veen, Krug, & Carter, 2008; Wickelgren, 1977; Woodworth, 1899; for a review, see Pachella, 1974). Cognitive scientific approaches to the SAT have been limited to the study of reaction time (RT) and accuracy to infer the dynamics of control; however, with the relatively recent advent of electrophysiological and functional imaging techniques, it is now possible to examine the neural and physiological correlates of these processes.

The inverse trading relationship between speed and accuracy is robust and evident across numerous species including humans (Band, Ridderinkhof, & van der Molen, 2003; Fitts, 1966; Schouten & Bekker, 1967) and non-human primates (Snyder, Dickinson, & Calton, 2006). It is also evident in multiple species' behaviour, such as predator-prey

detection, and navigation (for a review, see Chittka, Skorupski, & Raine, 2009). Despite the inter-species prevalence of SAT in decision-making, there is still a great deal to learn about how and where SAT demands are modulated in the brain and whether component processes of performance are differentially affected.

For over a century, the question of how we accommodate speed-accuracy demands placed on performance has been a main concern of experimental psychology. Lange (1888/2009) found that adopting differential preparatory strategies, or ways of reacting, along a continuum from "extreme muscular reactions" to "extreme sensory reactions" (p. 489), differentially impacts the speed and accuracy of responding in a similar manner as that found in present day SAT literature. Lange (1888/2009) defined "extreme muscular reactions" as a strategy whereby "the test subject was thinking exclusively about his attention to the preparation of those muscles with which to react" and "extreme sensory reactions" as a strategy whereby a subject placed "greater exclusive attention to sensory input (i.e., principally the avoidance of preparatory movement innervation)" (p. 489).

Lange (1888/2009) conducted a simple RT experiment whereby participants were first presented with an auditory warning signal (bell tone) that informed them a primary stimulus was about to be presented. Subsequently, an auditory primary stimulus (the release of an electromagnetic hammer) was presented following an interval of approximately 20-40 seconds informing participants to make a manual response. Participants were given substantial practice and instructed to "not think *at all* about the imminent sensory stimulus, but rather [to concentrate] as much as possible on preparing their own reaction" (i.e., adopt an extreme muscular preparatory strategy), or to "*strictly*

[avoid] any preparatory motor innervation [and] concentrate his entire preparatory attention on the anticipated sensory input and simultaneously focus on the immediate conversion of the impulse to movement", (i.e., adopt an extreme sensory preparatory strategy; Lange, 1888/2009; p.487-488).

Lange's (1888/2009) behavioural findings are strikingly consistent with those found in modern SAT literature. He found that when instructed to adopt an "extreme sensory reaction" (p. 489) strategy, participants made substantially fewer anticipatory errors than when instructed to adopt an "extreme motor reaction" (p. 489) strategy. Furthermore, when adopting an "extreme motor reaction" (p. 489) strategy, the participants made faster responses, yet more anticipatory errors than when implementing an "extreme sensory reaction" strategy. Although Lange (1888/2009) found that implementing these different strategies resulted in an SAT, there is no functional imaging or electrophysiological study to date that has found clear evidence for increased activity in sensory regions, suggesting greater attention being placed on *perceiving* the features of a stimulus when emphasizing response accuracy (see Forstmann et al., 2008; Ivanoff et al., 2008; Rinkenauer, Osman, Ulrich, Müller-Gethman, & Mattes, 2004).

Although response time and accuracy metrics are the primary dependent variables in experimental psychology, there currently exists little consensus on how to interpret them simultaneously. It is not uncommon for researchers to focus on one measure (e.g., response time), and ignore the other (e.g., error rate). Pachella (1974) argued that disregarding errors assumes an independent relationship between RT and accuracy: that "the RT for correct responses is not affected by the overall error rate for an experimental

condition" (p.62; see also Ratcliff, 2002). The SAT, however, is hard and fast evidence against the proposal that RT and accuracy are unrelated (for a review see Pachella, 1974).

To illustrate how an SAT function (SATF) may be derived, consider a hypothetical experiment in which participants are instructed to make a response to the presentation of one stimulus while inhibiting responses to another. In this hypothetical experiment, participants are instructed to complete this task under three conditions. In one condition, participants are instructed to balance the speed and accuracy of their responses; in a second condition participants are instructed to emphasize the speed of their responses at the cost of accuracy; and in a third condition participants are instructed to emphasize the accuracy of their responses at the cost of speed. Plotting a measure of the resultant response accuracy as a function of response time would result in an SATF like that illustrated in Figure 1.

The SATF (Figure 1) illustrates the close inverse mathematical relationship between the speed and accuracy of performance that may be used to infer the dynamics of information processing. Disregarding or removing erroneous responses from an RT analysis not an optimal strategy because some of the remaining "correct" responses may be guesses (Salthouse & Hedden, 2002), thus potentially tainting the measurement of information processing. As explained by Wickelgren (1977),

> "Obtaining an entire speed-accuracy tradeoff function provides much greater knowledge concerning information processing dynamics than is obtained by a reaction-time experiment, which yields the equivalent of a single point on this function. For this and other reasons, speed-accuracy tradeoff studies are often

preferable to reaction-time studies of the dynamics of perceptual, memory, and cognitive processes." (p. 67).

Put simply, by having participants perform under various conditions of speed-accuracy emphasis, one may best capture the dynamics of information processing.

The purpose of the current study is to use modern functional magnetic resonance imaging (fMRI) techniques to better understand how, and when, the brain responds to the relative importance of speed and accuracy of decision-making. Specifically, I aim to determine whether emphasizing the accuracy of a decision results in a shift of attention to the target object and whether emphasizing the speed of a decision results in changes to motoric centers of the brain (c.f. Lange, 1888/2009). The remainder of this section provides a discussion of the manipulations used by prior researchers to evoke SAT in performance. The main theoretical accounts of SAT are then considered and a brief review of recent studies of SAT and response preparation is provided.

Generating a SAT

The dynamics of perceptual decision-making has received increasing attention in recent years and across a wide variety of paradigms (for a review, see Bogacz, et al., 2009). There are a number of techniques researchers have employed to encourage the trading of speed for accuracy, and vice versa, for the purpose of obtaining an SATF. These techniques include the following: providing incentives or rewards, enforcing deadlines for responding, giving feedback regarding response accuracy and/or speed, and providing verbal or visual instructions (for a review, see Pachella, 1974; Wickelgren, 1977). Here, I will discuss each technique in turn.

Incentives

Financial incentives have been used to induce SAT performance in a number of studies (Banks & Atkinson, 1974; Bijleveld, Custers, & Aarts, 2010; Simen et al., 2009; Snodgrass, Luce, & Galanter, 1967). A recent study conducted by Bijleveld, Custers, and Aarts (2010) examined the impact of consciously perceived and subliminal performance based rewards on SAT in a simple arithmetic task. These authors provided financial rewards on a trial-by-trial basis for responses that were fast and accurate and found that high rewards increased the amount of effort (i.e., responding faster but still maintaining high levels of accuracy) that participants directed to the task regardless of whether the reward was consciously perceived or not; however, they found that only consciously perceived rewards induced an SAT in performance.

The rewards used by Bijleveld et al. (2010) did not emphasize response speed *at the cost of* accuracy, but rewarded performance that was both fast and accurate. Thus, these results may represent only a small region of the SATF closer to the asymptote, as subjects maintained near-perfect accuracy. To obtain a more representative distribution of responding along the SATF using this technique, it appears one must use consciously perceived incentives that are not only dependent on changing the speed of responses while maintaining accuracy, but are dependent on increasing accuracy at the cost of speed and increasing speed at the cost of accuracy. Regarding the use of incentives to induce SAT, Franklin and Okada (1983) commented that participants might continue to emphasize accuracy over speed regardless of whether incentives encourage speed over accuracy. Thus, properly inducing an SAT with this method is highly dependent not only on the reward contingency and the subjective magnitude of the reward in relation to the

contingency (Simen et al., 2009). It appears that, although used successfully in a number of studies, using incentives involves a great deal of control regarding the specific payoff contingencies and reward schedules to ensure participants make the appropriate tradeoffs.

Response Deadlines

In the response deadline method, participants are informed prior to each trial or block to respond within a specified period of time following the onset of a target (e.g., Lien, Ruthruff, Remington, & Johnston, 2005; Ruthruff, 1996). This method has been combined with the use of incentives to enforce responding within a specified period of time: responses made after the target and before the expiration of the response deadline were rewarded, whereas responses made prior to the target or after the deadline were penalized (e.g., Snodgrass, Luce, & Galanter, 1967). The deadline method is effective in obtaining SATFs and it is easy to implement because deadlines may be held constant, randomized on a trial-by-trial or block-by-block basis, and participants may be informed of the deadlines prior to trials or blocks (Miller, Sproesser, & Ulrich, 2008).

Kleinsorge (2001) used a changing deadline method where responses were compared with the average of correct responses from the trials in the previous block. To emphasize speed, participants were instructed to be faster if the average RT of correct responses in the previous block was faster than their current average; however, if the average correct RT was faster than that of the previous block, the participants received a reward. Therefore, participants were encouraged to continually increase the speed of their responses. The use of a changing response deadline is an effective means of having participants change the speed of their performance and may be implemented with minimal interference to the task itself; that is, participants may be informed at the end of

a period of time to change the speed of their responding. This technique may also be combined with other methods of SAT modulation to further induce SATs in performance.

Feedback

A number of studies have induced SATs by providing speed and/or accuracy feedback on a trial-by-trial, or block-by-block, basis (e.g., Ivanoff et al., 2008; Snodgrass et al., 1967). For example, Franklin and Okada (1983) evaluated how such feedback affects RT and accuracy in a recognition memory task. Participants completed a task in which they were first presented with a warning signal indicating that a series of numbers ranging from 0-9 (memory set) would be presented (e.g., 2, 6, 3, 5). They were required to remember the "memory set" and indicate whether a later set of numbers presented in the same manner and ranging from 0-9 (memory probe) matched the memory set by making a positive response or making a negative response if the memory probe did not match the memory set. Participants were randomly assigned to one of two conditions: accuracy-informed or time-informed. In the accuracy-informed condition, participants were provided trial-by-trial visual feedback indicating whether their response was correct or incorrect. At the end of a block of trials, participants were then shown the overall accuracy score for the block. In the time-informed condition, participants were provided trial-by-trial RT feedback, and at the end of each block of trials they were shown their average RT for the block. Equivalent emphasis was placed on the speed and accuracy of responding and participants were told their feedback was simply to help them improve.

Franklin and Okada (1983) found that performance reflected the type of feedback provided. That is, when provided response-time feedback, participants produced fast and accurate responses. When provided accuracy feedback, they increased their accuracy but

at the cost of response speed (i.e., they slowed down their responding). The authors interpreted their findings to mean that to induce a change in the way participants respond (i.e., faster or more accurate), feedback must correspond to the metric (RT or accuracy) that ought to change.

Instructions

The most widely used method for obtaining SATFs is the use of instructions, verbal or visual, that inform participants of whether to place differential emphasis on the relative speed *or* accuracy of their performance (e.g., Gopher, Armony, & Greenshpan, 2000; Reddi & Carpenter, 2000; Ruthruff, 1996; Swensson, 1972; van Veen, Krug, & Carter, 2008). Band et al. (2003) used this technique in their investigation of the effects of the SAT on motor activation in go/no-go and response-priming tasks. Trials began with the presentation of a fixation point, followed by a cue that corrected identified the response on 80% of trials. On the remaining 20% of the trials, the cue would provide erroneous (i.e., invalid) response information. Half of their participants were verbally instructed to be as fast as possible with minimal regard for accuracy while the other half were instructed to balance speed and accuracy. They found the expected SAT pattern of responding: faster, yet less accurate, responding following speed instructions relative to instructions to balance speed and accuracy. Unlike the use of incentives, the use of instructions is relatively easy to implement across different modalities (i.e., verbal or visual), and does not require special considerations regarding schedules of reward and contingencies.

The methods to induce an SAT differ in their limitations (e.g., type of rewards used, reward contingencies, and the types and contingencies of feedback), and for this

reason a number of studies have used combinations of these techniques to ensure that the appropriate tradeoffs occur. Examples of such combinations include the following: instructions and feedback (e.g., Carrasco & McElree, 2001; Forstmann et al., 2008; Ivanoff et al., 2008; Ratcliff, 2002); response deadlines and feedback (e.g., Ruthruff, 1996); and response deadlines, incentives, and feedback (e.g., Kleinsorge, 2001; Snodgrass et al., 1967). Using one or more these techniques will induce behavioural tradeoffs along the SATF, and each of these methods has associated costs and benefits (e.g., rewards may induce behavioral SAT but require a great deal of control regarding reward schedules and contingencies), that must be considered before implementing them in an experimental paradigm. In the current study, I will use visual instructions and feedback to induce an SAT. This approach has proven successful in a recent fMRI study (Ivanoff et al., 2008).

Mechanisms of the SAT

The previous section discussed the techniques that can be used to induce an SAT. The focus of this section is to discuss some of the main theoretical accounts of the relationship between RT and accuracy to provide a theoretical foundation for discussing recent fMRI studies of SAT. There are two primary classes of models commonly used to account for SAT: (1) models involving mixtures of guesses and stimulus-directed responses such as the fast-guess and deadline models, and (2) models involving the accumulation of stimulus-based evidence to a decision criterion.

Fast-guess and Deadline Models

The fast-guess model, first proposed by Ollman (1966), relies on the assumption that participants can make two types of responses: stimulus-controlled responses and fast

guesses (cf. Yellott, 1971; for a review, see Pachella, 1974). Stimulus-controlled responses are those produced after having taken sufficient time to process a stimulus, thus ensuring as accurate a response as possible. On the other hand, fast guesses are defined as those responses where the participant does not process a stimulus, but randomly guesses a response. This model accounts for SAT in the following way: when forced to make fast responses, participants must make more fast guesses, and when given sufficient time participants will make more stimulus-controlled responses. Thus, trading speed for accuracy is the result of reducing the relative proportion of responses that are fast guesses (Ollman, 1966; Pachella, 1974).

The fast-guess model has received little support as an explanation of the SAT. Because fast guesses are not guided by partial stimulus processing, the fast-guess model predicts that a decrease in RT is the result of increasing the proportion of fast guesses. Therefore, when responding extremely fast, there should be similar deficits in accuracy independent of task difficulty. A number of studies that have examined performance across various levels of task difficulty have shown clear violations of this assumption (e.g., Ruthruff, 1996; Swenson, 1972). Although it cannot be ruled out that participants may, at times, resort to guessing when told to emphasize the speed of their responses, the fast-guess model is, by itself, not sufficient to explain the SAT.

The deadline model is an adaptation of the fast-guess model proposed by Ollman (1966; see also Yellott, 1971). It assumes that one may change the ration of fast guesses to slow stimulus-based responses to induce an SAT. According to this model, responses are generated after sufficient stimulus processing, or upon the expiration of a time deadline. Fast responses are not simply random guesses (such as in the fast guess model),

but are the "best guesses" guided by some amount of stimulus processing. Therefore, fast but less accurate responses are due to setting early deadlines that permit only partial processing of a stimulus. Slow, but more accurate, responses reflect longer time deadlines that permit greater stimulus processing. A temporal threshold is in stark contrast to models of information accumulation whereby a decision is reached once an evidentiary (non-temporal) threshold is reached. Unlike fast guessing, this model does not predict similar changes in accuracy associated with decreases in RT across varying levels of task difficulty, and it is this assumption of the deadline model that can explain findings of increased error rates under speed stress in difficult, relative to easier, experimental conditions. The rationale is that difficult discriminations require greater information processing and more time to process than easy discriminations. Therefore, with increased emphasis placed on speed, the accuracy of difficult discriminations will suffer more than discriminations requiring less time to process (Ruthruff, 1996).

The deadline model provides a rather intuitive and simplistic explanation for how we trade speed for accuracy; however, this account of SAT modulation has received little support. A major assumption of the deadline model that has failed to generalize to SAT findings is the "deadline model inequality" described in detail by Ruthruff (1996). This assumption may be illustrated by considering a task with two levels of difficulty (e.g., easy and hard), and two SAT conditions, one emphasizing speed and another accuracy. According to the inequality prediction, the cumulative distribution function of RTs (a plot of the probability that some RT will be less than or equal to a given value of RT) for the easy discrimination/speed emphasis (ES) condition should always be less than or equal to the sum of the easy discrimination/accuracy emphasis (EA) and hard

discrimination/speed emphasis (HS) conditions (Ruthruff, 1996). In other words, the cumulative distribution functions for each condition (i.e., ES, EA, HS) should be similarly shaped and simply shifted so that they do not cross over.

Ruthruff (1996) conducted two control experiments, each with ten subjects instructed to make a discriminatory response before specified response deadlines. Both tasks involved discriminating the relative brightness of two white squares presented to the left and right of a central fixation point. Participants were informed to make a left-key response if the square on the left was brighter than the right and a right key-press if the stimulus on the right was brighter than the left. The tasks were performed under two conditions of relative speed stress (i.e., accuracy or speed) and there were four levels of discrimination (i.e., easy, medium, moderate, and hard). In the accuracy condition, participants were not required to respond within a specified period of time and in the speed condition, they were instructed to respond prior to 390 milliseconds (ms) after the presentation of the stimulus. In the first experiment, participants were provided immediate feedback in the form of an auditory tone if their response latency was longer than the imposed deadline in the speed condition. In the second experiment, participants were given feedback only as to the time of their response, and not whether it was made before or after the imposed deadline.

The results of both control experiments conducted by Ruthruff (1996) were in clear violation of the "deadline model inequality" previously described as the cumulative distribution functions for the EA and HS conditions overlapped substantially. Consistent with previous research (for a review, see Wilding, 1974), Ruthruff (1996) concluded that neither the fast-guess and deadline models, nor combination of the two, were able to

account for the trading relationship found between speed and accuracy. Instead, he suggested that models involving the accumulation of information to a response criterion better account for the SAT.

Models of Accumulating Evidence

A second class of mathematical models, referred to here as models of accumulating evidence or sequential-sampling models, have had great utility in describing the findings from choice-decision tasks involving speeded decision-making (Pew, 1969; Ruthruff, 1996; Smith & Ratcliff, 2004). These models include diffusion (e.g., Ratcliff, 1978), random walk (e.g., Link & Heath, 1975), and accumulator models (e.g., McMillen & Holmes, 2006; Smith & Vickers, 1988). Although specific models vary in their parameters and accumulator dynamics, they share the assumption that noisy sensory evidence is accumulated from some starting point (baseline) to a criterion level (decision threshold), at which point a decision or response is made (Figure 2a; for a review, see Smith & Ratcliff, 2004). This decision process is in stark contrast to fast-guess models where fast responses are simply random guesses. A commonly used analogy to illustrate information accumulation and the relationship between speed and accuracy is that of reading: the more time we are given to read an article, the more information we may accumulate, and thus the more accurate we are in our understanding of what we have read. In the context of choice-RT tasks, the more time we are given to process a stimulus, the more we may accumulate information about that stimulus and thus the more accurate we are in selecting a discretionary response.

Although models of information accumulation may differ in their specific parameters and how they are implemented, they share the assumption that stimulus-based

evidence is accrued in the form of what Osman et al. (2000) call a "growth function." The growth function reflects accumulating evidence across time, beginning at some baseline and growing to reach a specific threshold resulting in a decision (e.g., response selection, stimulus discrimination). In the case of response selection, RT reflects the time it takes for the evidence to accrue along the growth function to reach threshold. The growth function is assumed not only to be influenced by the accumulation of sensory-based evidence, but may also be affected by noise or decision biases. Using the above example of reading, even if one is given sufficient time to read an article one may still make errors due to prior letter or word combination expectancies. These models may not only be applied to response-selection, but may account for numerous cognitive processes such as stimulus discrimination, decision-making, response-selection, and response execution/inhibition.

As discussed so far, models of information accumulation describe how sensory evidence is accumulated to a decision threshold; however, the question still remains as to how these models account for the SAT. One way these models have accounted for the SAT is by changing the baseline-threshold distance. This may be accomplished by either lowering the threshold (Figure 2b) or raising the baseline (Figure 2c). The assumption made when decreasing the distance between the baseline and threshold is that the growth function requires less time and less evidence to reach threshold. Furthermore, shorter distances between the baseline and threshold increase the probability that internal or external noise may reach supra-threshold levels by chance (see Osman et al., 2000).

One specific type of sequential-sampling model that has tried to account for SAT is the diffusion model (for a review, see Smith & Ratcliff, 2004). There are a number of

variations of diffusion models; however, they all involve a single evidentiary total being calculated, with the evidence in favor of one choice being evidence against another (Link & Heath, 1975; Smith & Ratcliff, 2004). This form of the diffusion process has two or more thresholds, one for each decision. For example, in a two choice task involving left and right responding, evidence for a right response may be given a value of +1 and approach the "right" threshold. Evidence for a left decision may be given a value of -1 and approach the "left" threshold. If evidence accumulated in favor of a left response is greater than that accrued for the right response, and this amount of differential evidence reaches the "left" threshold, then a decision to respond left would occur. In the context of this model, errors occur when the noise and variability in the stimulus quality is high, resulting in the growth function reaching the wrong decision threshold (for a review, see Smith & Ratcliff, 2004). Diffusion models permit the combination of accuracy and RT variables to generate a "single measure of stimulus information, drift rate, which drives the decision process" (Ratcliff, 2002, p.290). The drift rate plays a particularly important role in the decision-process. It reflects the rate of accumulation of evidence in support of one or more decisions across time. The sign of the drift rate (i.e., negative or positive) indicates the direction of accumulation toward a positive or negative boundary (e.g., right and left response) and the magnitude of the drift rate reflects the rate of accumulation (i.e., unit of evidence per unit time). A second parameter of diffusion models that is a key to understanding the SAT is the threshold (or boundary) separation. This parameter reflects the magnitude of information needed to accumulate from a starting baseline to the decision threshold (Ratcliff, 2002). Boundary separation is analogous to the baseline-threshold distances depicted in Figure 2.

Ratcliff (2002) conducted a two-choice brightness discrimination study to test the diffusion model and how it may account for SAT. Participants in the study were first presented with a fixation cross at the center of a gray screen. Next, a stimulus was displayed, consisting of a 64 x 64 square of black and white pixels presented on the gray background, followed by a mask. Six levels of stimulus brightness were used in the experiment, accomplished by using six values for the probability of a pixel being white: .350, .425, .475, .525, .575, and .650. Additionally, there were three conditions of stimulus duration defined by the amount of time the stimulus was presented: 50, 100, and 150 ms, resulting in a total of eighteen conditions. Participants were instructed to identify the brightness of the square. In addition to the manipulations of brightness and duration, participants were required to switch between accuracy and speed emphasis on a block-by-block basis. In the speed condition, participants were instructed to respond as fast as possible, and in the accuracy blocks participants were instructed to respond as accurately as possible. For responses in the accuracy condition there was no feedback about RTs; however, if a response was incorrect, "ERROR" was presented on the screen. Accuracy feedback was not provided in the speed condition; however, RT feedback was provided.

Ratcliff (2002) varied the duration and brightness of the stimulus to vary the amount of processing time and the amount of information available. By combining these manipulations with SAT instructions, Ratcliff was able to acquire a distribution of responses ranging from chance to perfect accuracy. As predicted by the SATF illustrated in Figure 1, Ratcliff (2002) found that responses in the speed condition were faster and less variable than responses in the accuracy condition. Moreover, correct responses were slower than incorrect responses in both the speed and accuracy conditions.

Upon fitting the resultant data using a diffusion model (see Ratcliff & Rouder, 2000), it was apparent that drift rate varied normally from trial to trial and increased as a function of stimulus duration (i.e., processing time), until reaching a maximum asymptotic value determined by the brightness of the stimulus (i.e., evidence). Ratcliff (2002) concluded that drift rate accounted for the small trial-by-trial variations in speed and accuracy within a single SAT condition (i.e., speed versus accuracy) whereas the only variable successful in accounting for SAT between speed and accuracy instructions was boundary separation. Based on these findings, Ratcliff (2002) suggested that the SAT is not modulated by changing the relative rate of accumulation, but is the result of changing the distance between the baseline and threshold. Two fundamentally different, and mathematically equivalent, mechanisms may be employed to change the magnitude of threshold (boundary) separation: (1) variable threshold, and (2) variable baseline (see Hanes & Schall, 1996; Ivanoff et al., 2008; Ratcliff, 2002; Reddi & Carpenter, 2000; Smith & Ratcliff, 2004).

The variable threshold account of SAT, illustrated in Figure 2b, holds a constant baseline while the threshold is varied. The assumption is that the growth function is similar regardless of speed-accuracy emphasis. Moreover, information accrual is generally a passive process (i.e., there is no greater "effort" with speed or accuracy emphasis). According to this proposal, the SAT is the result of a decision being triggered by more or less information. When instructed to be fast, the threshold is lowered closer to the baseline resulting in faster, yet less accurate responding due to less sensory evidence being accumulated and the increased noise. In contrast, when instructed to be accurate,

the threshold may be elevated relative to the baseline to accommodate greater accumulation of evidence (for a review, see Bogacz et al., 2009).

The variable baseline account of SAT, illustrated in Figure 2c, holds a constant threshold is necessary to trigger a decision (Hanes & Schall, 1996), while the baseline is shifted closer to, or further from, a threshold. According to this proposal, the baseline shift occurs before the stimulus is presented. It is often construed as a decision bias, based on prior expectations (e.g., Laming, 1968). The baseline-shift may also be construed as a generalized increase in activity across a set of separate accumulators (see Smith & Ratcliff, 2004, for a discussion of this sort of model). This might occur when all responses show some level of priming. Thus, when instructed to be fast, the baseline is raised closer to a particular threshold, decreasing decision time while making it more likely that noise will trigger an erroneous decision. In contrast, when instructed to be accurate, the baseline remains further from the threshold to accommodate greater accumulation of evidence, thus reducing the likelihood that noisy stimulation may cause the decision process to reach threshold (for a review, see Bogacz et al., 2009). This account of the SAT has received empirical support from recent fMRI investigations of SAT and electrophysiological investigations of response preparation and SAT (see below for a complete discussion of this research).

Another model of the SAT explicitly pinpoints a neural mechanism for how fast responses are executed under demands to respond quickly. According to this "release-from-inhibition" hypothesis, the striatum (i.e., the caudate/putamen complex), an input region in the basal ganglia circuit, releases inhibitory control over the thalamus, midbrain, and brainstem (Bogacz & Gurney, 2007; Brown, Bullock, & Grossberg, 2004;

Lo & Wang, 2006). Before a fast response can be made, the inhibitory control of the basal ganglia over other motoric brain regions must be released, resulting in faster responding (Lo & Wang, 2006). This mechanism may also result in inaccurate performance as the selected response may be generated before the stimulus is presented. The striatum and pre-SMA are known to form a "closed-loop motor circuit" involved in preparation of voluntary action plans, with the striatum reducing inhibition in motor regions to permit faster, yet more error-prone response selection (Baunez et al., 2001; Forstmann et al., 2008; Lo & Wang, 2006).

Recent fMRI Investigations of the SAT

Mathematical models of information accumulation provide a theoretical context for behavioural and functional studies of decision-making but are limited in their ability to determine whether the SAT is implemented as a variable threshold or variable baseline. For example, Ratcliff's (2002) study suggested that a variable baseline-threshold distance was able to account for the relationships between RT and accuracy found in two-choice discrimination SAT studies. It was not possible, however, to determine whether this was the result of a change to the baseline *or* threshold (cf. Ratcliff 2006). Although these behavioural studies can provide insights into the dynamics of information processing, functional neuroimaging - such as fMRI analysis of transient blood-oxygen level dependent (BOLD) signal- is better suited to test whether SAT is modulated by a changing baseline or threshold because it can provide a continuous measure of activity over time.

fMRI is frequently used to detect transient changes in nuclear magnetic resonance (nmr) signal caused by changes in cerebral blood flow and blood-oxygen concentrations

related to changes in regional neural activation (for a review, see Logothetis et al., 2001; Logothetis, 2003). In this technique, the BOLD signal is sensitive to transient changes in deoxyhemoglobin concentration during task performance. This BOLD signal, in turn, may be mapped onto an anatomical MRI image for localization of the activity. By investigating BOLD signal changes in relation to specific task events, researchers may infer the dynamics of neural activity in specific cortical regions across time and related to specific stages of task performance (for a review, see Buckner, 1998).

In the context of models of information accumulation, changes in BOLD signal have been understood to reflect the accumulation of neural evidence from some baseline toward a decision or response threshold (Logothetis, 2003). Because BOLD fMRI does not provide an absolute measurement of deoxyhemoglobin, transient changes in BOLD signal are relative to a particular baseline. Therefore, to identify whether SAT is modulated by changes in baseline and/or threshold activation, the transient changes in BOLD signal due to stages of cognitive processing during task performance must be disentangled from a sustained level of baseline signal related to changes in SAT instruction. Once separated, activity in specific neural regions may be evaluated according to the predictions of the variable threshold versus variable baseline accounts of the SAT.

As stated earlier, it is difficult to disentangle the variable threshold and variable baseline hypotheses using behavioural data because all that is typically measured is the duration of all processing stages (i.e., RT), from sensation to action. However, it may be possible to continuously measure the neural activity associated with the decision-processes using event-related fMRI. According to the variable threshold hypothesis (see

Figure 2b), a region that integrates neural information to a threshold ought to demonstrate greater *prolonged* neural activity following the presentation of the stimulus for accuracy than for speed conditions. The prolonged activity reflects the greater duration of information processing under accuracy conditions. However, baseline activity, to a "speed" or "accuracy" cue would be equivalent. In contrast, the variable baseline hypothesis predicts that baseline (i.e., pre-stimulus) activity ought to be greater following speed than accuracy instructions. Once the stimulus is presented (and evidence is available), the evidentiary distance to a fixed threshold would be less in the speed condition than it would be in the accuracy condition. Thus, following the presentation of the stimulus, there would be less neural activity in the speed than the accuracy condition. Three recent fMRI studies (Forstmann et al., 2008; Ivanoff et al., 2008; van Veen et al., 2008) have investigated SAT modulation in the context of information accumulation models and were concerned mainly with how SAT is modulated in the brain (i.e., changing baseline or threshold), where in the brain this modulation is accomplished, and what stages of cognitive processing are affected.

van Veen et al. (2008) investigated the SAT during the performance of a Simon task (i.e., responses are selected according to the non-spatial feature of a spatial stimulus; see Simon, 1969). Twenty participants were instructed to respond to the non-spatial feature of a visual stimulus; that is, participants were instructed to respond left to a red square and right to a green square (this instruction was counterbalanced across participants) regardless of whether the target was presented to the left or right of a central fixation point. An incongruent trial is one where the target location is presented in the opposite location of the required response (e.g., a red stimulus coding for a left response

is presented on the right). A congruent trial is one where target location and the required response correspond (e.g., a red stimulus coding for a left response is presented on the left) and involves less response conflict (DeJong et al., 1994; Kornblum & Lee, 1995; O'Leary & Barber, 1993). The Simon effect refers to the performance advantage (i.e., faster and more accurate responding) for congruent versus incongruent trials (Simon, 1969).

Trials were divided into mini-blocks of four, eight, or twenty trials with seven mini-blocks per run. At the beginning of every mini-block, participants were given an instructional cue (a large uppercase "A" or "S") indicating that they should emphasize the accuracy or speed of their responses. This instructional cue lasted 1000ms, after which time the cue became smaller and served as a central fixation point during the remaining trials in the mini-block. Two square placeholders flanked the central fixation on the right and left. Targets were presented as red or green squares within the placeholders for 150ms. The trial ended after a 2850ms fixation screen. Speed and accuracy instructions were held constant for the duration of each mini-block. Congruent trials comprised 2/3 of all trials whereas incongruent trials comprised the remaining 1/3. On congruent trials the response indicated by the stimulus identity and the response corresponding to the location of the stimulus are the same and do not conflict. On incongruent trials, however, they conflict (see Hommel, 1993). Thus, encountering conflict on an incongruent trial was less likely than encountering a non-conflicting congruent trial. A smaller proportion of incongruent trials, relative to congruent, has been shown to increase the level of conflict in some tasks (for a review, see Ridderinkhof, 2002).

Behaviourally, van Veen et al. (208) found a Simon effect and the expected SAT, and the Simon effect (i.e., conflict) was larger in the speed condition than it was in the accuracy condition. To separate the baseline activity related to the SAT instructional cue from transient trial-related activity, they performed a multiple regression analysis using separate regressors for the baseline and transient BOLD signal changes in both speed and accuracy mini-blocks. Event-related analyses were also performed on the SAT cue to illustrate the time-course of neural activity related to the SAT cue and the Simon trials. To determine whether the neural activity related to the SAT cue was sustained across the Simon task in the mini-block (as would be expected in a neural region responsible for a baseline shift), , van Veen et al. (2008) used a block-design analysis whereby a separate baseline regressor accounted for the first five and last eight scans of each mini-block. They predicted that an area responsible for changing its baseline activity to accommodate SAT demands would demonstrate higher fMRI activity for speed, relative to accuracy instructions, for the initial five scans of each mini-block.

By conducting voxelwise paired *t*-tests between speed and accuracy baseline regressors, van Veen et al. (2008) found evidence for greater sustained baseline activation following speed instructions in a distributed network of brain regions (for a summary, see Table 1), found to be involved in the preparation and execution of movements. The dorsolateral prefrontal cortex (DLPFC), supplementary motor area (SMA), anterior cingulate cortex (ACC), and regions known to be involved in motor processes such as the thalamus, basal ganglia, and cerebellum, were all susceptible to the SAT manipulation. This analysis did not reveal any region demonstrating significantly greater sustained baseline activity for accuracy relative to speed instructions, and no speed-accuracy

differences were found in visual sensory regions indicating that adopting a sensory or perceptual attentional strategy did not contribute to the SAT.

According to the variable baseline hypothesis, regions involved in SAT modulation should exhibit reduced transient BOLD activation following a response signal in the speed condition relative to the accuracy condition, and van Veen et al. (2008) found activation patterns in the DLPFC to support this hypothesis. To determine whether DLPFC activity is related to activation in other brain regions identified by the main speed versus accuracy contrast (see Table 1), van Veen et al. (2008) conducted a psychophysiological interaction analysis (for a review, see Friston et al., 1997). A psychophysiological interaction analysis is a correlational method used to identify whether the connectivity between brain regions changes under different experimental manipulations. Using the left and right DLPFC as seed regions in this analysis revealed patterns suggesting that the DLPFC controls SAT by changing the baseline activity in motor, pre-motor, and executive regions. These authors suggested that the DLPFC provides a top-down influence on other regions involved in motor planning and executive control by controlling their baseline level of activation. However, another possible explanation for the involvement of the DLPFC is that it is involved in overcoming response conflict (e.g., McDonald, Cohen, Stenger, & Carter, 2000). Thus, it would be expected that greater sustained DLPFC activity would accompany situations involving greater response conflict. In-line with this prediction, the speed-accuracy difference in sustained baseline activation, averaged across the left and right DLPFC, was significantly greater for participants who made more errors in the speed relative to accuracy condition.

Although van Veen et al. (2008) suggested that the DLPFC controls SAT by modulating baseline activation in motor and executive regions, it is equally probable that SAT-related differences in the DLPFC may reflect conflict resolution processes involved in Simon task performance. For participants to maximize accurate and timely responding, the detection of response conflict (or situations where relevant and irrelevant task dimensions compete during response selection) must be supplemented by a means for conflict resolution. The prefrontal cortex (PFC) is believed to play a particular role in resolution of this conflict through attentional control by maintaining and controlling attention to relevant task information while suppressing irrelevant information (for a review, see Van Veen et al., 2006; Miller & Cohen, 2001). According to a conflict-based model proposed by Van Veen et al. (2006), the ACC detects response conflict and the PFC exerts attentional control to maximize processing of relevant task dimensions for correct responding. Because speed emphasis has been shown to increase the level of conflict involved in tasks such as the Simon task (see Ridderinkhof, 2002), it is possible that the change in baseline DLPFC activation is related to resolving greater response conflict under speed instructions, and not necessarily directly related to the SAT.

Ivanoff et al. (2008) conducted an fMRI investigation of the SAT in a motion discrimination task. This task involves discriminating the direction of coherent motion of dots in a cloud of randomly moving dots and is frequently used to investigate the dynamics of information processing and perception (for detailed description, see Gold & Shadlen, 2007). Furthermore, these tasks allow the experimenter to quantitatively increase or decrease perceptual difficulty by changing the proportion of dots moving coherently in one direction. To identify regions involved in specific stages of

performance in the discrimination task, twenty-one participants performed a block-design localizer task where participants were required to respond to trials involving 60% motion coherence and passively view trials involving a static version of the display. Because they predicted that the SAT would be modulated in a subset of regions involved in performance during the localizer task, they contrasted brain activation in moving versus static displays to reveal a distributed network of brain regions that would be later probed using the event-related SAT task. This method of localization has been suggested as a means of ensuring independent analyses, as non-independent correlation analyses have been shown to greatly inflate implausibly strong relationships between neural activity and behaviour (for a review, see Vul, Harris, Winkielman, & Pashler, 2009).

To probe the brain regions identified from the localizer task, thirteen participants performed an event-related motion discrimination task involving SAT manipulation. As explained previously, these tasks require participants to discriminate the direction of coherent motion in a cloud of randomly moving dots and allow the experimenter to quantitatively increase or decrease the difficulty by changing the relative number of dots moving coherently in one direction. In this task, participants were visually cued at the beginning of every block with 'SPD' (speed) or 'ACC' (accuracy) for 3s, indicating that they were to emphasize the relative speed or accuracy of their responses. Following the SAT cue, a fixation period lasted 3s, and was followed by a random motion display was presented for 6s in a red square outline. The outline then turned green, indicating that a trial had begun. Participants were instructed to make a left button press if they detected coherent motion in a leftward direction, and a right button press if they detected coherent motion in a rightward direction. The green frame was then changed to red, indicating the

trial was over, with the stimuli returning to randomly moving dots when participants made a response. The random display remained with a red outline for 13.5s before turning green, indicating the beginning of the next trial. Participants were instructed to respond as soon as they could detect motion in the speed condition and to take as much time as needed to ensure an accurate response in the accuracy condition. Feedback was provided according to the type of SAT cue: RT feedback was provided at the end of every run for the speed blocks, and accuracy information was given at the end of every run for the accuracy blocks. Participants completed 4-5 runs, with three blocks per run and seven trials per block.

The event-related task used by Ivanoff et al. (2008) involved three types of randomly presented trials: coherence, baseline, and trials used to ensure participants were vigilant in differentiating the motion stimuli. Coherence trials comprised 3/7 of the trials in a block. On these trials a set of dots started to move coherently either left or right at 0s, 4.5s, or 9s, following the beginning of the trial (i.e., when the outline turned green) and the proportion of dots moving coherently increased by one percent per second. Baseline trials comprised 2/7 of trials in a block and involved continuous random motion throughout the entire trial. The remaining 2/7 of trials were not included in the analysis and involved motion coherence beginning at the onset of the trial, with the proportion of coherently moving dots increasingly rapidly at two percent per second.

Behavioural analyses revealed the expected SAT, with participants responding faster and less accurately in the speed relative to the accuracy condition. Furthermore, by using the decision criterion (c) from signal detection theory (Macmillan & Creelman, 1991), Ivanoff et al. (2008) were able to detect a greater response bias when participants

were instructed to emphasize response speed over accuracy. To identify differences in neural activation related to SAT instruction, the hemodynamic responses were response-locked and baselined to the onset of motion coherence. Regions involved in information accumulation were expected to exhibit increasing activation from some baseline level at the onset of motion coherence with the activation at the time of a response corresponding to the decision threshold. Therefore, by analyzing the entire hemodynamic response function (HRF), from speed and accuracy conditions, Ivanoff et al. (2008) were able to detect differences in threshold levels of activation between these two conditions. Results of this analysis revealed that sensory and primary motor regions were not differentially affected by SAT manipulation; however, some lateral prefrontal and medial frontal regions did demonstrate differential activity following speed and accuracy emphasis (see Table 1). The accrual of neural activity in the posterior lateral PFC (pLPFC) and bilateral pre-SMA was found to be greater following accuracy emphasis than speed, reflecting the greater accrual of information predicted by the variable threshold and baseline hypotheses.

To determine whether the changes in transient BOLD signal between speed and accuracy were due to a change in baseline versus threshold, Ivanoff et al. (2008) analyzed activity during the baseline trials. Because no motion coherence was present in these trials, they argued that any SAT differences during these trials reflected the resting baseline for speed versus accuracy conditions. Consistent with the variable baseline hypothesis illustrated in Figure 2c, the right pre-SMA demonstrated greater baseline activity following speed relative to accuracy instructions, and greater coherence (stimulus-related) activity following accuracy than following speed instructional cues.

This pattern of activation in the pre-SMA led the authors to conclude that when speed is emphasized increased baseline activity in the pre-SMA increases the internal readiness to respond. In contrast, the pLPFC activity was correlated with the c (the criterion metric of signal detection theory), suggesting that this region seems to play a role in setting the evidentiary threshold (i.e., Figure 2b). Similar to van Veen et al. (2008), Ivanoff et al. (2008) did not find any evidence that adopting differential sensory versus motor strategies modulates SAT, as no effect of SAT instruction was found in primary motor or sensory regions. In other words, Ivanoff et al. (2008) did not find evidence supporting Lange's (1888/2009) proposal that the SAT is the result of adopting differential sensory versus motor preparatory sets. Rather, Ivanoff et al. (2008) suggest that the SAT is controlled by differentially changing the internal preparation to respond via the pre-SMA, with increased preparation resulting in faster and less accurate performance. Furthermore, they suggest that individuals may control the amount of external sensory evidence needed to accrue to reach a decision via the pLPFC.

Although these findings lend further support for a variable baseline account of the SAT in medial frontal cortical regions, the motion coherence task used by Ivanoff et al. (2008) involved an element of conflict similar to the Simon task in van Veen et al's (2008) work. In a Simon task, the goal is to respond to the non-spatial feature (i.e., colour) of a stimulus, and ignore the location of the stimulus. In a motion coherence task, the goal is to find dots that move with a common fate, and ignore those that move in orthogonal or the opposite directions. Prior research has demonstrated Simon-like effects from motion coherence stimuli (Bosbach, Prinz, & Kerzel, 2004), suggesting that Ivanoff et al.'s task is not necessarily response-conflict free.

Recall that the "release-from-inhibition" hypothesis predicts greater activity in the striatum on 'speed' than on 'accuracy' trials. This activity in the striatum is presumed to reflect a greater release from inhibition in other motor regions of the brain involved in response preparation and execution (i.e., thalamus, pre-SMA, brainstem, etc.). To test this hypothesis, Forstmann et al. (2008) conducted a study of nineteen participants performing a motion coherence task (discussed previously) with participants being cued at the beginning of a trial with a "SN", "NE", or "AK", indicating to emphasize speed, balance speed and accuracy, or emphasize accuracy, respectively. If participants were instructed to emphasize speed, they received feedback at the end of a trial indicating they were "too slow" if their RT exceeded a 450ms criterion. If participants were instructed to balance speed and accuracy (i.e., "NE" cue), they were provided feedback indicating they were "too slow" if their RT exceeded 750ms, and "incorrect" if their response was not correct. If participants were instructed to emphasize accuracy, they received feedback stating "incorrect" if their response was not correct. They were not provided feedback as to the accuracy of their responses in the speed-emphasis condition, and likewise not provided feedback on their RT in the accuracy-emphasis condition.

Behavioural results revealed a tradeoff between speed and accuracy with responses being faster and less accurate following speed instruction relative to neutral or accuracy, with the greatest SAT found between speed and accuracy conditions. To identify brain regions responsible for the SAT, Forstmann et al. (2008) conducted a conjunction analysis between two contrasts: speed versus neutral and speed versus accuracy. This method of analysis is used to identify activation in brain regions common to both contrasts (for a review, see Nichols et al. 2005). Results of the conjunction

analysis revealed two distinct brain regions that increased activation following speed instruction in absence of the target stimulus; the right anterior striatum and right pre-SMA (see Table 1).

To elucidate the roles of the striatum and pre-SMA in the SAT, Forstmann et al. (2008) correlated percent BOLD signal change in the anterior striatum and pre-SMA with various parameters from an accumulator model (i.e., linear ballistic accumulator model; for a review, see Brown & Heathcote, 2008). They found that individual activity in both the right anterior striatum and pre-SMA negatively correlates with the individual caution parameters estimated from the model. The caution parameter of the linear ballistic model is an estimate of the baseline-threshold distance. It does not, however, provide an estimate for the baseline or threshold separately. Thus, those participants who had greater accuracy-speed differences in the baseline-threshold distance also had greater speed-accuracy activity level differences in the striatum and pre-SMA. Consequently, Forstmann et al. (2008) suggested that as time pressure increased, individuals increased baseline activation in the striatum and pre-SMA to permit faster, and thus less inhibited, responding.

Although Forstmann et al.'s (2008) findings provide support for the involvement of the basal ganglia and pre-motor cortical regions in modulating SAT demands by differentially exerting or releasing inhibitory control over motor regions in the brain following instructions to emphasize speed, two issues concerning their findings and methodology warrant discussion. First, although they identified medial, middle, and inferior frontal, and superior temporal regions as having greater activation following accuracy instructions relative to speed, they failed to discuss these findings and

seemingly restricted their analyses to regions exhibiting greater activation during speed relative to accuracy instructions. Therefore, it is still unknown what neural mechanisms, if any, are differentially implemented when emphasizing accuracy over speed. Secondly, the SAT cues were randomly presented at the beginning of each trial and changed from trial to trial permitting the analysis of BOLD signal change due to the cue separate from target-related activation. One issue with this technique is that it requires participants to change response strategies from trial to trial and in a random fashion to accommodate the unpredictable SAT demands of each trial, much like the paradigms used in the task switching literature (Monsell, 2003). A robust and well-replicated finding in the task switching literature is that when individuals are required to switch between tasks there is an increase in reaction time and reduction in accuracy (i.e., the "switch cost"; Dove, Pollmann, Schubert, Wiggins, & von Cramon, 2000; for a review, see Monsell, 2003). Therefore, Forstmann et al's (2008) findings may simply reflect how individuals make faster or slower responses when switching between trials in tasks with different speed-accuracy emphasis.

The studies conducted by Forstmann et al., (2008), Ivanoff et al., (2008), and van Veen et al., (2008), have provided strong support for the involvement of the pre-SMA in shifting baseline-related activity during the SAT. Forstmann et al. (2008) proposed that a threshold shift in the basal ganglia circuit whereby increased activation in the basal ganglia and pre-SMA following a cue to emphasize speed results in an increased readiness to respond. The findings of van Veen et al. (2008) and Ivanoff et al. (2008) provide evidence in favor of a lateral prefrontal role in the SAT. Forstmann et al. (2008) did not find evidence suggesting lateral prefrontal regions were involved in modulating

SAT. This finding is not surprising considering that the prefrontal cortex has been implicated in resolving and accommodating task conflict. It is possible that a higher proportion of coherent motion (60% in Forstmann et al., 2008) do not produce as much conflict as less coherent motion (7-10% in Ivanoff et al., 2008). While this proposal is speculative, it would be consistent with of the susceptibility of lateral prefrontal regions by the SAT as observed by van Veen et al. (2008) and Ivanoff et al. (2008). In other words, the lateral prefrontal cortex may not play a significant role in the SAT; it may simply reflect the resolution of increase stimulus/response conflict in speed conditions.

Response Preparation and the SAT

A second source of support for the variable baseline hypothesis has come from response cueing studies that investigate the effect of prior response information on the SAT. The response-cueing paradigm was first introduced by Rosenbaum (1980) to investigate response preparation. This method involves two stimuli, a response-cue and target stimulus, separated by a foreperiod (or preparatory interval; see Band, Ridderinkhof, & van der Molen, 2003; Mattler, 2005; Rosenbaum, 1980; Rosenbaum & Kornblum, 1982; Sangals, Sommer, & Leuthold, 2002). The response-cue provides information that permits the selection and preparation of a particular response, such as the direction of a response (i.e. left versus right). On the other hand, the target stimulus provides information about when (of if) the response is to be executed. The selection and preparation of a response is believed to occur during the preparatory interval prior to target presentation. Response-cueing is a technique that has previously been employed in electrophysiological and functional imaging studies to examine neural and physiological

changes during stimulus perception, response selection and preparation, and response execution (e.g., Mattler, 2005; Rosenbaum & Kornblum, 1982).

Electrophysiological studies have investigated the effect of response-cueing on underlying cortical activity by examining a readiness potential waveform extracted from electroencephalography (EEG) recordings found prior to a left or right motor response (Coles, 1989; Eimer & Schlaghecken, 1998; Leuthold, Sommer, & Ulrich, 1996). This lateralized readiness potential (LRP) is a difference wave calculated by subtracting ipsilateral activity in electrodes centered over the precentral gyri from activity in the corresponding contralateral electrodes. The resultant LRP waveform has been taken to reflect the accumulation of information to a decision threshold in motor and pre-motor cortical regions (Leuthold, Sommer, & Ulrich, 1996; Sangals, Sommer, & Leuthold, 2002). For example, the accumulation of evidence in favor of selecting a right response would result in a greater LRP waveform recorded in electrodes over the left frontal cortex. The preparatory LRP following a response-cue is thought to reflect underlying cortical processes related to response selection, preparation, and differential strategies at these stages of task performance related to modulation of SAT demands (Leuthold et al., 1996; Sangals, et al., 2002; Ulrich, Leuthold, & Sommer, 1998).

Band, Ridderinkhof, and van der Molen (2003) investigated the SAT using EEG time courses of response preparation in a modified go/no-go task. Participants were instructed to balance speed and accuracy or to emphasize speed at the cost of accuracy. The researchers used a response-cueing type of design involving a prime (S1) that indicated which response was *likely*. A probe (S2; following 1500ms) followed the response cue and indicated whether the primed response was to be executed or inhibited.

By manipulating the SAT instruction, they believed they could modulate the extent to which subjects prepare the primed response as well as the strength of inhibition required on no-go trials. Furthermore, having two stimuli that code for different response parameters allowed for functional and behavioural analyses of specific cognitive processes occurring at and between the presented stimuli (e.g., decision-making activity during the 550ms presentation of S1; preparatory activity 200ms prior to S2 onsets when S1 was no longer present; response execution activity to S2) (Band et al., 2003; Leuthold et al., 1996). Band et al. (2003) found an LRP during the foreperiod (i.e., the time period following S1 and prior to S2), suggesting that participants had prepared their response during this interval. This preparatory LRP waveform was larger following speed instruction, suggesting that faster responding may be the result of greater response preparation during this foreperiod.

A second study conducted by Sangals et al. (2002) examined RT, accuracy, and LRPs during performance of a go/no-go response-cueing task with varying degrees of emphasis on response speed. Participants were provided visual response-cues indicating partial or full information about the response they should prepare (i.e., an upward or downward movement of the left or right index finger). A visual target stimulus followed and consisted of the numbers 1, 4, 6, or 9. Each number indicated which one of four possible movements (i.e., left/up, right/up, left/down, or right/down, respectively) had to be made. The letter 'X' was presented 10% of the time and indicated that a response was to be withheld (i.e., it was the 'no-go' signal). Therefore, while participants were able to prepare for one dimension of their response (i.e., up/down or left/right), it was not until the target stimulus was presented that they were provided with complete response

information. Time pressure was manipulated from high to low by imposing rewards or fines for RTs falling within or outside specific time periods (i.e., high time pressure would result in a reward for RTs falling within a window determined following each experimental block).

Sangals et al. (2002) found that increasing speed demands of the task was accompanied by a reduction in RT and an increase in false alarm errors; however, no bias toward a specific response direction was observed, indicating participants utilized the response-selection information provided by the response-cue. Increased emphasis placed on response speed did not result in a difference of LRP onset, but was found to increase the amplitude. This finding is consistent with the idea that response preparation is responsible for the shift in baseline activity with an emphasis on response speed.

These electrophysiological findings are consistent with recent functional imaging studies (Ivanoff et al., 2008; van Veen et al., 2008), suggesting that baseline shifts in response preparation play a key role in the SAT. Greater response preparation on trials with a speed emphasis can account for faster responses to the 'go' stimuli and more false alarm errors to 'no-go' stimuli. With an elevated baseline, noisy sensory information from target stimuli could inadvertently trigger the prepared response, even following a 'no-go' stimulus.

Summary

The key findings from electrophysiological and functional imaging studies suggest that SAT is modulated by adopting a motor preparation strategy (e.g., Band et al., 2003; Forstmann et al., 2008; Ivanoff et al., 2008; Sangals et al., 2002; van Veen et al., 2008). First, increasing the emphasis on response speed increases activity in the pre-

SMA, a neural region implicated in response selection and preparation. Ivanoff et al., (2008) suggested that the greater activity in the pre-SMA may reflect a greater internal urge to respond. Second, Forstmann et al., (2008) suggested that the basal ganglia play a vital role in the SAT by increasing or decreasing its inhibitory control over the thalamus, midbrain, and brainstem. These two findings, combined with similar results from other electrophysiological and functional imaging studies, suggests that SAT is modulated by adopting a motor preparation strategy (e.g., Band et al., 2003; Sangals et al., 2002; van Veen et al., 2008). That is, when emphasizing speed over accuracy one may increase their preparation *of* a response via increased activity in the pre-SMA. Similarly, one may increase their preparation *to* respond via increased activity in the basal ganglia. However, because the tasks used these studies did not sufficiently separate processes involved with SAT instructions from those involved with response preparation and those involved with response execution, the processes effected by SAT-related changes in the pre-SMA and basal ganglia are still unknown.

Two additional key findings are of interest for the current study. First, the lateral prefrontal cortex has been implicated in the SAT (Ivanoff et al., 2008; van Veen et al., 2008); however, its role may be more closely tied to resolving conflict than the SAT. No fMRI study that has found the PFC to be involved with modulating the SAT has used stimuli that do not require the resolution of conflict. Therefore, it is still unknown whether the involvement of the PFC in the SAT is related to increased conflict resolution processes when emphasizing response speed or related to some other cognitive process. Secondly, no study to date has found clear evidence for regions of the brain that selectively increase their activity under accuracy conditions. This finding may simply be

due to the inability of prior studies of the SAT to disentangle processes related to SAT instructions from processes involved with response preparation and response execution.

fMRI Analysis of the SAT during Task- and Response Preparation

The purpose of the current study is to identify, using fMRI, the neural correlates of the SAT during performance of a response-cueing go/no-go task. Unlike previous fMRI investigations of the SAT, neural activity related to SAT instruction will be disentangled from neural activity related to response preparation to investigate whether individuals adopt sensorimotor strategies to accommodate SAT demands (cf. Lange, 1888/2009). A modified go/no-go task will be used with a sequence of three different visual signals indicating: i) whether to emphasize speed ('SPD') or accuracy ('ACC') when responding; ii) what response will be required (a left or right key-press, indicated by the gender of a face image); and iii) whether the planned response is to be executed or withheld ('Go' or 'No-Go', indicated by an image of either a single- or two-level house). Therefore, this task permits the isolation of the effects of SAT instructions on response preparation, inhibition, and execution (Falkenstein, Hoorman, & Hohnsbein, 1999; Gomez, Ratcliff, & Perea, 2007; Kiehl, Liddle, & Hopfinger, 2000; Konishi et al., 1998; Simmonds, Pekar, & Mostofsky, 2008). Because the use of a response-cue permits differential analysis of the processes involved in response preparation (Band, Ridderinkhof, & van der Molen, 2003; Mattler, 2005; Falkenstein et al., 1999; Gomez et al., 2007; Kiehl et al., 2000; Konishi et al., 1998; Rosenbaum, 1980; Rosenbaum & Kornblum, 1982; Sangals, Sommer, & Leuthold, 2002; Simmonds et al., 2008), this task will allow for a detailed analysis of the effect of SAT manipulation on strategies employed during response preparation.

To further ensure that participants make appropriate tradeoffs between speed and accuracy, feedback is provided at the end of every experimental run informing

participants of their RT during blocks emphasizing response speed and accuracy during blocks emphasizing accuracy. This combination of instructions and feedback has been shown to induce SATs in a number of previous studies and across various tasks (for a review, see Franklin & Okada, 1983; e.g., Carrasco & McElree, 2001; Forstmann et al., 2008; Ivanoff et al., 2008; Ratcliff 2002).

Based on prior research, it may be expected that individuals make faster, albeit less accurate, responses by increasing the internal readiness to respond and placing greater importance on preparing a forthcoming motor response (Forstmann et al., 2008; Ivanoff et al., 2008). There is recent fMRI and electrophysiolgical evidence that further suggests that the PFC is critically involved in modulation of SAT demands by increasing baseline activation following speed instructions relative to accuracy (Band et al., 2003; Forstmann et al., 2008; Ivanoff et al., 2008; Sangals et al., 2002; van Veen et al., 2008).

The separation of SAT preparation, response preparation, and response execution/inhibition provides distinct benefits from prior fMRI investigations of the SAT. First, by providing SAT instructions at the beginning of every block, cortical activation related to the SAT instructions may be examined across an entire block of trials, apart from momentary transient activation related to the onset of the cue itself. Secondly, we may identify stimuli-based processing during response selection and response execution/inhibition processes independently. The analysis of neural activity patterns during the response preparatory interval will permit the investigation of SAT-related changes in neural activation during response preparation independent of whether the response is to be executed or inhibited. If individuals increase their internal readiness to respond when speed is emphasized, relative to accuracy, then neural regions involved in

this process may be expected to have greater preparatory activity during this period. Lastly, if a region that increases its baseline activity to accommodate speed emphasis controls the SAT, then examination of its activity following speed instructions should reveal greater sustained activation across an entire block of trials, independent of transient stimulus-related changes in activity. Simply put, this task permits the separation of transient stimuli-based changes in neural activity from sustained SAT-related changes. It permits the investigation of SAT effects on sensory and motor stages of cognitive processing.

There are three key goals of the current study discussed in the next sections: determine whether there are regions responsible for achieving greater response accuracy; investigate whether increased activity following speed instructions in the pre-SMA and basal ganglia is related to response preparation processes; determine whether regions of the PFC are involved in modulating SAT demands when conflict is removed from the task design; determine whether there is support for Lange's (1888/2009) sensory versus motoric response strategies in the context of the SAT.

Accuracy and Visuo-spatial Attention

An advantage of the current paradigm is related to the use of face and house stimuli and the response-cueing technique. Because face and house stimuli have been shown to elicit functionally specific sensory activation in a region of the fusiform gyrus (FFA) (Kanwisher, McDermott, & Chun, 1997; Mauer, et al., 2007; O'Craven & Kanwisher, 2000) and the parrahipocampal gyrus (PPA) (Epstein & Kanwisher, 1998; Marois, Yi, & Chun, 2004; Mauer et al., 2007), respectively, the use of face and house stimuli will provide a distinct advantage over the stimuli used in previous fMRI

investigations of SAT (e.g., random motion displays and Simon stimuli). In other words, the use of face and house stimuli will permit the examination of changes in neural activation in distinct objective-selective sensory regions during specific stages of task performance. If individuals increase the accuracy of their performance by increasing visual attention, then it is hypothesized that increased activation following accuracy instructions in sensory and attention regions of the brain will occur during the entire duration of accuracy trials following the onset of SAT instructions. A rejection of the null for this hypothesis would provide support for Lange's (1888/2009) idea that slower and more accurate responding may be achieved by increasing perceptual attention. That is, when emphasizing accuracy, individuals may increase activation in regions of the brain involved in visuo-spatial attention to increase the perceptibility of stimuli.

Speed Instructions and Response Preparation

The response-cueing technique permits the analysis of the impact of SAT manipulation during a period where participants may select and prepare a response prior to the target stimulus. As previously discussed, this technique has shown to elicit differential preparatory activation in the prefrontal cortex in electrophysiological studies of SAT, yet has not been investigated using fMRI. Ivanoff et al., (2008) and van Veen et al., (2008) found greater activation in the pre-SMA following speed instructions suggesting that individuals may respond fast by increasing the preparation of a specific response. Therefore, it is hypothesized that by separating response preparation processes from SAT cue-related and target-related processes increased activity in the pre-SMA following speed instructions should occur only during a period when participants may prepare a specific response. In the context of the current task, if increased activation in

the pre-SMA following speed instructions is in fact due to increased preparation of a response, then it may be hypothesized that this increase should occur only during the preparatory period between the presentation of the face cue and before the presentation of the house target.

Forstmann et al., (2008) have suggested that modulation of threshold activity in the basal ganglia plays a vital role in increasing preparation *to* respond by increasing or decreasing its inhibitory control over the thalamus, midbrain, and brainstem. If increased activation in the basal ganglia is in fact related to increased response readiness then it is hypothesized that an increase in activation following speed instructions will occur prior to and be closely tied to the execution of a response (i.e., prior to and during the onset of the house targets). This finding would coincide with prior findings that increased activation in the input nuclei of the basal ganglia is related to reduced inhibitory control over motor regions of the cortex, thereby permitting faster and less inhibited responding (see Lo & Wang, 2006). Likewise, if individuals reduce their internal urge to respond when emphasizing the relative accuracy of their responses, reduced basal ganglia activity may be expected following accuracy instructions during the interval just prior to and during the presentation of house targets.

A rejection of the null for these two hypotheses would provide support for Lange's (1888/2009) idea that faster and less accurate responses may be achieved by increasing motoric attention. In other words, individuals may place greater attention on preparing a specific response (reflected by increased activation in the pre-SMA) and preparing to respond (reflected by increased activation in the basal ganglia) when emphasizing speed over accuracy.

PFC, SAT, and Conflict Resolution

A secondary aim of this study is to disentangle the effect of SAT on response preparation processes with little involvement by processes involved in conflict resolution. As discussed previously, Ivanoff et al. (2008) and van Veen et al. (2008) had found evidence for increased activation following speed instructions in lateral prefrontal cortical regions and while Forstmann et al. (2008) reported finding greater activation in the left medial frontal gyrus for speed relative to neutral instructions, the results of their conjunction analysis failed to implicate this region as being responsible for modulating SAT demands. The differences between these findings may represent the relative lack of response conflict involved with the highly coherent stimuli used by Forstmann et al. (2008). Therefore, it may be expected that the use of highly coherent stimuli that require little conflict resolution should elicit activation patterns in lateral prefrontal cortical regions similar to that found by Forstmann et al. (2008).

Methodology

Participants

Nineteen volunteers (11 females and 8 males) aged 20 - 26 (mean = 23), with normal or corrected-to-normal vision, participated in the study for pay and were included in all subsequent analyses. In accordance with local research ethics boards, full informed consent and MRI pre-screening measures were provided before participation. The Saint Mary's University, Capital Health, and National Research Council research ethics boards approved the study. All participants were interviewed prior to participation to ensure they met the criteria outlined in Table A1 in the Appendix. Table A1 in the Appendix also provides a summary of other exclusionary criteria. Twelve participants participated in a

single two-hour scanning session starting at 4:30pm (participants 1-10, 18-19), while seven participants participated in a two-hour scanning session starting at 10am (participants 11-17).

At the beginning of every scanning session participants met with a senior research administrator prior to being scanned and were required to pass an MRI pre-screening process to ensure their safety. All participants were debriefed and provided exit questionnaires immediately following all MRI scanning sessions to ensure no one experienced adverse effects due to the MRI scanning. Table 2 lists the slice thickness used for each subject, the number of functional runs acquired, whether scans were acquired in the morning or afternoon, and participants' age, handedness, and sex.

fMRI Data Acquisition

Imaging was conducted on a 4 Tesla magnet (Oxford Magnet Technology, Witney, UK) using an INOVA^{TM} console (Varian Inc., Palo Alto, CA), 36 mT/m imaging gradients (Tesla Engineering Ltd., West Sussex, UK), 950 V amplifiers, and a transverse electromagnetic quadrature radiofrequency coil.

Anatomical images. A whole-brain T1-weighted 3-D anatomical image was acquired once for every subject using a magnetization prepared fast low angle shot (MPFLASH) scanning sequence (echo time [TE]= 5ms, repetition time [TR] = 10.1ms, inversion time [TI] = 500 ms, flip angle [FA] = 11°, FOV = 240mm x 240mm, 256 x 256 matrix, 170 axial slices, 0.94 mm slice thickness). A 4-shot spiral sequence was used to acquire an in-plane T1-weighted anatomical image for every subject at the beginning of each scanning session (TR = 1000 ms, TE = 3 ms, TI = 500 ms, FOV = 24 cm x 24 cm, FA = 60°, 25 axial slices, 3.75 or 4.75 mm thickness, 0.5 mm gap).

Functional images. Subjects underwent 6-8 T2*-weighted fMRI scans per scanning session (1-2 localizer runs and 4-6 go/no-go runs) that were acquired using a 2-shot spiral out sequence (TR = 850 ms, volume acquisition time = 1700 ms, TE = 15 ms, TI = 500 ms, FA = 60°, FOV = 24 cm x 24 cm, 64 x 64 matrix, 25 slices, 3.75 or 4.75 mm slice thickness and 0.5 mm gap, 283 volumes per run). The change in slice thickness from 3.75mm to 4.75mm was made to accommodate subjects with larger head sizes, thereby maximizing cerebral coverage. This prescription change is likely to matter very little, because all images were analyzed at $1mm^3$, as described below (fMRI preprocessing).

Stimuli

Five hundred and four novel and expressionless facial stimuli (252 male and 252 female stimuli) were randomly generated using FaceGen Modeller 3.3 (Singular Inversions Inc., Toronto, ON). This software permits the generation of realistic 3D, computer-generated, faces while maintaining control of sex, symmetry, age, gaze direction, facial expression, and the removal of all facial and head hair. All faces differ along the race, gender, attractiveness, and age dimensions thereby ensuring no face stimulus was presented more than once. Five hundred and four novel house images were collected from freely available images found on realty websites, ensuring no house was presented more than once. The face and house stimuli were gray scaled, presented centrally, and subtended visual angles of 6.8° x 6.8°.

The localizer and preparatory go/no-go tasks were programmed and presented using MATLAB R2007b 7.5.0 (The MathWorks Inc., Natick, MA) on a MacBook Pro with a 2 GHz Intel Core Duo processor, 1 GB 667 MHz DDR2 SDRAM, and an ATI

Radeon X1600 128 MB visual card, running Mac OS X version 10.4.11. All images were back-projected onto a blank screen at the end of the scanner where participants viewed the images through a mirror. Participants responded by pressing their right or left index finger on one of two MRI compatible button boxes (Current Designs, Inc., Philadelphia, PA).

Task Procedure

Localizer task. Immediately following the T1-weighted in-plane anatomical scan, participants underwent block-design fMRI runs, lasting 481.1s each (i.e., 283 volumes *1.7s volume acquisition time). Each run began with a 11.9s fixation period to allow for spin alignment and consisted of 8 fixation blocks that alternated with 9 task blocks. Blocks lasted 27.2s. Task blocks alternated based on the stimuli used (houses or faces) and were counterbalanced so each of two runs began with a different task block (e.g., Face-Fixation-House-Fixation… or House-Fixation-Face-Fixation…). During face task blocks, participants completed 16 trials and were instructed to make a right button press in response to male face stimuli and a left button press in response to female face stimuli. During house task blocks, participants completed 16 trials and were required to make a right button press in response to two-level homes and withhold responding to one-level homes. Face blocks consisted of 8 male faces and 8 female faces presented in random order. House blocks consisted of 14 one-level homes and 2 two-level homes. House and face stimuli were presented for 1.2s followed by a central fixation cross for a quasi-randomly selected inter-trial interval (ITI) of 0.2, 0.3, 0.4, 0.6, 0.7, or 0.8s. During fixation blocks, participants were instructed to stare at the centrally located fixation cross (1.3°x1.3° visual angle). Participants completed 9 face blocks, 9 house blocks, and 16

fixation blocks across both runs. Figure 3 illustrates the block-design task and temporal sequence of stimuli presentation for the localizer runs.

Event-related task. Following the localizer runs, participants underwent 4-6 event-related fMRI runs per scanning session where they performed a go/no-task involving a preparatory response-cue. Each run lasted 481.1s, consisting of three alternating blocks that varied in their emphasis on speed and accuracy. Participants were given a 500ms visual cue of "SPD" or "ACC" at the beginning of every block of trials, indicating that they should respond as fast as possible with minimal regard for accuracy or as accurately as possible with minimal regard for response speed, respectively. With the exception of one participant (11) the speed/accuracy emphasis was alternated and counterbalanced across runs (i.e., ACC-SPD-ACC or SPD-ACC-SPD) so participants performed the same number of speed and accuracy blocks across the entire scanning session. Due to an input error, participant 11 completed six accuracy blocks and nine speed blocks[1]. Providing visual feedback regarding RT and accuracy of performance has been shown to induce a behavioural SAT (for a review, see Franklin & Okada, 1983) and for this reason it was provided at the end of every run in the following manner. To provide feedback regarding performance in speed blocks, participants were presented with, "SPD - Good! During Speed (SPD) blocks, you were responding fast enough!", if their average RT in speed blocks for their first run was faster than 1s. In subsequent runs, the speed criterion was lowered by 100ms, but only if they again managed to beat the

[1] fMRI and behavioral analyses were conducted with and without participant 11 followed by a comparison of the two resultant data sets. The results of this comparison indicated that inclusion of participant 11 did not unduly influence the data set; therefore, there was no evidence to warrant removal of their data.

criterion. For example, if they were faster than 1s on the first run, they would be encouraged to respond faster than 900ms on the second run. If they failed to respond faster than 900ms on the second run then the criterion would remain at 900ms for the third run; however, if they responded faster than 900ms then they would be encouraged to respond faster than 800ms on the third run. This method of RT feedback constantly encouraged participants to respond faster in subsequent runs. If they failed to meet the RT criterion they were presented with, "[average RT for speed blocks in a run] seconds. You need to respond more quickly during Speed (SPD) blocks".

To provide feedback regarding performance in accuracy blocks, participants were presented with, "ACC - Good! During Accuracy (ACC) blocks, you were very accurate!", if their percent correct responses in accuracy blocks for that run was greater than 90% in the first run with this criterion remaining if they failed to meet it; otherwise they were encouraged to respond more accurately by 2.5%. For example, if they were more accurate than 90% on the first run, they would be encouraged to be 92.5% accurate on the second run. If they failed to meet the 92.5% criterion on the second run then the criterion would remain the same for the third run; however, if they were more accurate than 92.5% then they would be encouraged to be 95% accurate on the third run. This method of accuracy feedback constantly encouraged participants to maintain high levels of accuracy in accuracy blocks on a run-by-run basis. If they failed to meet the accuracy criterion, they were presented with, "[their average percent correct for accuracy blocks in a run] %. You need to respond more accurately during Accuracy (ACC) blocks".

Each block consisted of 6 trials with 1 or 2 short stimulus onset asynchrony (SOA) trials and 5 or 6 long SOA trials. Long SOA trials had a 11.7s SOA between

response cue and target presentation. Short SOA trials had a 1.7s SOA and were excluded from fMRI analyses. Short SOA trials served to lessen the predictability of target onset to encourage participants to remain vigilant and begin response preparation immediately following the presentation of the facial response-cue. Figure 4 provides an illustration of the temporal sequence of stimuli presentation for the event-related go/no-go task.

Participants were instructed to prepare a left response to a female face stimulus and a right response to a male face stimulus. They were to execute their planned response upon presentation of the two-level house targets (*go* trial) and withhold their planned response to one-level house targets (*no-go* trial). Blocks consisted of 50% go trials, 50% no-go trials, 50% male faces, and 50% female faces, with random assignment and equal numbers of right go, right no-go, left go, and left no-go trials. Table 2 lists the specific slice thicknesses used for each subject, the number of functional runs acquired, as well as participants' age, handedness, and sex.

fMRI Pre-processing

Brain Voyager QX Version 10.4 (Brain Innovation, Maastricht, The Netherlands) was used to pre-process the data and generate statistical parameter maps (SPMs). All functional T2*-weighted images were spatially aligned to the T1-weighted in-plane anatomical image acquired at the beginning of every scanning session, corrected for motion artifacts using trilinear/sinc interpolation and referenced to the first *functional* volume acquired in each scanning session (i.e., the first volume acquired in the first localizer scan), and corrected for linear drift. Localizer scans were subjected to additional spatial smoothing using a 4mm full width at half maximum Gaussian filter. The high-

resolution 2D T1-weighted anatomical images were spatially aligned to 3D T1-weighted anatomical images, normalized to the Talairach brain atlas (Talairach & Tournoux, 1988), with 3D volumetric time-courses being generated for every fMRI run.

Functional Localizer Analyses

Three-dimensional localizer functional data sets were combined and a group analysis was conducted using random-effects multiple-regression, corrected for serial correlations, with predictors. Separate predictors were defined by boxcar functions convolved with a canonical double-gamma model of the hemodynamic response (Boynton, Engel, Glover, & Heeger, 1996; Friston et al., 1995).

A conjunction analysis and two contrasts were used to identify regions of interest (ROIs). First, to identify neural ROIs common to both the face and house blocks of trials, multiple comparison *t* tests were conducted on the group averaged activation during face response blocks versus activation during fixation blocks (face-fix contrast), and group averaged activation during house response blocks versus activation during fixation blocks (house-fix contrast), correcting for false positives using a false discovery rate (FDR) of $q(\text{FDR})<.05$ (Genovese, Lazar, & Nichols, 2001)[2]. The face-fix and house-fix contrasts were used to identify any regions that were not revealed in the conjunction analysis. We

[2] FDR is an adaptive technique used to correct for the proportion of false positives when one performs multiple comparisons. In the context of neuroimaging, if a one-sample t-test were performed on all acquired voxels in an fMRI data set to determine what voxels demonstrate activation significantly greater than zero, with a significance level of $p<0.05$, then 5% of all tested voxels would be found active when in fact they were not. Staying in the context of one-sample t tests among voxels, the FDR procedure is applied to the entire data set and involves setting an expected rate of false positives (q) among those voxels declared significantly active. This method has been shown to be less constraining than other methods for controlling false positives, such as Bonferroni correction (for a detailed explanation, see Holm, 1979), and is less sensitive to rejecting true positives (see Genovese et al., 2001; cf. Nakagawa, 2004).

expected these three analyses to reveal neural regions associated with different stages of information processing (i.e., sensation, perception, response preparation, response selection, response execution, and response inhibition) associated with the task.

ROIs were chosen using a maximum ROI size of $14mm^3$, with the exception of a $5mm^3$ maximum size for the lentiform nucleus due to anatomical restrictions. Those ROIs identified from the localizer data were later probed in the event-related task. This method of localization has been used in previous literature (e.g., Ivanoff et al., 2008) and is a suggested means of increasing statistical power and framing mind-brain relationships (for a review, see Saxe, Brett, & Kanwisher, 2006). By identifying ROIs using a separate localizer task, statistical analyses performed on the event-related data in those ROIs will remain completely independent from the analysis used to identify them, thereby avoiding the error of non-independence described in detail by Vul, Harris, Winkielman, and Pashler (2009).

Event-related Data Analysis

ROIs defined in the localizer task were probed by extracting pre-processed time-courses for each ROI acquired in the preparatory go/no-go task and analyzed using custom software programmed and implemented using MATLAB R2007b 7.5.0 (The MathWorks Inc., Natick, MA). ROI time courses for every subject and run were assessed for spikes and signal dropout. Spikes were defined as activation in a particular volume exceeding an upper or lower bound of 3 standard deviations from the average BOLD signal during the run in which it was acquired. Spikes were subsequently replaced by the average MR signal in the same voxel from the immediately neighboring volumes (i.e., pre- and post-spike).

Event-related time-courses for each trial and participant were separated by speed and accuracy, averaged across trials and participants, and locked to the onset of each type of stimulus (SAT, Face, and House) and baselined to the average of the BOLD signals from the volume of the stimulus (n) and the volume just prior (n-1). The average of the BOLD signal from the two volumes provides an estimate of baseline activation less susceptible to an artifact or noise. For each time-course, the average area under the hemodynamic function (AUC) was calculated for speed and accuracy over nine volumes following stimulus presentation. Activation following the face cue was subjected to a second analysis where AUC was averaged for only the eighth and ninth volumes following the presentation of the face stimulus to evaluate activity immediately before the presentation of the target.

Behavioural Analyses

Accuracy was calculated using all trials and was estimated in two ways. First, the proportion of correctly made responses to go targets was calculated (i.e., hits). In most studies of response preparation, the hit rate is quite high (e.g., Band et al., 2003; Sangals et al., 2002). Secondly, and more importantly, the proportion of responses made to no-go targets was calculated (i.e., false alarms). In previous studies (e.g., Band et al., 2003; Ivanoff et al., 2008; Sangals et al., 2002), the false alarm rate increase with an emphasis on the speed of responding. RTs to the target stimuli were analyzed to calculate the magnitude of differences between RTs following accuracy and speed instructions. Response time was calculated from the onset of the target stimulus (i.e., house) to the execution of a response.

Results

Reaction times were vincentized (Ratcliff, 1979) into quintiles for trimmed and untrimmed responses for speed and accuracy conditions. The vincentized plots are illustrated in Figure 5. When untrimmed, it is apparent from these distributions that the slowest responses in the speed condition substantially overlap with the fastest responses in the accuracy condition. By removing those trials in the first quintile (i.e., fastest 20% of responses) in the accuracy condition and last quintile (i.e., slowest 20% of responses) in the speed condition, the distributions for speed and accuracy are more temporally distinct. The average RT for those responses removed from the speed condition was 992.42ms, and the average RT of those responses removed from the accuracy condition was 608.29ms. Once trimmed, the only overlap apparent in the distributions is briefly between the fifth quintile from the speed condition and the first quintile of the accuracy condition, with responses in the speed condition being significantly faster than accuracy for all quintiles ($p<.05$). Because this approach does not eliminate trials for which there was an inappropriate SAT mental set and no response (i.e., no-go trials), trimming resulted in merely 10% of trials in the speed condition and 10% of trials in the accuracy condition being removed. Therefore, it may be argued that these RT cut-offs removed a minimal number of trials in which participants may not have implemented the appropriate mental set. Additional analyses were performed on the fMRI data for only those trials that were removed. The results of these analyses revealed little difference between brain activation in the speed and accuracy conditions. This finding further supports the argument that participants may not have implemented the proper SAT mental sets in

those trials that were removed as a result of this trimming procedure. Only trimmed RTs were used in the fMRI data analyses.

Behaviour

Localizer task. To determine whether performance differed between face and house blocks, paired *t*-tests were performed on the average correct RTs and percent corrects for each run. Results of the paired *t*-tests performed on correct RT revealed no difference in RT between face (M=742.17ms) and house blocks (M=739.10ms; $t(36)=0.21$, $p=.79$). Analysis of the percent correct in the face (M=86.74%) and house blocks (M=86.86%; $t(36)=0.27$, $p=.83$) also revealed no significant difference. The RTs and accuracy scores for the localizer task is provided in Table 3. Participants 1, 4, and 5 confused the instructions on their second localizer run during house blocks. As a result, they made left responses to one-storey homes and right responses to two-level homes[3]. Incorrect responses were not removed from analysis as the localizer data was analyzed by fitting a synthetic HRF in a block-design.

Event-related task. Responses following speed instruction (M=583.40ms) were 305.50ms faster than responses following accuracy instruction (M=888.90ms), $t(18)=5.82$, $p<.0001$. Although the hit rate (i.e., number of hits /total number of go-trials x 100) did not differ significantly between speed (M=97.72%) and accuracy [M=97.75%; $t(18)=0.05$, $p=.96$] conditions, the false alarm rate (i.e., number of false alarm errors ÷

[3] A comparison of the data with and without these runs revealed no differences in the statistical parameter maps, group reaction times, or group accuracy. It may be argued that although they were not following instructions they were still maintaining vigilance to the task in a similar manner to that in face blocks.

total number of no-go trials x 100) was greater in the speed condition (M=11.55%) than in the accuracy condition [M=8.23%; $t(18)$=2.26, p<.05]. Table 4 provides a summary of RT, hit rate, and false alarm rate, for all participants.

Localization of Regions of Interest

Results of the conjunction analysis (i.e., face-fix ∧ house-fix) revealed a distributed network of ROIs in prefrontal, medial frontal, superior and inferior parietal, medial and superior occipital, and extrastriate cortices, as well as subcortical structures such as the midbrain, basal ganglia, and thalamus. The only ROI that was identified in the face-fix contrast that was not present in the conjunction analysis was the right pre-SMA. This region was identified as being functionally distinct to the face-fix contrast and was anatomically defined as the pre-SMA (as opposed to the SMA) due to it being anterior of the anterior commissure and restricted to Brodmann area 6 (for a review, see Picard & Strick, 2001). The house-fix contrast revealed a network of ROIs in the superior parietal, posterior cingulate, and middle frontal cortices that were not revealed in the conjunction analysis. Table 5 provides a summary of ROIs identified using the conjunction analysis and those ROIs identified using the individual face-fix and house-fix contrasts.

Event-related Analyses

Short SOA trials were removed from the event-related analyses because they did not permit the separation of response preparation from execution during the short (1.7s) presentation of the face stimuli. Three analyses of hemodynamic time-courses were performed according to the stimuli in the event-related task (i.e., SAT instruction, face, and house). A fourth analysis was performed on those ROIs identified as being significantly modulated by SAT instruction when time-locked to the SAT stimulus.

SAT stimuli. At the time of the SAT instruction, participants saw either "ACC" or "SPD" and they were instructed to prepare for accurate responding or rapid responding, respectively. To analyze activation in each localized ROI related to processing of SAT instructions, hemodynamic time courses for each run were separated by SAT instruction (i.e., "SPD" or "ACC"), time-locked to the onset of the SAT cue, and baselined to the average of the first volume in each block and the volume preceding it. The first seven volumes following the onset of the SAT cue were averaged across events and participants. The differences in sustained activation related to speed or accuracy instructions were assessed statistically by measuring the AUC. Paired *t*-tests (uncorrected)[4] were conducted on the average AUC in the speed and accuracy conditions in a 11.9s (i.e., 7-volume) window. Table 5 provides a summary of the mean accuracy-speed difference in average AUC for the period defined for each analysis, the standard error of the mean (SEM), and the significance of the paired *t*-tests between the average AUC for speed versus accuracy for all ROIs.

Statistical analysis revealed significantly greater activation following the accuracy SAT cue relative to the speed cue in the right cuneus (Figure 6), left cuneus (Figure 7) left extrastriate cortex (Figure 8), left superior occipital cortex (Figure 9), left superior parietal lobe/precuneus (Figure 10), right superior parietal lobe/precuneus, right posterior cingulate (Figure 11), left DLPFC (Figure 12), bilateral pre-motor cortices, right SFG, left superior occipital cortex, right ventral precuneus, and left FFA (*ps*<.05; see Table 5).

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[4] Because ROIs were identified using FDR corrected analyses in the separate localizer task, and because paired *t* tests in the event-related analyses were constrained to those ROIs (not all voxels), all paired *t* tests performed in the event-related analyses were not corrected for multiple comparisons (for a review, see Saxe, Brett, n& Kanwisher, 2006).

No ROI demonstrated significantly greater activation following speed instruction relative to accuracy.

Sustained SAT cue-related differences in activation. Those ROIs that demonstrated significantly greater activation following accuracy relative to speed instructions in the SAT cue analysis (*ps*<.05, see Table 5) were subjected to a secondary analysis to determine whether the differences were only present during the SAT cue interval or were sustained over entire trials. HRFs in these ROIs were separated by SAT instruction (i.e., "SPD" or "ACC"), time-locked to the onset of the face stimulus and initially baselined to the average of the volume of the face stimulus and the last volume of the SAT cue interval. Subsequently, the first fourteen baselined volumes following the onset of the face stimuli were averaged across runs for each participant. These average time-points were then adjusted by adding the average of the last two volumes of the SAT stimulus window to all points along the HRF. The differences in sustained activation related to speed or accuracy instructions were assessed statistically by determining the average AUC of all fourteen volumes following the onset of the face cue. Paired *t*-tests (uncorrected)[3] were conducted on the average AUC in the speed and accuracy conditions in the fourteen-volume window following the presentation of face cues.

This analysis revealed significantly greater sustained activation in the right cuneus ($t(18)=2.64$, $p<.05$; see Figure 6), left cuneus ($t(18)=2.78$, $p<.05$; see Figure 7), left extrastriate cortex ($t(18)=2.11$, $p<.05$; see Figure 8), left superior occipital gyrus ($t(18)=2.66$, $p<.05$; see Figure 9), left superior precuneus/parietal lobe ($t(18)=3.19$, $p<.01$; see Figure 10), and right posterior cingulate ($t(18)=3.00$, $p<.01$; see Figure 11), following

accuracy relative to speed instructions. No ROI demonstrated a similar pattern of sustained activation when following speed instructions.

Face stimuli. The perceived gender of the face stimulus informed participants to prepare either for a left or right key-press response. To analyze activation in each ROI beginning at the onset of the face-cue and reflecting processes related to response selection and preparation, hemodynamic time courses for each run were separated by SAT instruction (i.e., "SPD" or "ACC"), time-locked to the onset of the face cue, and baselined to the average of the volume of, and the volume prior to, the onset of the face stimuli. Subsequently, the first seven volumes following the onset of the face stimuli were averaged across runs for each participant to achieve the average hemodynamic response reflecting processes involved in face perception, response selection, and response preparation prior to the presentation of target stimuli (i.e., houses). The differences in sustained activation related to speed or accuracy instructions were assessed statistically by determining the AUC for volumes following the onset of the face stimulus. Paired *t*-tests were conducted on the average AUC in the speed and accuracy conditions in the seven-volume window following the presentation of the face. Table 5 provides a summary of the mean accuracy-speed difference in average AUC for the time period defined for each analysis, the standard error of the mean (SEM), and the significance of the paired *t*-tests between the average AUC for speed versus accuracy for all ROIs.

This analysis revealed significantly greater activation when emphasizing response speed relative to accuracy in the right pre-SMA (see Figure 13); however, no ROI

demonstrated greater sustained activation across this window when emphasizing accuracy relative to speed.

To identify ROIs that demonstrated differential activation for speed versus accuracy instructions just prior to responding we conducted paired t-tests on the average AUC for the last volume (i.e., 7th volume) prior to the appearance of the target stimuli and the first volume when the target stimuli appeared (i.e., 8th volume) following the presentation of the face stimuli). Results of this analysis are summarized in Table 5. The left lentiform nucleus was the only ROI to demonstrate a difference in activation during this narrow window, with significantly greater activation when emphasizing the speed of responding relative to accuracy (see Figure 14).

House stimuli. The number of levels in the house stimulus informed participants to either execute or withhold responding. To analyze activation in each ROI beginning at the onset of the target stimulus (i.e., house) and reflecting processes related to response execution and inhibition, hemodynamic time courses for the first seven volumes following the presentation of the house were subjected to a 2(SAT instruction: speed and accuracy) x 2(response type: CR and Hit) repeated measures analysis of variance (ANOVA).

The results of the ANOVA did not reveal any significant interaction of SAT instruction and response type, indicating that these two factors were orthogonal; however, there were significant main effects. First, there was a significant main effect of SAT instruction on activation in the left SMA [$F(1,18) = 4.47, p<.05$], left pre-SMA [$F(1,18) = 4.66, p<.05$], and the right middle frontal cortex [$F(1,18) = 6.19, p<.05$]. The time-courses for these ROIs are depicted in Figures 15-17, respectively, separated by the

factors included in the ANOVA. All three ROIs exhibited greater activation when emphasizing accuracy relative to speed with no ROI having demonstrated the opposite pattern. Secondly, there was a significant main effect of response type on activation in the right cerebellum [$F(1,18) = 9.64$, $p<.01$] and the right SPL/precuneus region [$F(1,18) = 5.47$, $p<.05$]. Figures 18 and 19 illustrate the time-courses in these ROIs split according to the factors included in the ANOVA. As illustrated in Figure 18, increased activation in the right cerebellum was greater when participants made hits relative to correct rejections (CRs). In contrast, shown in Figure 19, increased activation in the right SPL/precuneus region was greater when making CRs relative to when making hits. No analysis was conducted on trials when participants made false alarm errors, as there were too few to analyze.

General Discussion

The purpose of the current study was to elucidate the neural mechanisms responsible for the SAT. Unlike previous research, SAT cue-related processes will be disentangled from processes involved with stimulus perception, response preparation, and response execution/inhibition. Using this methodological approach it was possible to investigate *when* SAT modulation occurs during task performance and whether there is a subset of brain regions responsible for achieving greater accuracy.

Behavioural analyses show that the use of an SAT cue and performance feedback successfully elicited an SAT. That is, participants responded significantly faster and made more errors (i.e., greater false alarm rate) when emphasizing speed over accuracy. This finding is not surprising, considering the number of prior SAT studies that have used these methods for eliciting SAT in performance (e.g., Forstmann et al., 2008; Ivanoff et al., 2008; Ratcliff, 2002).

There are several key findings from the current study. First, with the exception of the left DLPFC (Figure 12) having greater activity during the SAT cue interval when emphasizing accuracy over speed, there were no sustained effects of the SAT cue on lateral PFC regions such as the right DLPFC or bilateral pLPFC/IFJ. Second, consistent with prior SAT literature (Forstmann et al., 2008; Ivanoff et al., 2008) there was greater activity in the right pre-SMA when emphasizing response speed than accuracy during the response preparation interval (i.e., during presentation of the face stimulus). Furthermore, there was greater activity in the left lentiform nucleus just prior to the presentation of the response target (i.e., house) when emphasizing response speed. Third, although the left FFA exhibited greater activation during the SAT cue interval when emphasizing accuracy

instructions, this increase was not maintained over the entire interval, and this pattern was not found in other object selective visual regions such as the right FFA, left PPA, and right PPA. Finally, there was a sustained effect of SAT manipulations in the following non-selective visual processing regions: right cuneus, left cuneus, left extrastriate cortex, left superior occipital gyrus, left superior precuneus/parietal lobe, and right posterior cingulate. These findings will be discussed in the context of perceptual and motoric attention and the theoretical implications of these findings for our understanding of SAT modulation.

Conflict and the Lateral Prefrontal Cortex

One of the main aims of the current study was to minimize stimulus-response conflict from the task used to elicit an SAT in performance. Conflict is often greater when speed is emphasized (e.g., Ridderinkhof, 2002; van Veen et al., 2008), thus confounding SAT modulation and conflict resolution. As discussed in the Introduction, Ivanoff et al. (2008) found greater activity under speed than accuracy instructions in a region of the lateral PFC, the pLPFC, when there was no motion coherence (i.e., no sensory evidence) in the display. Likewise, van Veen et al. (2008) found greater activity under speed than accuracy conditions to the SAT cue (i.e., before sensory evidence is available) in the DLPFC, another region of the lateral PFC. Although these authors suggested these findings reflect a reduction of the amount of sensory evidence needed to accrue when responding fast, it is equally plausible that these findings reflect the resolution of increased conflict when responding to Simon and motion coherence stimuli under speed stress. A number of prior studies have identified the lateral PFC to have an integral role in resolving response conflict (for a review, see Van Veen et al., 2006;

McDonald, et al., 2000; Miller & Cohen, 2001). In the present study, there was reduced stimulus-response conflict in the design.

Analyses of the left DLPFC (Figure 12) revealed significantly increased activation only during the SAT cue interval when emphasizing accuracy over speed and a trend in the same direction was found in the right DLPFC. Furthermore, analyses of the time-courses in these regions and in the left and right IFJs did not indicate that this greater activation following accuracy instructions was sustained over the block of trials. The transient SAT-related difference in activation during the SAT cue interval in the left DLPFC leaves open the possibility that the DLPFC may be responsible for implementing the SAT, but not in maintaining it over the length of the block. Results of the IFJ do not suggest that it plays a role in either initiating or maintaining the SAT.

Differences between the stimuli used in the current study and those used by van Veen et al. (2008) and Ivanoff et al. (2008) might explain why lateral PFC regions (i.e., DLPFC and IFJ) did not show evidence of greater sustained activity in the speed than the accuracy condition. That is, unlike the stimuli in van Veen et al.'s (2008) and Ivanoff et al.'s (2008) studies, the faces and house used in the current study were highly discriminable (this is supported by the finding that no errors were made when identifying the gender of the face, and few errors were made to the number of levels of the house). More importantly, the stimuli in the current study do not inherently induce response conflict, as is the case with the motion coherence and Simon stimuli. Although it may be argued that identifying the gender of some of the faces or the stories of some of the houses in the current study was challenging, it was not the case that a feature of a face (e.g., a beard on a female face) or a house (e.g., a bungalow with extensive cathedral

ceiling), providing conflicting information. Thus, the lack of robust lateral PFC involvement in the SAT could be due to the virtual absence of conflict in the current design.

Motoric Attention and Speed Emphasis

Response preparation and the SAT. The pre-SMA is a region that has been implicated in the literature as playing a vital role in planning and preparing actions (e.g., Cunnington, et al., 2002; Humberstone, et al., 1997; Weilke et al., 2001). Two recent fMRI studies of the SAT have identified this region as playing a role in modulating SAT by increasing baseline activation (Ivanoff et al., 2008; van Veen et al., 2008), and changing threshold activation (Forstmann et al., 2008), following speed instructions. Although the elevated baseline activation when emphasizing speed in these studies may be assumed to reflect increased response preparation, two specific limitations did not permit these researchers to make this assumption. First, in these three investigations (i.e., Ivanoff et al., 2008, Forstmann et al., 2008; van Veen et al., 2008), the participants were not provided advance information permitting the preparation of a specific response. Thus, it is not clear what kind of response preparation their task entailed. Secondly, Forstmann et al. (2008) presented SAT cues randomly on a trial-by-trial basis. This technique may not have permitted participants to adopt a specific strategy for responding quickly or accurately, but required them to frequently change response strategies in an unpredictable pattern. As discussed in the Introduction, trial-by-trial switching between two tasks (i.e., speed and accuracy) results in a well-replicated increase in reaction time and reduction in accuracy (i.e., switch cost; Dove et al., 2000; Monsell, 2003). Although these three fMRI investigations of the SAT have found increased baseline activation in the pre-SMA when

emphasizing speed, the limitations of their designs may only permit the conclusion that elevated pre-SMA activity is related to faster versus slower responding and not necessarily increased response preparation.

Based on these prior SAT findings of increased activation in the pre-SMA following speed emphasis, combined with non-SAT findings linking this region closely to the preparation of a response, it may be hypothesized that separating response preparation processes from other task processes would reveal that this increase occurs strictly during a period when individuals prepare a forthcoming response. Consistent with this hypothesis, and with the findings from Forstmann et al. (2008) and Ivanoff et al., (2008), the event-related analyses suggested greater activation in the right pre-SMA when emphasizing speed over accuracy, but only during an interval where participants were instructed to visually process facial information to select and prepare a response (see Figure 13). We did not find any effect of the SAT in this region during the interval when the SAT cue was presented or following target presentation, suggesting that the pre-SMA does is not susceptible to the SAT during pre-task adjustments or during response execution, respectively.

The pre-SMA plays a key role in the generation and switching of motor plans in monkeys (e.g., Matsuzaka & Tanji, 1996; Shima, Mushiake, Saito, & Tanji, 1996) and the generation of self-initiated motor plans in humans (e.g., Deiber et al., 1999; Jäncke, Himmelback, Shah, & Zilles, 2000; for a review, see Picard & Strick, 2001). For example, Dieber et al. (1999) had participants perform a sequence of self-initiated and visually initiated manual responses using the five fingers of their right hand while undergoing fMRI. In the self-initiated condition participants were told to respond either

fast or slow and were free to perform a series of right manual button presses at their own speed. Following every button press a red light would be presented and recorded. In the visually initiated condition, the responses made in the self-initiated condition were played back to the participant in a random or fixed manner and at a fast or slow rate. Analysis of the BOLD response in the pre-SMA revealed greater activation when performing self-initiated, relative to visually-initiated, movements and greater activation when making fast, relative to slow, responses. These results were interpreted to suggest that the pre-SMA plays a vital role in the planning of self-initiated movements with greater activity when those motor plans must be executed quickly. Therefore, one interpretation of the current findings may be that increased activity in the right pre-SMA under speeded conditions reflects increased commitment to a right or left response via a more developed motor plan or representation.

Release from inhibition and the SAT. Analysis of the time-courses in the left lentiform nucleus, a region that comprises the putamen and globus pallidus of the basal ganglia, revealed significantly greater activation during the volumes just prior to, and at the onset of, the target presentation when emphasizing response speed. There is a substantial literature identifying the putamen, and more generally the basal ganglia, as being part of a "closed-loop motor circuit" involving the striatum and pre-SMA (see Introduction section; Bogacz & Gurney, 2007; Forstmann et al., 2008; Lo & Wang, 2006; for a review, see Mink, 1996). In the context of SAT, the basal ganglia might perform two important functions. First, to prevent anticipatory or premature responses the output nuclei of the basal ganglia provide constant inhibitory control over motor regions in the thalamus, midbrain, and brainstem. Secondly, activation of the input nuclei of the basal

ganglia (including the putamen) results in a reduction in inhibitory control over motor regions via suppression of output nuclei (see Lo & Wang, 2006). Less inhibitory control over motor regions will cause faster responding. Forstmann et al. (2008) provided initial support for the release-from-inhibition account of the SAT; they found increased activity in the basal ganglia when participants were instructed to emphasize speed over accuracy. However, their design did not permit them to separate SAT cue-related processes from response preparation and execution processes, thereby limiting their interpretation of this finding.

Similar to Forstmann et al. (2008), we found increased activity in an input region of the basal ganglia, the left lentiform nucleus, when participants emphasized speed over accuracy. However, by separating SAT cue-related processes from response preparation and response execution/inhibition processes we have determined this increase in activation occurs just prior to, and possibly during, the execution of the response (see Figure 14). That is, we found no effect of SAT modulation in this region during processing of the SAT cue, across the entire preparatory interval, or following the presentation of the target stimulus (with the exception of the first volume).

It is interesting to note that, in the current study, the only two ROIs (i.e., pre-SMA and lentiform nucleus) exhibiting an increase in activation when emphasizing response speed relative to accuracy are closely linked (Bogacz & Gurney, 2007; Forstmann et al., 2008; Lo & Wang, 2006) as part of a "closed-loop motor circuit." However, the pre-SMA exhibited increased activation during response selection and preparation across the duration of the preparatory interval, whereas the lentiform nucleus exhibited a similar increase just before the target appeared. Considering that the input nuclei of the basal

ganglia receive excitatory input from cortical regions such as the pre-SMA (Forstmann et al., 2008; Graybiel, 1997), it is feasible that faster responding may be achieved via increased attention placed on preparing the motor response (pre-SMA) with a subsequent release of inhibitory control to permit the prepared response to be expressed as fast as possible. Future research may be directed toward determining whether the increased preparatory activity in the pre-SMA *causes* the subsequent increase in activity found in the lentiform nucleus.

Perceptual Attention and Accuracy Emphasis

One of the central goals of this study was to determine whether individuals increase the accuracy of their performance by increasing visual attention. The three recent fMRI studies of the SAT have found evidence for increased activation in medial frontal, lateral prefrontal, and basal ganglia regions when emphasizing speed (Forstmann et al., 2008; Ivanoff et al., 2008; van Veen et al., 2008); however, no SAT study has found evidence to suggest that greater accuracy is achieved by increasing activation in a subset of neural regions involved with perceptual attention. In stark contrast to these prior findings, we have identified a distributed network of parietal, occipital, and posterior cingulate regions as playing a key role when accuracy is emphasized. These same regions have been implicated in visual processing and visuo-spatial attention (Brefczynski & DeYoe, 1999; Heinze et al., 1994; Hopfinger, Buonocore, & Mangun, 2000; Martinez et al., 1999; Tootell, 1998).

Object-selective visual processing. Face and house stimuli were used in our design with the intention of being able to observe the effects of SAT manipulation in visual regions that have been identified as playing a specific role in perceiving and

processing categorically-specific stimuli. The FFA, a region in the fusiform gyri, has been functionally defined as being a region involved in visual processing of face stimuli (Kanwisher, Tong, & Nakayama, 1998; Mauer, et al., 2007). Furthermore, the PPA, a neural region in the parrahipocampal gyri has been functionally defined as being involved in visual processing of house stimuli (Epstein, Harris, Stanley, & Kanwisher, 1999; Epstein & Kanwisher, 1998; Mauer et al., 2007). The results of the localizer analysis successfully identified activity in these regions in both the left and right hemispheres. The event-related analyses failed to find clear and lasting effects of the SAT in these regions. As shown in Tables 5 and 6, the left FFA demonstrated greater activation only during the SAT cue interval; however, this SAT difference was not sustained across any other event-related analyses. Likewise, in Tables 5 and 6, the right FFA, left PPA, and right PPA were unaffected by the SAT. It is clear from these findings that there is little or no effect of the SAT on activity in these object-selective visual regions. One possible explanation for this finding is that it might be more effective to increase attention under accuracy instructions in non-specific visual regions to improve perceptual processing of both types of stimuli rather than to attend to more holistic processing of the face and house stimuli.

Non-selective visual processing. Prior research has identified the extrastriate cortex, comprised mainly of Brodmann areas 18, 19, and 30, to play a key role in maintaining visuo-spatial attention (Brefczynski & DeYoe, 1999; Heinze et al., 1994; Hopfinger, et al., 2000; Martinez et al., 1999; Tootell, 1998; Yantis et al., 2002). It is even suggested by Martinez et al. (1999) that regions in the extrastriate cortices receive top-down attentional signals and are highly involved in influencing the perceptibility of visual stimuli.

To identify the cortical regions involved in maintaining and directing spatial attention, Hopfinger et al. (2000) performed an fMRI investigation of spatial attention in a cueing task. Their task involved a centrally presented cue of crossed-over blue and yellow arrows pointing in opposite directions along the x-axis of the visual display. Participants were instructed to attend to only one of the arrows (i.e., blue *or* yellow) that cued the subsequent location a target would be presented. Two targets were used: a checkerboard with white and black squares; and a checkerboard with a small proportion of white squares replaced by gray squares. Participants were to make a left button press to one type of checkerboard and make a right button press to the other. Participants were instructed to respond to only the checkerboard that was cued by the relevant arrow (i.e., yellow or blue). Consistent with prior findings that the extrastriate is affected by spatial attention, Hopfinger et al. (2001) found increased extrastriate activity prior to the appearance of target stimuli when participants anticipated the spatial location that the target would appear.

Results of the current study have identified, for the first time, a number of low-level non-selective visual and attention regions that demonstrate greater sustained activity when emphasizing accuracy over speed of responding. A number of ROIs exhibited significantly greater activation during the SAT cue interval when emphasizing accuracy over speed; however, when adding the average of the last two volumes of the SAT cue interval to the time-courses in these ROIs, only the left superior occipital cortex (Figure 9), the left extrastriate cortex (Figure 8), and bilateral cuneus (Figures 6 and 7) had sustained this increase in activation across the entire block duration. It is interesting to note that activation in similar regions of the extrastriate cortex has been strongly related

to shifts in spatial attention that are externally cued by visual signals (e.g., Hopfinger, et al., 2000; Yantis et al., 2002). In the current study, participants were provided no cues instructing them where or when to direct their attention, but simply to achieve high accuracy. Therefore, it is quite possible that when instructed to achieve greater accuracy, there is a greater allocation of attentional resources to the stimulus.

Another subset of neural regions implicated as playing a key role in visuo-spatial attention in prior research includes the SPL (BA 7) and the posterior cingulate cortex (e.g., Corbetta, 1998; Corbetta, et al., 1998; Hopfinger et al., 2000; Mesulam, Nobre, Kim, Parrish, & Gitelman, 2001; Yantis et al., 2002). Specifically, these regions have been identified as providing top-down control of visuo-spatial attention. For example, Hopfinger et al., (2000) found that a region in the superior parietal cortex, occupying the same Brodmann area as the SPL/precuneus identified in the current study, was active not only to the cue stimuli (i.e., blue and yellow arrows) that indicated which location to attend, but also to the target presentation (i.e., checkerboards).

Similarly, Yantis et al. (2002) used fMRI to determine what brain regions are involved with maintaining and shifting spatial attention. In this study, participants were instructed to maintain fixation at center while detecting the numbers "3" or "7" in a series of rapidly appearing visual displays containing random letters. Participants were instructed to make a response by simultaneously pressing left and right buttons with their thumbs if a number was detected. At the beginning of a run, a visual cue was presented to the left or right of center indicating at what location the subsequently presented number would be presented. If participants detected the number "3" they were to maintain

attention to the same side of the visual display and if they detected the number "7" they were to switch their attention to the opposite side.

Yantis et al. (2002) found evidence that activity in left and right extrastriate cortices reflected the current location of attention. Furthermore, they found evidence suggesting that transient activity in superior and inferior parietal regions reflected the deployment of attention, but not the current position of attention. The findings of Yantis et al. (2002), and Hopfinger et al. (2001), combined with other prior research (e.g., Corbetta, 1998; Corbetta et al., 1998) suggests that the extrastriate cortex is not only involved in specific orienting of spatial attention but may be more generally related to orienting of attention to detect targets in the central visual field and in the periphery. Furthermore, shifts in visuo-spatial attention may be controlled via top-down control mechanisms provided by regions of the parietal cortices, such as the SPL.

Meshing nicely with the findings of prior research (e.g., Corbetta, 1998; Corbetta, et al., 1998; Hopfinger et al., 2000; Mesulam, et al., 2001) the left SPL/precuneus (Figure 10) and the right posterior cingulate cortex (Figure 11) identified in the current study both demonstrated significantly greater activation when emphasizing accuracy over speed. Additionally, an analysis of the HRF in the right SPL/precuneus revealed a significant main effect of response type (i.e., CRs and hits), with CRs eliciting greater activation in this region relative to hits following the presentation of the house stimuli. One speculative, yet feasible, explanation for this finding may be that response inhibition requires a prolonged period of attention to the stimuli across its entire duration. In contrast, hits were made substantially faster than the 1.7s that houses were presented and perhaps control of visuo-spatial attention may be released once a response is made. This

explanation fits nicely with the proposed role of this region in controlling visuo-spatial attention for the purpose of target detection (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000).

Perceptual Versus Motoric Attention

It has been suggested in prior literature (Ivanoff et al., 2008; van Veen et al., 2008) that faster responding is partly accounted for by increased baseline activity in the pre-SMA; however, by separating SAT cue-related processes from response preparation processes we have found no evidence that the pre-SMA increases baseline activity to speed *instructions*, as evidenced by the non-significant SPD/ACC difference during the SAT cue interval. Analysis of the face-locked time-course in the pre-SMA did exhibit greater transient activity following speed emphasis during a period when participants were able to select and prepare a response. Because increased activation in this region has been linked with the generation and execution of self-initiated movements, it is feasible that this region may increase its level of transient activity following speed emphasis, reflecting greater commitment to, and preparation of, an internally-generated motor plan.

Another possible explanation for our findings is that when emphasizing speed participants were implementing a two-part system of motoric attention involving the preparation *of* a particular response and the general preparation *to* respond. The preparation of a particular response may be explained in the same manner as described in the previous paragraph; the greater pre-SMA activity reflects a greater commitment to, and preparation of, a specific motor plan. The preparation to respond may be explained by our finding that the left lentiform nucleus increases activity just prior to responding. As described previously, this region is involved in exerting inhibitory control over other

motor regions, with increased activity reflecting release of inhibitory control. Therefore, it is possible that increased activity in this region following speed instruction may reflect an increase in preparation to respond.

By implementing a long preparatory interval in our paradigm, we have successfully temporally resolved the effects of the SAT on pre-SMA and the lentiform nucleus. The current results suggest that individuals may achieve fast, but error-prone, responses by implementing two complementary processes. First, when provided with advance response information under speed stress a specific motor plan is generated. In cases where advanced response information is unavailable (e.g., Forstmann et al., 2008; van Veen et al. 2000), it is possible that all response alternatives are simultaneously selected. It is also possible that a specific response is selected and prepared randomly (or pseudo-randomly, based on information from the prior trial information; response repetition effects, Soetens, Boer, & Hueting, 1985). Greater response preparation is also generally associated with increased propensity for errors (e.g., Bertelson, 1967). Second, the lentiform nucleus of the basal ganglia may release inhibitory control over motor regions just prior to the execution of the prepared response. This account of the SAT provides further support from neurophysiological research that identifies the basal ganglia and pre-SMA as sharing a close relationship whereby the pre-SMA provides excitatory input to the input nuclei of the basal ganglia, including the lentiform nucleus of the putamen (Forstmann et al., 2008; Graybiel, 1997). Although Forstmann et al. (2008) alluded to a similar idea, this is the first fMRI investigation of SAT to examine when SAT effects occur in these regions and to provide evidence that suggests the emergence of these processes are serial and not parallel.

The current findings add to the literature suggesting that the pre-SMA and basal ganglia play a key role in setting the speed of responding along the SATF. However, this still begs an important question: how does accuracy improve in an SAT task? Is it a passive accrual process or does it result from increased attention under conditions to emphasize accuracy? The finding that low-level visual regions in the extrastriate and occipital cortices increase activation when emphasizing accuracy are consistent with previous findings that these regions are involved in influencing the perceptibility of visual stimuli (e.g., Martinez et al., 1999). Considering that no prior study has found a sustained increase in activation when emphasizing the accuracy of responding, the SAT has commonly been discussed as the passive accrual of evidence as processing time increases. The SAT-related activity in low-level sensory and attention regions suggests an alternative explanation: more attentional resources may be deployed to visual regions under instructions to improve the accuracy of a perceptual decision.

Summary

The findings from the present investigation provide convincing evidence for Lange's (1888/2009) account of the SAT. First, to ensure fast responses, one may commit greater attention facets of the response, rather than to the perceptual qualities of the stimulus. Second, to ensure accurate responding one may divert greater attentional resources to the perception of the stimulus. These findings provide, for the first time, support for an account of the SAT that considers the mechanism by which responses are speeded and decision accuracy is improved.

In the context of the mechanisms of SAT discussed in the Introduction, it is possible that specific facets of Lange's (1888/2009) account of the SAT may reflect

contributions from the fast-guess, deadline, and accumulator models. As explained previously, increasing preparatory activity in the pre-SMA may reflect increased commitment or bias toward making a specific response while increased activation in the basal ganglia may result in faster and less inhibited responding. Although it is highly unlikely that participants would resort to guessing when provided 11.9s to evaluate the face stimuli, it is possible that participants may have resorted to simply guessing that a response would be required to the house stimuli. In other words, by increasing their preparation *to* respond, via increased activity in the basal ganglia, participants may have simply guessed that a response will be required. Although participants may have resorted to fast guessing during some trials it is unlikely to have accounted for the entire SAT found in the present study and the associated changes in neural activation.

The findings of the current study help to provide greater insight to our understanding of the neural regions and networks involved in the temporal dynamics of human decision-making. These findings lend support to the idea that attention resources may be controlled to maximize performance based on speed/accuracy demands.

Suggestions for Future Research

Two key suggestions for future research may be made. First, the pre-SMA and left lentiform nucleus was found to increase activation following speed emphasis; however, future research may be directed toward determining whether the increased preparatory activity in the pre-SMA *causes* the subsequent increase in activity found in the lentiform nucleus (Lo & Wang, 2006). An alternative possibility is that another region, one not identified, initiates response preparation in the pre-SMA and the release of inhibition in the lentiform nuclei. To identify a causal relationship, one might conduct

the same experiment using transcranial magnetic stimulation to disrupt the cortical connections between the pre-SMA and lentiform nuclei. Second, the analysis of activity in the SPL/precuneus indicated a significant main effect of response type (i.e., CRs and hits), with CRs eliciting greater activation in this region relative to hits following the presentation of the house stimuli. As stated previously, one speculative explanation for this finding may be that inhibition of responses to house stimuli requires a prolonged period of attention to the stimuli across the entire duration the house is presented (i.e., 1.7s). In contrast, because hits were made substantially faster than the 1.7s that houses were presented, it is feasible that control of attention may have been released once a response was made. Future research could address this idea by investigating activation in the superior parietal cortex related to different types of responses such as hits, CRs, false alarms, and misses (i.e., not responding to a 'go' target). For example, by increasing the proportion of go trials relative to no-go trials one could manipulate the propensity to respond, thereby inducing a possibly greater baseline-shift (e.g., Nieuwenhuis, Yeung, van den Wildenberg, & Ridderinkhof, 2003).

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Appendix

Table A1.

Eligibility criteria as outlined in informed consent documentation.

YOU MAY NOT PARTICIPATE IN THE STUDY IF
You have metal objects inside your body. MRI may be dangerous for anyone with metal implants or metal objects inside their body. The following list is not necessarily complete. Please discuss with the study staff if you have (or may have) any object in your body that was not there when you were born. • Surgery involving metal, such as: clips, rods, screws, pins, wires. • Heart pacemaker • Implanted electrodes, pumps or electrical devices • Cochlear (inner ear) implants • Intraocular lens (eye) implants (Cataract lens allowed except for Brain Imaging studies) •Any metallic foreign body, shrapnel or bullet (Please mention if you have ever been a grinder, metal worker, welder, wounded during military service, etc.) •Intrauterine contraceptive device (IUD) or contraceptive diaphragm •Dental work held in place by magnets •Non-removable dental braces and retainers •Metal dental work, unless it is composed predominantly of precious or semiprecious alloy or amalgam (*This exclusion is for brain imaging studies only)* •Tattooed eyeliner •Some tattoos (if you do, please discuss with the Investigator) •Non-removable metal jewellery (body piercing) •Nicotine, nitroglycerin and/or contraceptive patches •Claustrophobia
In the opinion of the investigators, you have a medical condition that could be made worse by any stress associated with participation in a research protocol. These conditions include: • heart and circulatory problems • seizure disorders • anxiety disorders • mental or psychiatric disorders

You should not participate if you are, or may be, pregnant. If there is a possibility that you are pregnant, we will provide you with a pregnancy test before you enter the study. There are well-known hormonal fluctuations across the human menstrual cycle. Some of these hormonal fluctuations influence sleep-wake cycles, but this influence is reduced by oral contraceptives. Therefore, females will be EXLCUDED from participating UNLESS (1) they are currently taking oral contraceptives and (2) participating 10 days after the end of menstruation (and before the start of the next menstrual period). Please inform the investigator and the MR Screening Officer of the last day of your menstruation and the drug name and dosage of your oral contraceptive.
Have a Body-Mass Index (BMI) greater than 30 or less than 18, as large deviations in BMI can be associated with sleep disordered breathing.
We are seeking volunteers with a particular type of sleep pattern. If any of the following apply to you, you will be excluded from participating. O Oral contraceptives temper hormonal changes that affect the sleep cycle. Females may be excluded from participating unless they are currently taking oral contraceptives. Please inform the investigator and the MR Screening Officer of the drug name and dosage of your oral contraceptive. O a chronic serious illness (e.g. asthma, diabetes, hemophilia) O a history of neurological disease or impairments (e.g., epilepsy, migraines) O sleep complaints O use of street drugs during the past year O smoking cigarettes or other tobacco products O a pattern of alcohol misuse (>14 drinks a week) during the past year O weight loss greater than 5% during the past month O regularly sleep less than 6 hours or more than 10 hours daily O take regular naps O have a history of shift work in the last six months O have taken an airplane flight in the last month crossing more than two time zones. O take large amounts of caffeine daily. Caffeine users may be included if their daily intake from all sources is not more than the equivalent of one cup of coffee, or three cups of tea, daily (approximately 150 mg of caffeine). Some prescribed and over-the-counter medications have an impact on sleep patterns. You will be excluded from participating if you have taken any medicine that affect sleep. Please inform the investigator of all medicines you have taken within the last month.

Tables

Table 1.

Summary of key brain regions identified in three recent fMRI investigations of SAT.

Study	Brain Region	Talairach Coordinates x	y	z
Van Veen et al. (2008)				
	Left DLPFC	-33	34	35
	Right DLPFC	33	34	39
	ACC/SMA/left PMC	-15	-4	53
	Left PMC	-31	-11	57
	ACC/SMA	0	1	53
	Right dorsal PMC	34	-10	55
	Right dorsal PMC	47	1	42
	Left ventral PMC	-54	9	7
	Left anterior Insula	-31	21	11
	Left IPL/supramarginal gyrus	-45	-48	40
	Precuneus	-3	-68	44
	Basal ganglia/thalamus	-2	0	9
	Left cerebellum	-40	-50	-25
	Right cerebellum	29	-62	-22
Ivanoff et al., (2008)				
	Left pre-SMA	-2	5	52
	Right pre-SMA	4	7	56
	Right pLPFC	53	11	26
Forstmann et al. (2008)				
	Right pre-SMA	4	5	45
	Right anterior striatum	16	7	5

Note.

All regions had greater baseline activity following speed instructions relative to accuracy. PMC = pre-motor cortex, DLPFC = dorsolateral pre-frontal cortex, ACC = anterior cingulate cortex, SMA = supplementary motor cortex, IPL = inferior parietal lobule, pre-SMA = pre-supplementary motor area, pLPFC = posterior lateral prefrontal cortex.

Table 2.

Participant and scanning protocol information.

PAR	Sex	Age	Handedness	# Loc. Scans	# E-R Scans	Slice	Scan Time
1	M	25	R	2	4	3.75	pm.
2	F	23	R	2	4	3.75	pm.
3	F	26	R	2	4	3.75	pm.
4	M	24	R	2	4	3.75	pm.
5	M	22	R	2	4	3.75	pm.
6	M	23	R	2	4	4.75	pm.
7	M	23	L	2	6	4.75	pm.
8	F	26	R	1	6	4.75	pm.
9	F	24	R	2	6	4.75	pm.
10	F	23	R	2	6	4.75	pm.
11	M	23	R	2	5	4.75	am.
12	F	23	R	2	6	4.75	am.
13	F	24	R	2	6	4.75	am.
14	F	23	R	2	6	4.75	am.
15	M	23	R	2	6	4.75	am.
16	F	20	L	2	6	4.75	am.
17	F	21	R	2	6	4.75	am.
18	F	20	R	2	6	4.75	pm.
19	M	26	R	2	4	4.75	pm.

Note.
PAR = participant number; # Scans = the number of functional localizer (Loc.) runs and event-related (E-R) runs completed; Slice = slice thickness measured in millimeters (mm); Scan Time = time scanning session occurred (10am or 4:30pm).

Table 3.

Average localizer task performance for house and face blocks with standard deviations shown in brackets.

	Face Blocks	House Blocks
Correct RT	742.17 (84.23)	739.10 (93.93)
Hit Rate		0.89 (0.09)
FA Rate		0.15 (0.17)
Percent Correct	86.74 (5.53)	86.86 (9.58)

Note.
RT = Response Time; FA = False Alarm.

Table 4.

Summary of behavioural results for every participant split by speed and accuracy conditions in the event-related task.

	RT (ms)		Hit Rate (%)		FA Rate (%)	
PAR	**ACC**	**SPD**	**ACC**	**SPD**	**ACC**	**SPD**
1	821.86	546.79	100.00	100.00	8.33	0.00
2	790.48	553.05	100.00	94.44	0.00	5.56
3	853.09	644.40	100.00	100.00	0.00	8.33
4	860.72	626.05	100.00	100.00	0.00	8.33
5	749.83	619.45	100.00	100.00	0.00	0.00
6	808.29	549.46	100.00	100.00	0.00	0.00
7	834.86	558.21	100.00	100.00	0.00	11.11
8	710.22	566.34	88.89	92.59	27.78	33.33
9	762.30	599.38	100.00	100.00	38.89	33.33
10	734.13	714.49	100.00	100.00	0.00	0.00
11	853.99	581.19	100.00	100.00	0.00	0.00
12	1537.79	615.33	85.71	81.48	0.00	11.11
13	990.15	486.04	100.00	100.00	22.22	38.89
14	864.79	681.09	96.43	96.15	5.56	5.56
15	1442.29	615.89	96.30	100.00	0.00	0.00
16	800.96	550.28	100.00	96.30	16.67	16.67
17	884.97	636.75	89.29	96.30	27.78	27.78
18	994.23	518.64	100.00	100.00	0.00	11.11
19	594.14	421.19	100.00	100.00	9.09	8.33
Avg.	**888.90**	**583.37**	**97.72**	**97.75**	**8.23**	**11.55**

Note.
PAR = participant number; RT = mean reaction time; FA = false alarm; ACC = accuracy condition; SPD = speed condition; Avg. = average.

Table 5.

ROIs identified with functional localizer task, mean accuracy minus speed differences in average AUC, and results of paired *t*-tests for accuracy versus speed in event-related analyses.

		Tal.		SAT Cue			Face Cue			
	B.As	X,Y,Z	Vox	2-8 Vol.	SEM		2-8 Vol.	SEM	8-9 Vol.	SEM
House-Fix										
MF	8, 9, 6	-46, 17, 42	1651	1.43	0.87		0.3	0.36	0.11	0.09
	6, 8	27, 22, 56	1523	0.63	0.76		-0.27	0.46	-0.04	0.1
MFG/IFG	10, 46	-41, 48, 5	770	1.14	1.09		1.01	0.57	0.21	0.13
MFG/SFG	10, 9	31, 49, 9	1770	0.69	0.7		0.25	0.28	-0.07	0.08
S. Occ.	19,39,31	-33,-76, 24	2141	1.31	0.47	*	-0.04	0.21	-0.03	0.07
	19,31	32, -76, 23	2711	0.48	0.58		0.36	0.45	0.13	0.09
V. PreCu	7, 19	-11,-76, 44	2055	3.55	1.92		-0.12	0.57	0.01	0.14
	7, 19	9, -76, 45	2669	4.8	1.73	*	-0.83	0.78	-0.03	0.19
PreCu	7, 31	-22,-64, 26	1167	1.16	0.6		0.08	0.2	-0.02	0.07
	7, 31	21, -62, 25	1590	0.69	0.54		0.25	0.25	0.09	0.06
SPL/PreCu	7	-8, -65, 55	2168	3.35	1.26	*	-0.45	0.92	-0.01	0.3
	7	12, -64, 55	2510	2.66	0.95	*	0.01	0.47	0.12	0.14
Temporal	37,22,20	-50, -53, -6	1056	1.01	0.79		0.08	0.35	0.03	0.1
	22,21,37	54, -43, -2	1833	-0.47	0.69		0.22	0.26	0.08	0.08
PPA	30,36,35	-22, -40, -6	1440	0.85	0.65		-0.03	0.22	0.06	0.06
		23, -38, -6	1652	0.77	0.39		0.24	0.23	0.03	0.06
PCC	29, 30	-12, -51, 9	1170	1.32	0.65		0.4	0.35	0.05	0.1
	29, 30	9, -49, 10	1974	1.35	0.53	*	0.4	0.35	0.08	0.09
Face-Fix										
Pre-SMA	6	8, 5, 65	2023	0.13	0.56		-0.69	0.29	* -0.11	0.11

Table 5 (cont.)

		Tal.		SAT Cue				Face Cue			
	B.As	X,Y,Z	Vox.	2-8 Vol.	SEM		2-8 Vol.	SEM	8-9 Vol.	SEM	
Conj.											
LN		-24, 6, 4	125	0.18	0.63		-0.26	0.27	-0.16	0.06	*
		23, 6, 4	125	-0.05	0.71		-0.16	0.32	-0.11	0.08	
Occipital Lobe	18,19	-40, -77, -6	2732	1.02	0.79		0.13	0.35	0.02	0.11	
	18,19	39, -77, -7	2652	1.21	0.93		0.5	0.66	0.22	0.18	
SMA	6	-6, -1, 57	1017	0.81	0.53		-0.11	0.25	-0.08	0.06	
Pre-SMA	6	-3, 7, 66	714	1.92	0.95		-0.43	0.38	-0.04	0.13	
Extra.S	18	-16, -81, -6	1111	1.54	0.65	*	0.46	0.37	0.02	0.08	
	18	15, -80, -5	1813	1.09	0.6		0.03	0.39	0.15	0.12	
Caudate		13, 7, 12	1562	0.47	0.67		-0.14	0.24	-0.07	0.07	
Insula/IFG	13	-32, 16, 7	2434	0.42	0.68		0.05	0.25	-0.04	0.06	
	13	33, 20, 7	2734	0.41	0.61		-0.07	0.2	-0.06	0.06	
IFG	47	46, 18, -2	564	0.26	0.96		0.24	0.38	-0.04	0.11	
Thalamus		-11,-12, 12	2666	0.31	0.45		-0.06	0.24	-0.06	0.07	
		8, -11, 11	2720	0.42	0.53		-0.19	0.25	-0.05	0.07	
DLPFC	46, 9	-44, 18, 27	1340	1.58	0.73	*	0.14	0.3	0.04	0.07	
	46, 9	43, 24, 24	2741	1.01	0.89		-0.08	0.23	-0.08	0.07	
IFJ	6, 9	-39, 2, 31	2573	1.21	0.64		0.13	0.18	-0.03	0.06	
	6, 9	38, 5, 31	2696	0.83	0.63		0.06	0.22	-0.05	0.07	
PM	6	-28, -6, 80	779	1.16	0.52	*	0.06	0.27	-0.09	0.07	
	6	32, -1, 53	1200	1.26	0.58	*	-0.06	0.26	-0.1	0.06	
	6	-48, 0, 46	1859	1.8	0.77	*	0	0.26	-0.07	0.09	
	6, 8, 9	45, 5, 43	1695	0.61	0.54		0.14	0.33	-0.06	0.09	
Midbrain		-8, -21, -6	1793	0.61	0.47		0.1	0.22	-0.02	0.06	
		7, -20, -7	1980	0.82	0.43		0.03	0.21	-0.03	0.05	
IPL	40	-37,-37, 39	1129	0.84	0.62		0.03	0.27	-0.07	0.08	
	40	38, -42, 43	993	0.17	0.51		0.2	0.28	0.08	0.08	
SPL	7	-28,-53, 44	719	1.59	0.76		-0.13	0.31	-0.11	0.07	
	7	28, -58, 44	1029	0.79	0.69		0.11	0.29	0.14	0.08	
M. Occ.	19,18	-29,-87, 10	2186	0.98	0.72		0.25	0.26	0.01	0.06	
	19,18	26, -90, 10	2401	-0.1	0.48		0.44	0.33	0.14	0.09	
Cerebell.		-8, -67, -18	2211	0.49	0.81		0.48	0.49	0.09	0.1	
		6, -66, -16	1650	0.73	0.62		0.39	0.48	0.1	0.11	

Table 5 (cont.)

		Tal.		SAT Cue				Face Cue		
	B.As	X,Y,Z	Vox	2-8 Vol.	SEM		2-8 Vol.	SEM	8-9 Vol.	SEM
Conj.										
M. Frontal	8,9	44, 22, 42	1433	0.96	0.74		-0.01	0.31	-0.11	0.08
S. Frontal	10,46	39, 44, 20	796	0.34	0.87		0.19	0.28	-0.13	0.06
LN/GP		-25, -21, 0	815	0.49	0.54		0.2	0.2	-0.03	0.05
		25, -21, 0	1854	0.66	0.44		0.11	0.18	-0.02	0.04
Cuneus	18,19,30	-10,-71, 10	1081	1.45	0.55	*	0.05	0.26	-0.03	0.07
	18,19,30	7, -70, 12	570	1.38	0.6	*	0.47	0.25	0.1	0.07
IFG	44	48, 11, 16	1971	0.98	0.75		-0.13	0.3	-0.11	0.08
M. Occ.	19	-43, -76, 6	1020	1.72	0.92		-0.35	0.34	-0.06	0.09
	19	40, -75, 7	1603	0.72	0.44		0.31	0.44	0.09	0.09
ACC	32	-5, 17, 39	757	0.49	0.53		0.05	0.19	0	0.07
	32	8, 19, 37	1509	0.85	0.61		-0.21	0.19	-0.08	0.06
S. Frontal	6, 8	7, 26, 55	890	1.15	0.66		0.05	0.28	0.02	0.08
	8,6	5, 38, 47	806	1.15	0.67		0.22	0.29	0.11	0.08
	6,32	4, 10, 51	2185	1.35	0.62	*	-0.05	0.28	-0.07	0.07
FFA	37,20	-37,-43,-14	1359	1.08	0.5	*	0.26	0.25	0.05	0.1
	37, 20	39,-42, -13	1739	0.46	0.57		0.44	0.29	0.09	0.06

Note.

1. Extra S. = extrastriate cortex; Cerebell. = cerebellum; SMA = supplementary motor area; Pre-SMA = pre-supplementary motor area; IFG = inferior frontal gyrus; DLPFC = dorsolateral pre-frontal cortex; IFJ = inferior frontal junction; PM = pre-motor; IPL = inferior parietal lobe; LN = lentiform nucleus; GP = globus pallidus; ACC = anterior cingulate cortex; M. Frontal = middle frontal cortex; S. Frontal = superior frontal cortex; FFA = fusiform face area; MFG = medial frontal gyrus; SFG = superior frontal gyrus; MF = middle frontal cortex; SPL = superior parietal lobe; PPA = parrahipocampal place area; M. Occ. = middle occipital cortex; S. Occ. = superior occipital cortex; PCC = posterior cingulate cortex; PreCu = precuneus; V. PreCu. = ventral precuneus; B.As = brodmann areas; Vol = volumes; Tal = Talairach coordinates (x,y,z); Vox = number of voxels in ROI; CR = correct rejection; Conj. = ROIs identified using conjunction analysis; House-Fix = ROIs identified using house-fix contrast; Face-Fix = ROIs identified using face-fix contrast.

3. Statistical significance of paired *t* tests between the average AUC for specified time

intervals in speed versus accuracy conditions; * = p<.05; ** = p<.01; SEM = standard error of the mean

4. 2-8 vol. and 8-9 vol.: Values represent mean accuracy-speed differences for the average AUC calculated across the time intervals of 2-8 volumes and 8-9 volumes following the presentation of the SAT cue and face stimuli in the event-related analyses. Negative values indicate greater average AUC for speed relative to accuracy instructions.

Table 6.
Results of 2 (SPD/ACC) x 2 (CR/Hit) repeated measures ANOVA in each ROI.

		CR/Hit			SAT			Interaction	
	B.As	F(1,18)	MSE		F(1,18)	MSE		F(1,18)	MSE
Conj.									
Lentiform Nucleus		2.51	0.62		3.22	0.86		1.37	2.35
		3.59	1.26		1.89	1.53		0.79	3.43
Occipital Lobe	18, 19	0.02	6.57		0.72	5.92		0.01	3.45
	18, 19	0.00	2.43		0.01	4.31		1.23	2.55
SMA	6	2.34	1.52		4.66	1.34	*	0.43	2.05
Pre-SMA	6	4.24	7.01		4.47	3.94	*	0.43	8.04
Extrastriate	18	0.01	3.18		0.54	4.07		0.24	2.15
	18	0.61	1.54		0.03	2.76		1.17	1.42
Caudate		1.53	0.81		3.19	1.04		1.44	3.51
Insula/IFG	13	1.90	1.05		0.02	1.32		0.77	1.57
	13	1.79	1.79		0.01	2.10		1.18	2.63
IFG	47	1.54	4.63		0.26	6.18		0.03	8.12
Thalamus		4.32	0.81		0.99	1.00		1.31	2.61
		3.18	0.76		0.79	1.40		2.84	3.33
DLPFC	46, 9	0.04	2.24		0.04	2.23		0.34	3.74
	46, 9	0.04	2.21		0.06	3.36		0.22	4.41
IFJ	6, 9	0.61	1.61		0.54	1.89		1.07	3.07
	6, 9	0.12	2.28		0.43	2.25		0.43	3.36
PM	6	0.12	1.19		4.05	1.77		0.60	2.47
	6	0.03	1.44		1.04	1.62		0.78	2.86
	6	0.44	2.63		1.42	2.49		0.02	6.14
	6, 8, 9	0.55	3.06		0.89	2.57		0.01	3.08
Midbrain		3.99	1.03		1.12	1.52		0.03	2.09
		2.64	0.85		1.54	1.24		0.00	2.03
IPL	40	1.08	1.73		1.29	2.18		0.50	3.70
	40	0.03	0.96		0.03	2.18		0.01	2.09
SPL	7	0.78	3.14		3.66	1.88		0.06	3.16
	7	1.83	1.52		0.01	1.43		0.14	3.38
Middle Occipital	19, 18	0.01	2.74		0.00	2.86		0.42	2.38
	19, 18	0.02	2.46		1.42	1.10		0.02	2.44
Cerebellum		3.42	9.17		0.09	10.33		0.30	9.57
		9.64	3.65	**	0.20	6.60		0.14	4.43
Middle Frontal	8, 9	0.83	6.65		6.19	2.90	*	0.16	4.09
Superior Frontal	10, 46	0.01	4.49		0.03	4.69		0.07	3.64
LN/GP		2.24	1.74		0.01	2.35		0.11	1.88

Table 6 (cont.)

		CR/Hit			SAT		Interaction	
	B.As	F(1,18)	MSE		F(1,18)	MSE	F(1,18)	MSE
Conjunction								
Cuneus	18, 19, 30	2.43	1.09		1.74	1.35	0.25	2.17
	18, 19, 30	1.45	0.94		2.13	2.15	0.00	1.45
IFG	44	1.35	2.75		0.24	3.35	0.03	3.93
Middle Occipital	19	0.02	2.89		0.02	5.30	0.93	5.58
	19	2.73	2.17		2.63	1.14	0.07	2.91
ACC	32	1.31	1.27		0.82	1.39	1.43	1.93
	32	1.36	1.45		2.67	1.41	1.99	1.91
Superior Frontal	6, 8	0.03	1.66		0.14	3.77	0.11	3.76
	8,6	1.81	1.89		0.86	3.22	0.02	2.36
	6, 32	0.88	1.62		2.94	1.61	0.99	2.32
FFA	37, 20	0.01	3.37		0.19	3.27	0.28	3.31
	37, 20	0.56	1.90		0.19	1.13	0.31	1.88
House-Fix								
Middle Frontal	8, 9, 6	0.53	1.84		1.60	3.25	0.94	6.82
	6, 8	0.03	3.39		0.44	6.84	0.00	7.59
MFG/IFG	10, 46	0.21	5.45		2.76	7.22	2.21	7.65
MFG/SFG	10, 9	0.00	4.03		0.02	5.90	0.31	3.22
Superior Occipital	19, 39, 31	0.15	2.52		0.59	1.82	0.23	3.53
	19, 39, 31	3.18	0.95		1.40	1.14	3.03	1.40
Ventral PreCu	7, 19	0.01	7.31		2.70	5.91	0.00	4.11
	7, 19	0.20	4.00		0.28	16.56	0.26	3.58
PreCu	7, 31	0.01	1.32		0.89	2.20	0.03	2.63
	7, 31	0.00	1.20		0.41	0.80	1.12	1.26
SPL/PreCu	7	0.22	5.71		1.97	13.49	2.01	7.68
	7	5.47	2.19	*	1.25	3.08	0.36	5.05
Temporal	37, 22, 20	0.39	4.14		0.25	4.59	0.12	4.69
	22, 21, 37	0.00	1.54		0.01	2.15	2.13	2.95
PPA	30, 36, 35	0.00	1.88		0.27	2.79	0.16	2.40
		0.83	1.04		2.73	0.90	0.01	0.95
PCC	29, 30	0.04	2.40		0.35	1.82	1.29	2.89
	29, 30	0.21	1.79		3.39	1.40	2.96	1.90
Face-Fix								
Pre-SMA	6	1.36	3.73		3.30	3.82	0.00	5.11

Table 6 (cont.)

Note.
1. SMA = supplementary motor area; Pre-SMA = pre-supplementary motor area; IFG = inferior frontal gyrus; DLPFC = dorsolateral pre-frontal cortex; IFJ = inferior frontal junction; PM = pre-motor; IPL = inferior parietal lobe; LN = lentiform nucleus; GP = globus pallidus; ACC = anterior cingulate cortex; FFA = fusiform face area; MFG = medial frontal gyrus; SFG = superior frontal gyrus; SPL = superior parietal lobe; PPA = parrahipocampal place area; PreCu = Precuneus; PCC = posterior cingulate cortex.
2. B.As = brodmann areas; MSE = mean squared error; * = $p<.05$; ** = $p<.01$.
3.Black boxes indicate the contrast used to identify the subsequent ROIs.

Figures

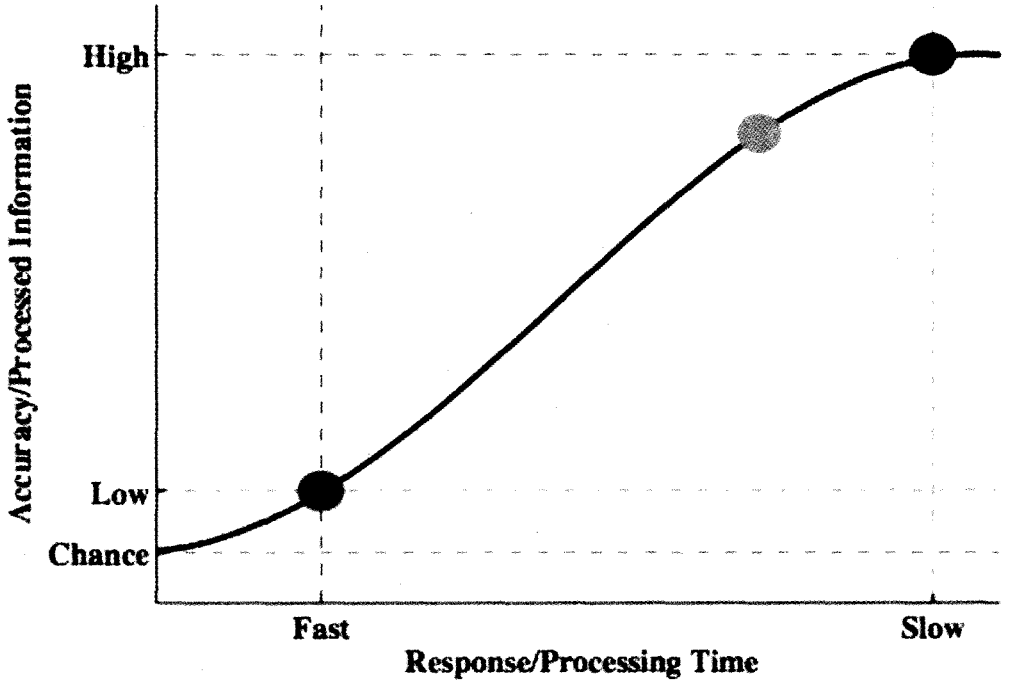


Figure 1. Simplified version of the SAT function (SATF) achieved by plotting the response speed or time taken to process a stimulus versus the response accuracy or amount of information processed. When responding fast (red), performance is less accurate relative to when responding is slow (blue). When instructed to balance the speed and accuracy of responding (green), responses are typically biased toward achieving relatively high levels of accuracy. The function has been understood to reflect information processing, with greater response times reflecting greater processing of stimulus information. When responding exceptionally fast, performance is expected to be at chance levels of accuracy (for a review, see Pachella, 1974).

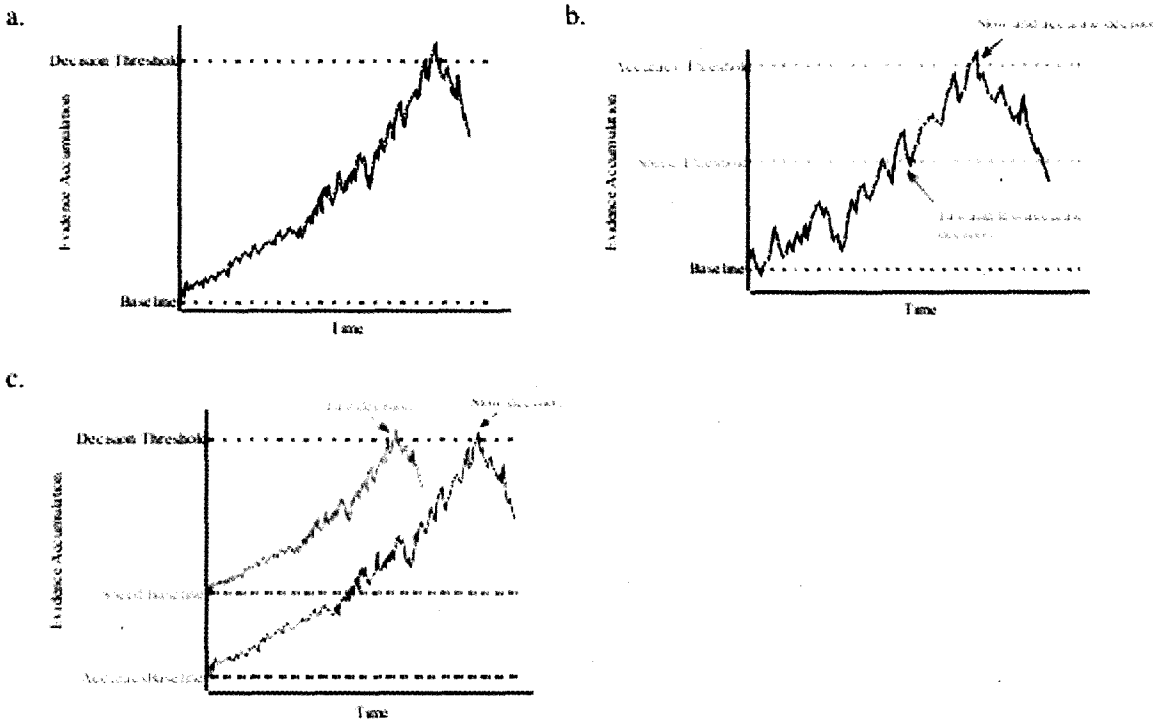


Figure 2. An illustration of a simple accumulator model with a single decision criterion and two ways that this type of model has accounted for the speed-accuracy tradeoff (SAT). (a) Evidence is accrued across time from a starting baseline toward a threshold in favor of one or more outcomes. Increased evidence reflects evidence accrued toward a decision (e.g., right hand response) while reduced evidence reflects evidence against the decision or toward another decision (e.g., left hand response). (b) The variable threshold account of SAT holds a constant baseline while the threshold criterion is varied. When instructed to be fast (red), the decision threshold may be lowered closer to the baseline resulting in faster yet less accurate responding and increasing the probability that noisy or irrelevant stimulation may incorrectly result in the growth function reaching threshold by chance. (c) The variable baseline account of SAT holds a constant threshold while the baseline is varied. When instructed to be fast (red), the baseline may be raised closer to the threshold, resulting in faster yet less accurate responding and an increased risk of noisy or irrelevant stimulation reaching threshold.

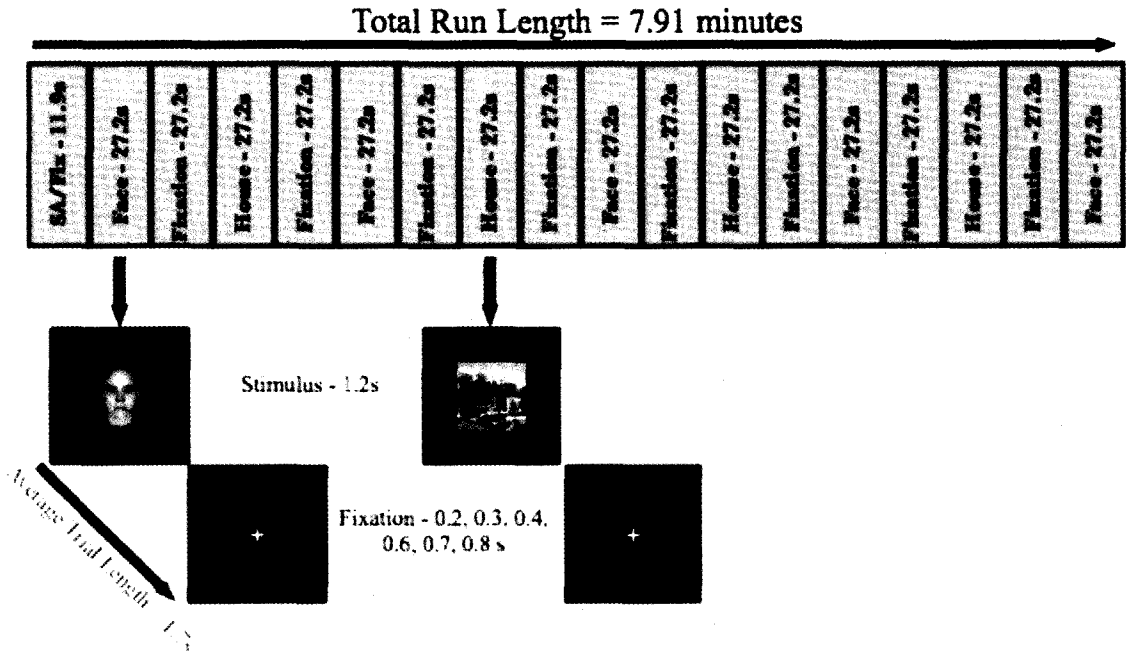


Figure 3. An illustration of the block-design task with an example of trials for face and house response blocks. Participants performed 16 trials per response block and a total of 9 face and 9 house blocks across two runs. On average, trials were 1.7 seconds with the total run length being 7.91 minutes. Note: "SA" – spin alignment block; "Face"- face response block; "House" – house task block.

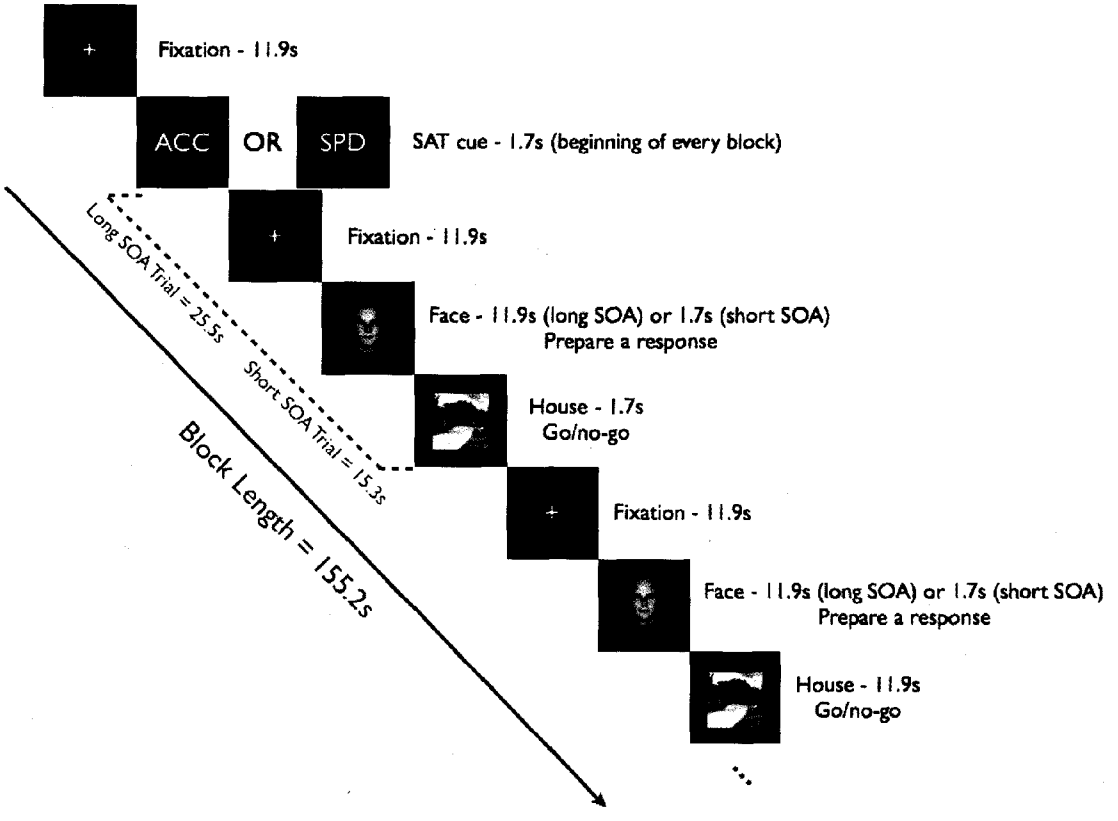


Figure 4. An illustration of the trial sequence in the response preparation go/no-go task. Participants underwent 3 blocks of 6 trials. There were fifty percent go-trials (two-storey house) and fifty percent no-go trials (one-storey house) with 4-5 long SOA and 1-2 short SOA trials. Participants were cued at the beginning of each block to be as fast as possible (SPD) or as accurate as possible (ACC). The speed-accuracy tradeoff cue (SAT cue) alternated for each block and was counterbalanced across runs. Participants were instructed to prepare a right response to male faces and to prepare a left response to female faces, with equal numbers of male and female faces presented in a block. A trial consisted of an 11.9s fixation period followed by a face stimulus (presented for 11.9s or 1.7s) which was then followed by a house stimulus (presented for 1.7s). Responses were prepared to face stimuli and executed/inhibited to house stimuli.

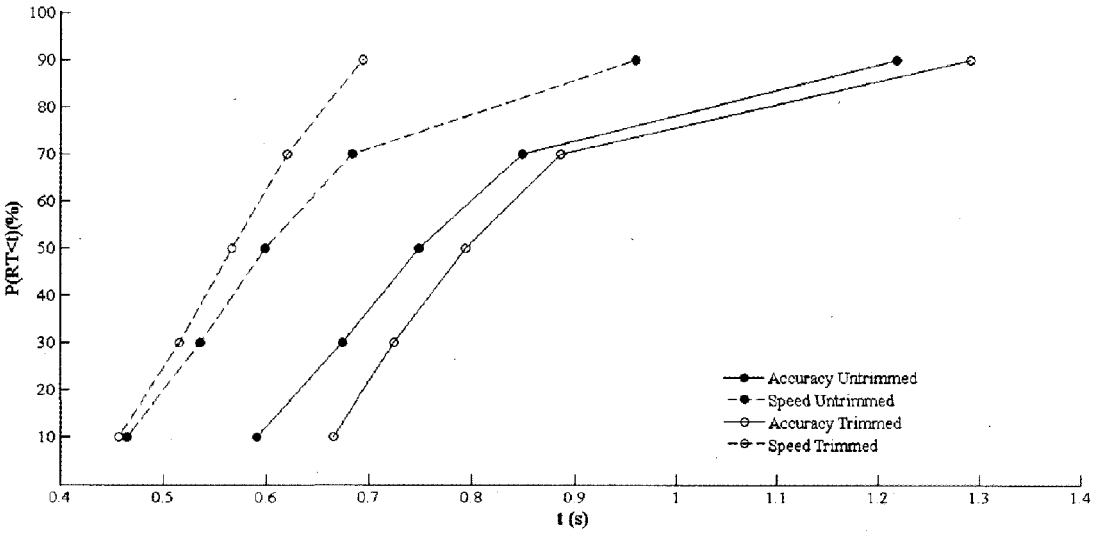


Figure 5. Vincentized plots of trimmed and untrimmed RTs in speed and accuracy conditions.

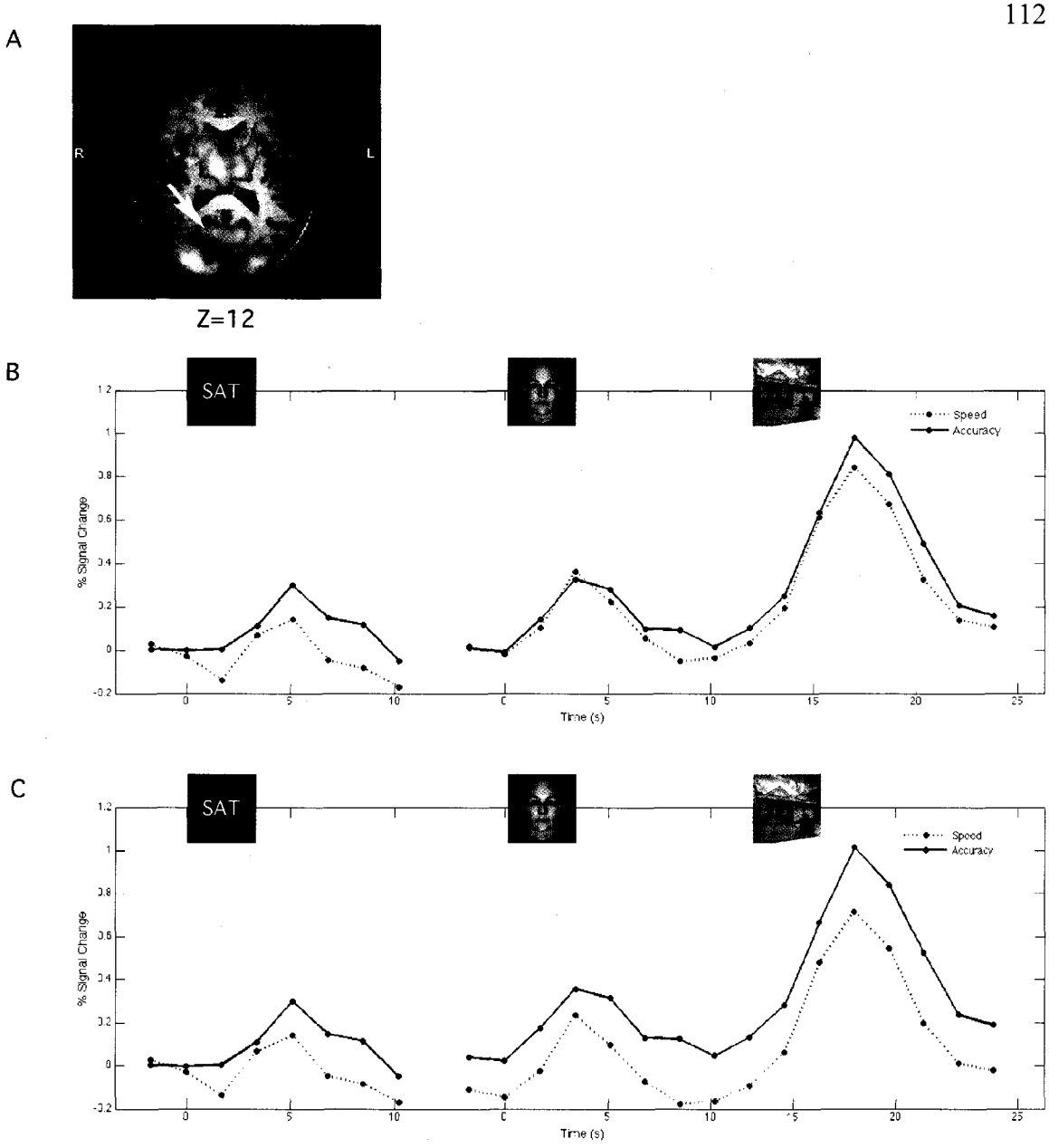


Figure 6. fMRI results for the right cuneus. (A) Axial view of the conjunction SPM from the functional localizer task with the location of the right cuneus indicated by the white arrow. (B) Speed and accuracy time-courses time-locked and baselined to the SAT cue and to the face cue. Accuracy was significantly above speed during the SAT cue interval (indicated by gray rectangle). There were no differences between speed and accuracy time-courses when time-locked to the face. (C) Speed and accuracy time-courses time-locked and baselined to the SAT cue and time-locked to the face cue but baselined to the average of the last two volumes during the SAT cue interval. When baselined to the last two volumes of the SAT cue the accuracy time-course was significantly greater than the speed time-course for the entire duration following the face cue (indicated by gray rectangle).

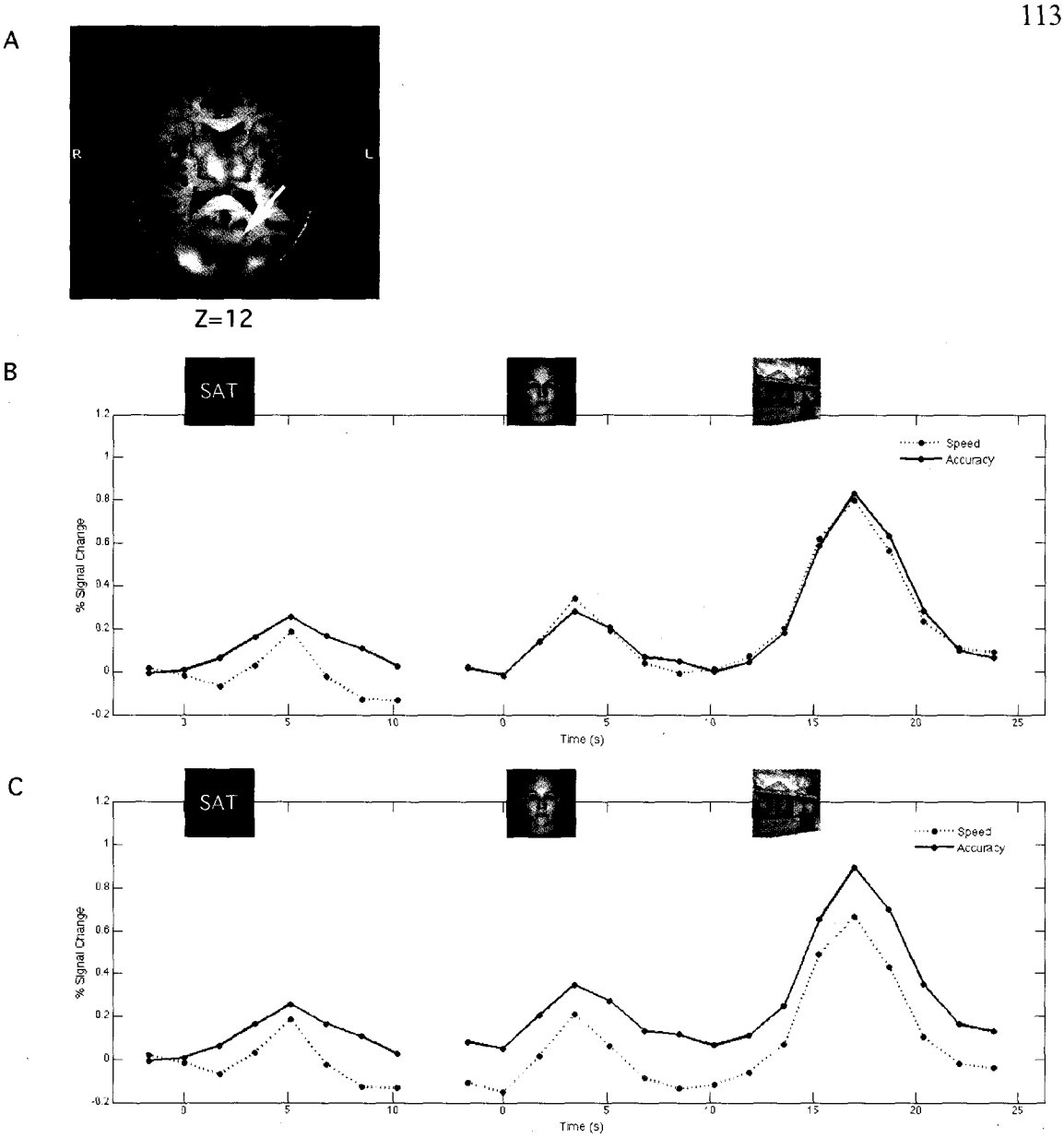


Figure 7. fMRI results for the left cuneus. (A) Axial view of the conjunction SPM from the functional localizer task with the location of the left cuneus indicated by the white arrow. (B) Speed and accuracy time-courses time-locked and baselined to the SAT cue and to the face cue. Accuracy was significantly above speed during the SAT cue interval (indicated by the gray rectangle). There were no differences between speed and accuracy time- courses when time-locked to the face. (C) Speed and accuracy time-courses time-locked and baselined to the SAT cue and time-locked to the face cue but baselined to the average of the last two volumes during the SAT cue interval. When baselined to the last two volumes of the SAT cue the accuracy time-course was significantly greater than the speed time-course for the entire duration following the face cue (indicated by the gray rectangle).

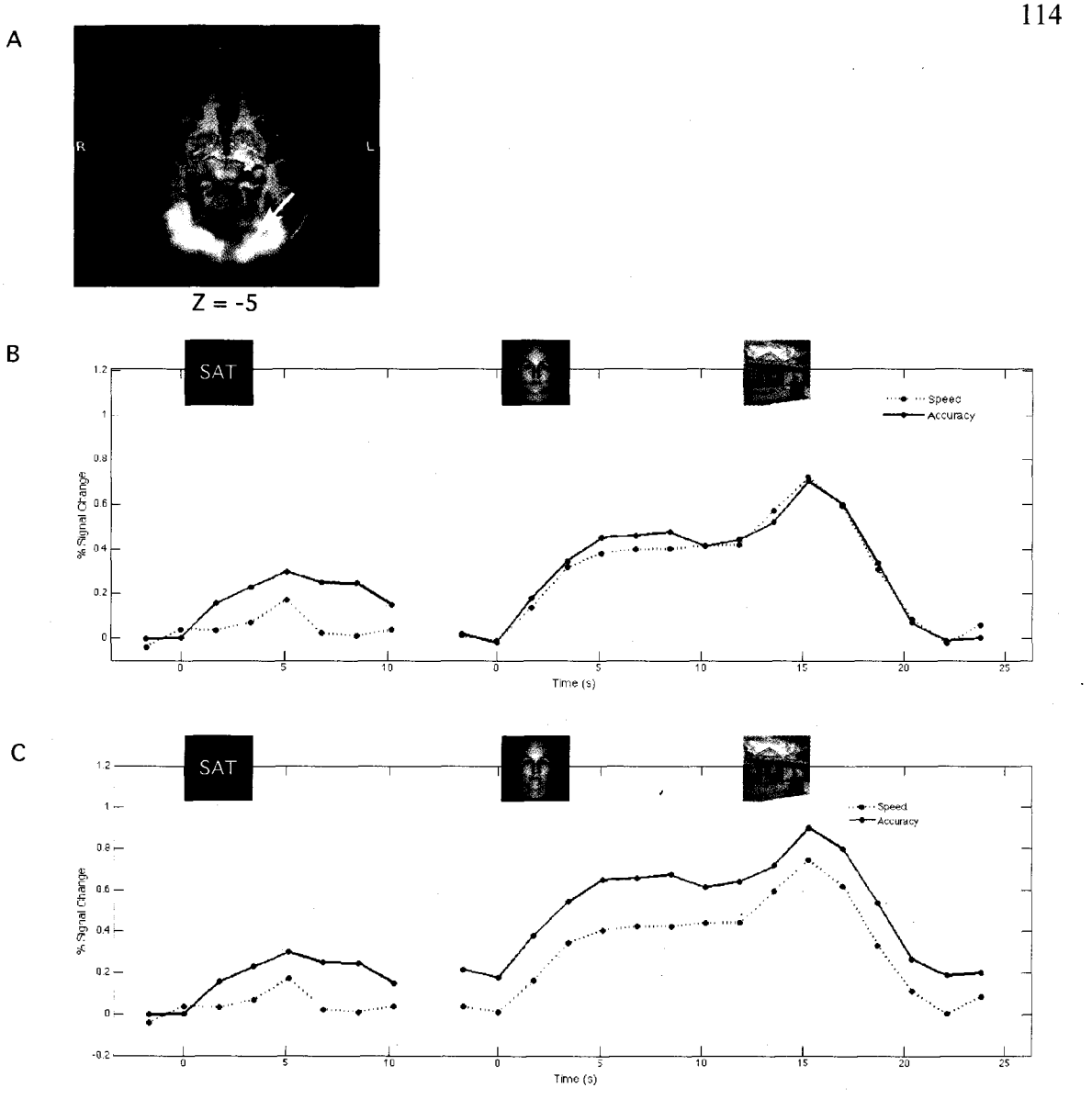


Figure 8. fMRI results for the left extrastriate cortex. (A) Axial view of the conjunction SPM from the functional localizer task with the location of the left extrastriate indicated by the white arrow. (B) Speed and accuracy time-courses time-locked and baselined to the SAT cue (baselined to average of volume of, and prior to, presentation of the SAT cue) and time-locked and to the face cue. Accuracy was significantly above speed during the SAT cue interval (indicate by gray rectangle). There were no differences between speed and accuracy time-courses when time-locked to the face. (C) Speed and accuracy time-courses time-locked and baselined to the SAT cue and time-locked to the face cue but baselined to the average of the last two volumes during the SAT cue interval. When baselined to the last two volumes of the SAT cue the accuracy time-course was significantly greater than the speed time-course for the entire duration following the face cue (indicated by gray rectangle).

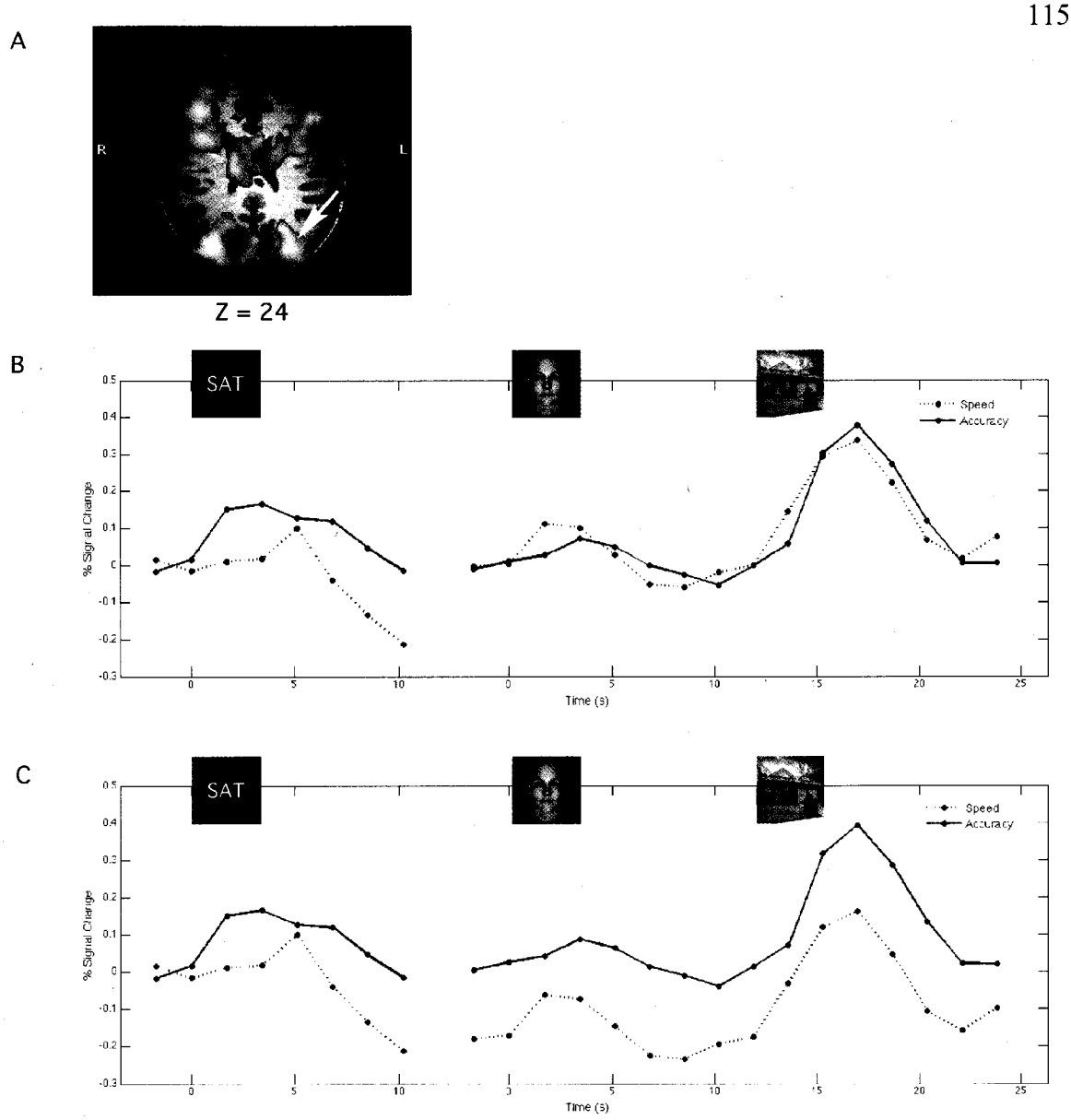


Figure 9. fMRI results for the left superior occipital cortex. (A) Axial view of the house-fix SPM from the functional localizer task with the location of the left superior occipital cortex indicated by the white arrow. (B) Speed and accuracy time-courses time-locked and baselined to the SAT cue and to the face cue. Accuracy was significantly above speed during the SAT cue interval (indicated by gray rectangle). There were no differences between speed and accuracy time-courses when time-locked to the face. (C) Speed and accuracy time-courses time-locked and baselined to the SAT cue and time-locked to the face cue but baselined to the average of the last two volumes during the SAT cue interval. When baselined to the last two volumes of the SAT cue the accuracy time-course was significantly greater than the speed time-course for the entire duration following the face cue (indicated by gray rectangle).

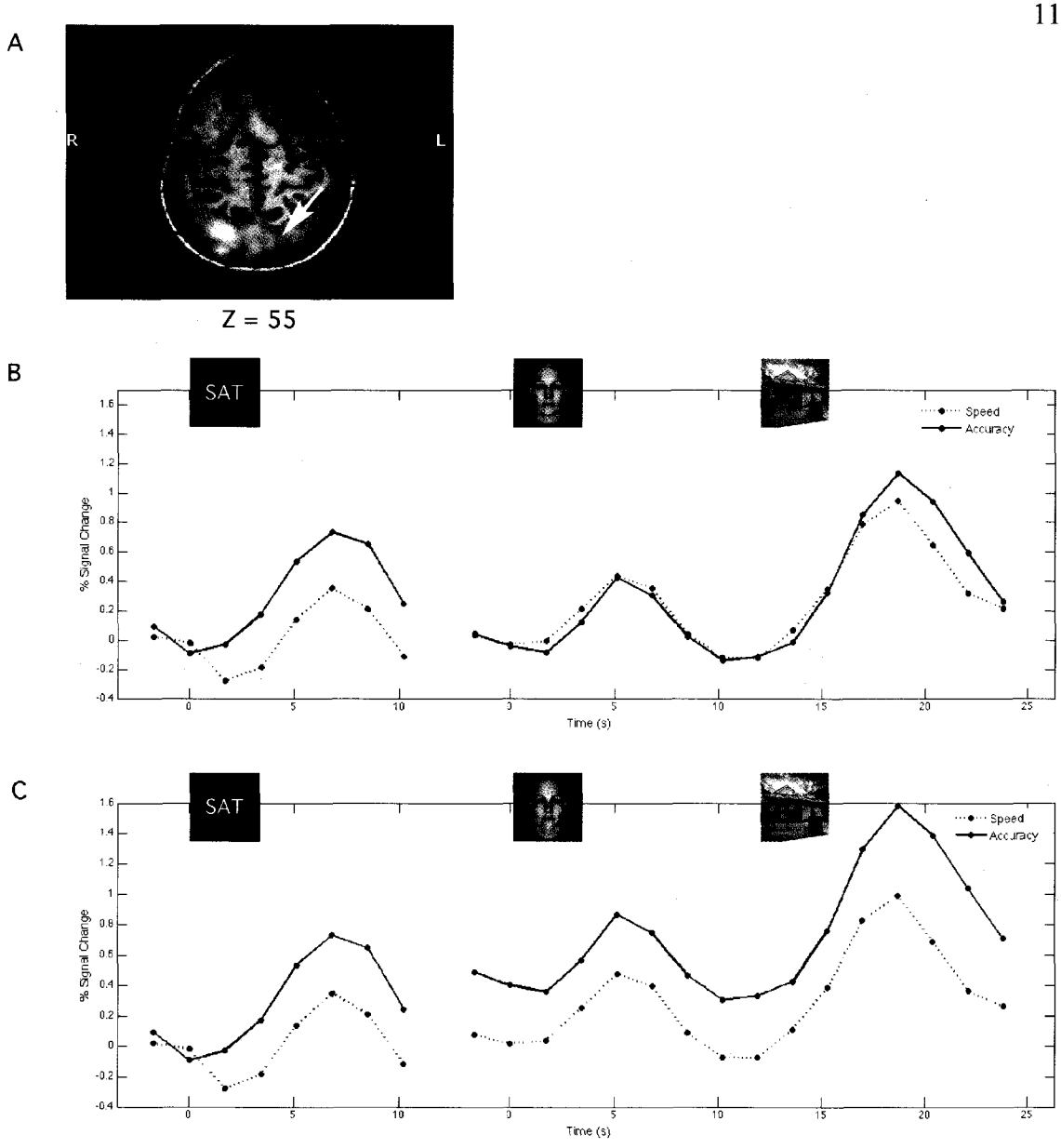


Figure 10. fMRI results for the left superior parietal lobe/precuneus (BA7). (A) Axial view of the house-fix SPM from the functional localizer task with the location of the left superior parietal lobe/precuneus indicated by the white arrow. (B) Speed and accuracy time-courses time-locked and baselined to the SAT cue and to the face cue. Accuracy was significantly above speed during the SAT cue interval (indicated by gray rectangle). There were no differences between speed and accuracy time-courses when time-locked to the face. (C) Speed and accuracy time-courses time-locked and baselined to the SAT cue and time-locked to the face cue but baselined to the average of the last two volumes during the SAT cue interval. When baselined to the last two volumes of the SAT cue the accuracy time-course was significantly greater than the speed time-course for the entire duration following the face cue (indicated by gray rectangle).

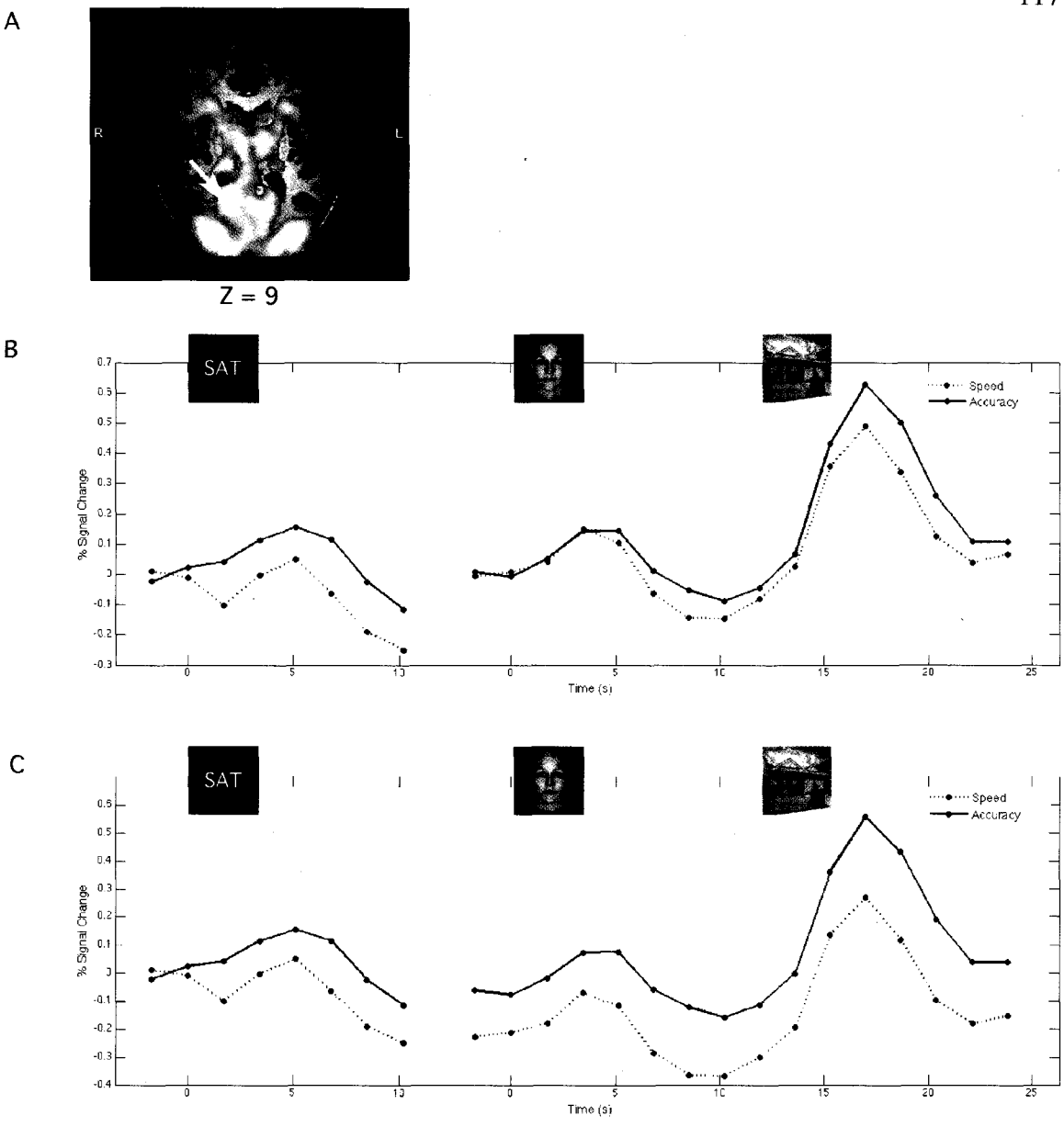


Figure 11. fMRI results for the right posterior cingulate. (A) Axial view of the house-fix SPM from the functional localizer task with the location of the right posterior cingulate indicated by the white arrow. (B) Speed and accuracy time-courses time-locked and baselined to the SAT cue and to the face cue. Accuracy was significantly above speed during the SAT cue interval (indicated by gray rectangle). There were no differences between speed and accuracy time-courses. (C) Speed and accuracy time-courses time-locked and baselined to the SAT cue and time-locked to the face cue but baselined to the average of the last two volumes during the SAT cue interval. When baselined to the last two volumes of the SAT cue the accuracy time-course was significantly greater than the speed time-course for the entire duration following the face cue (indicated by gray rectangle).

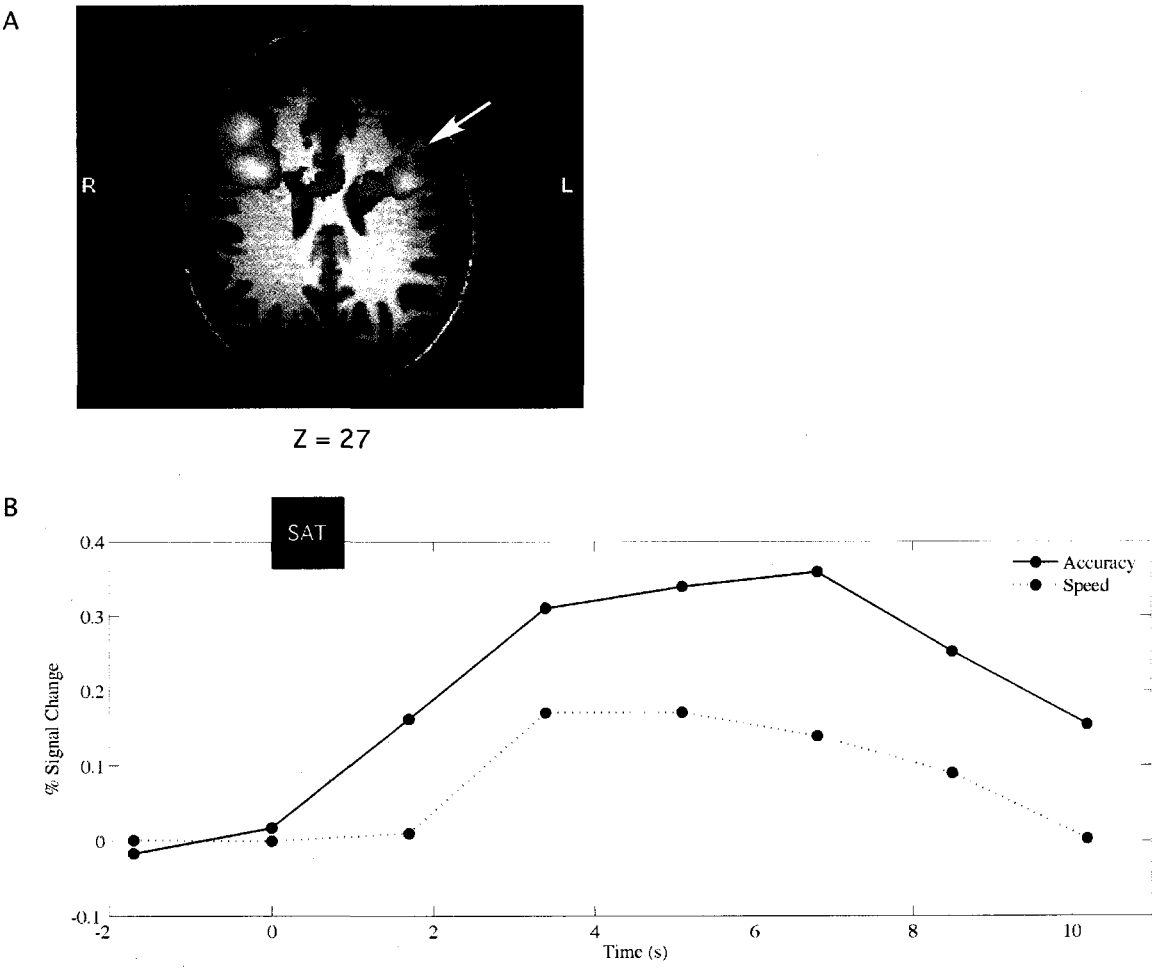


Figure 12. fMRI time-courses for the left DLPFC. (A) Axial view of the conjunction SPM from the localizer task with the location of the left DLPFC indicated by the white arrow. (B) Speed and accuracy time-courses time-locked and baselined to the SAT cue. Accuracy was significantly above speed during the SAT cue interval.

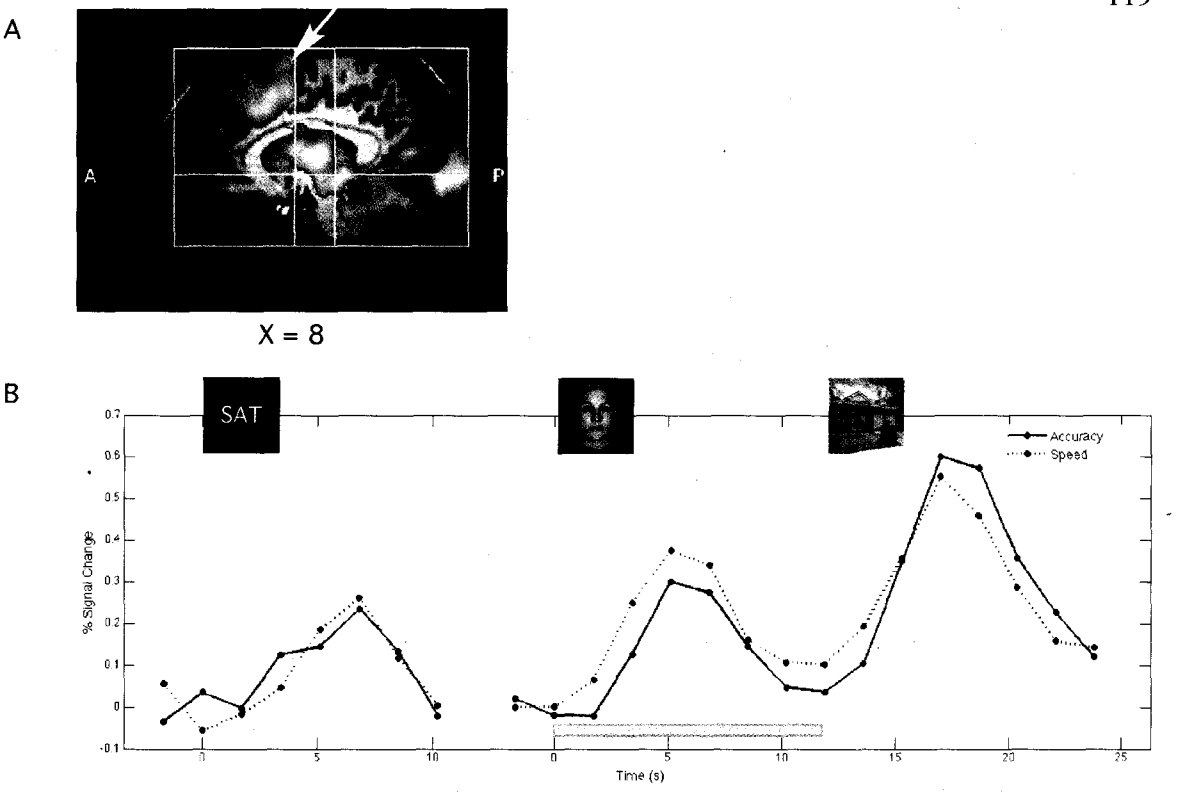


Figure 13. fMRI results for the right pre-SMA. (A) Sagittal view of the face-fix SPM from functional localizer task with the location of the right pre-SMA indicated by the white arrow. (B) Speed and accuracy time-courses time-locked to the SAT cue and to the face cue. Speed was significantly above accuracy from 0s to 11.9s (indicated by gray horizontal rectangle) following the face presentation.

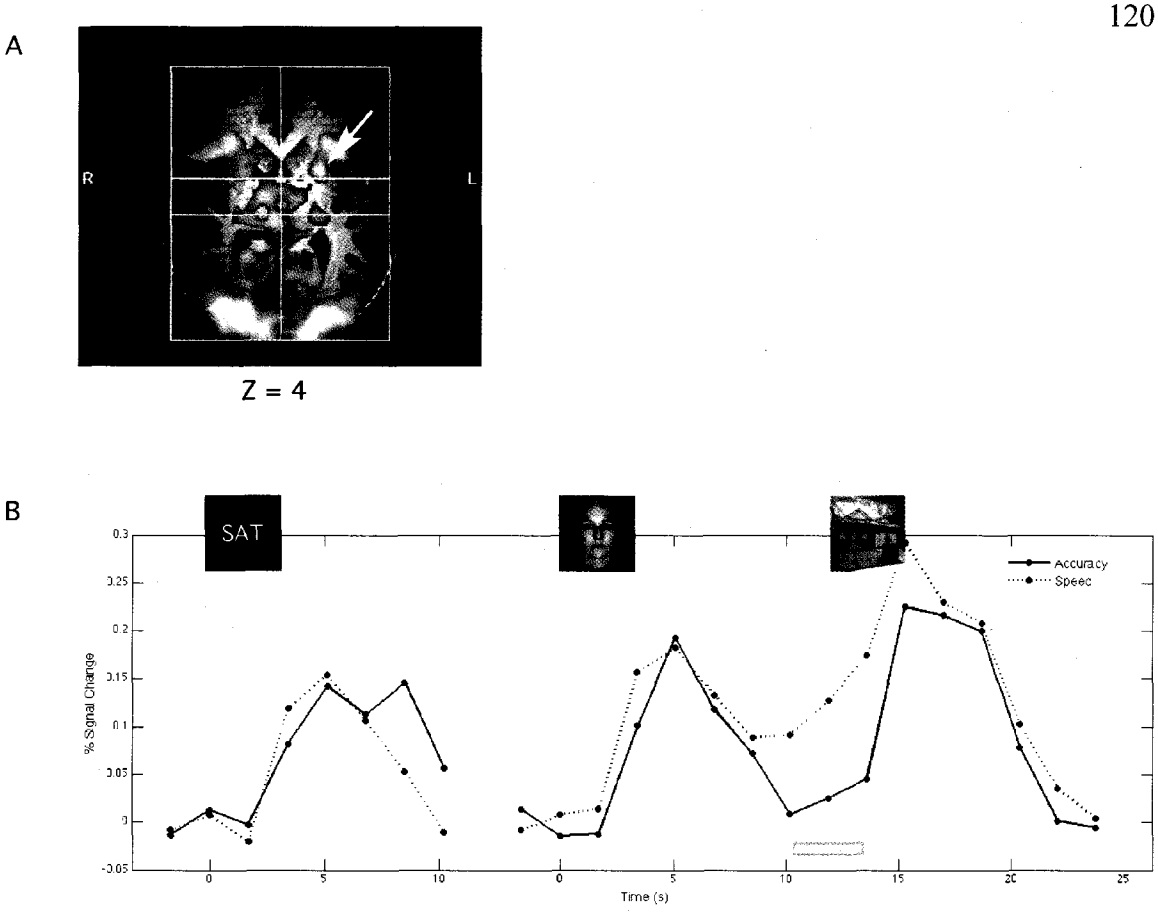


Figure 14. fMRI results for the left lentiform nucleus of the putamen. (A) Axial view of the conjunction SPM from functional localizer task with the location of the left lentiform nucleus indicated by the white arrow. (B) Speed and accuracy time-courses time-locked and baselined to the SAT cue and to the face cue. Speed was significantly above accuracy from 10.2s to 13.6s (indicated by gray rectangle) following the face presentation.

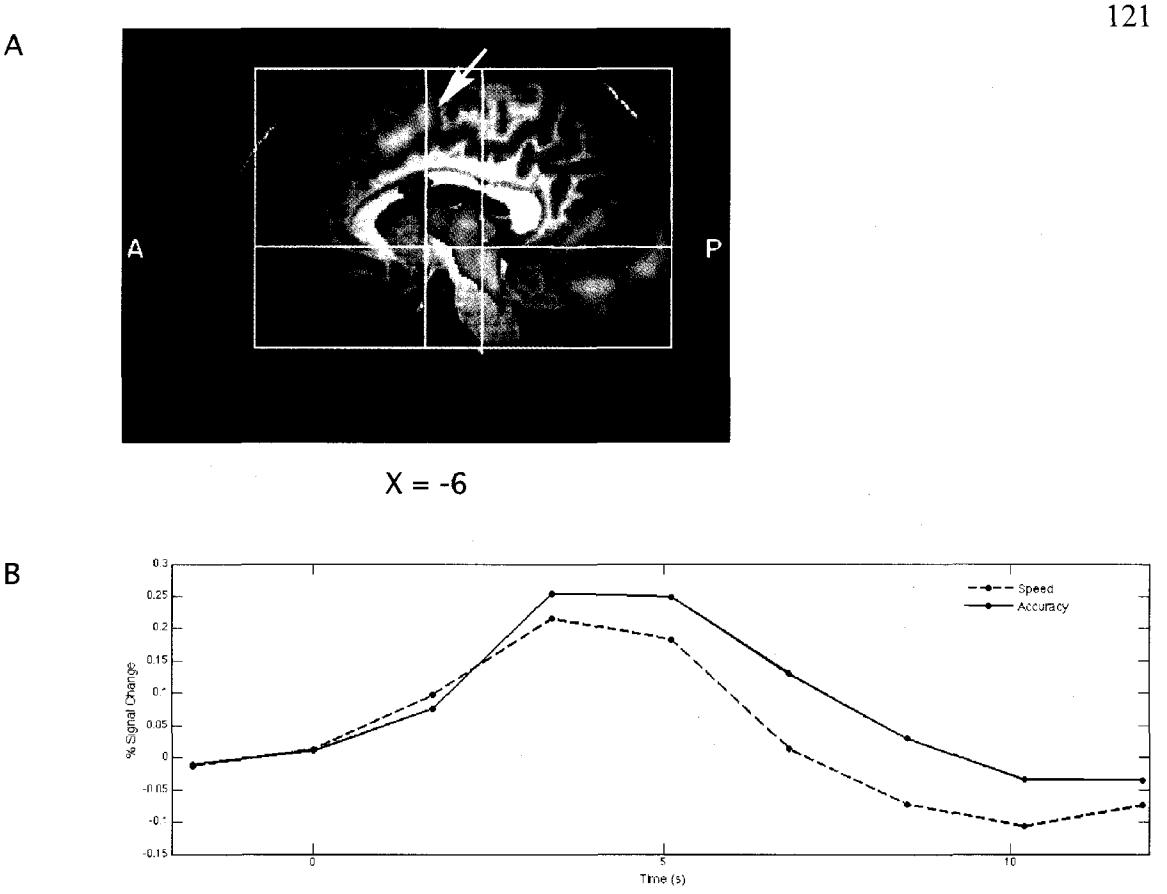


Figure 15. fMRI time-courses for the left SMA split by speed and accuracy. (A) Axial view of the conjunction SPM from the functional localizer task with the location of the left SMA indicated by the white arrow. (B) Speed and accuracy time-courses, time-locked to the house cue. Results revealed a main effect of SAT instruction on activation in this region, $F(1,18)=4.66$, $p<.05$, with greater activation following accuracy emphasis.

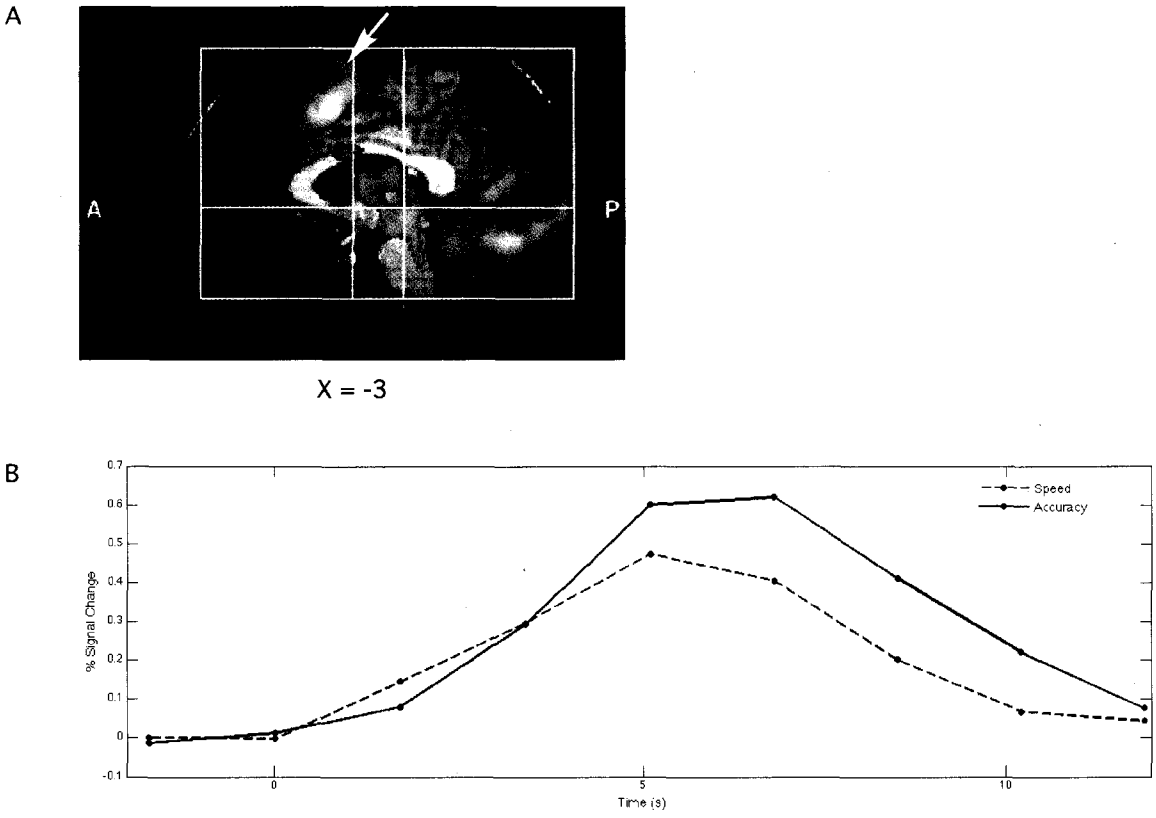


Figure 16. fMRI time-courses for the left pre-SMA split by speed and accuracy. (A) Axial view of the conjunction SPM from the functional localizer task with the location of the left pre-SMA indicated by the white arrow. (B) Speed and accuracy time-courses, time-locked to the house cue. Results revealed a main effect of SAT instruction on activation in this region, $F(1,18)=4.47$, $p<.05$, with greater activation for accuracy relative to speed instructions.

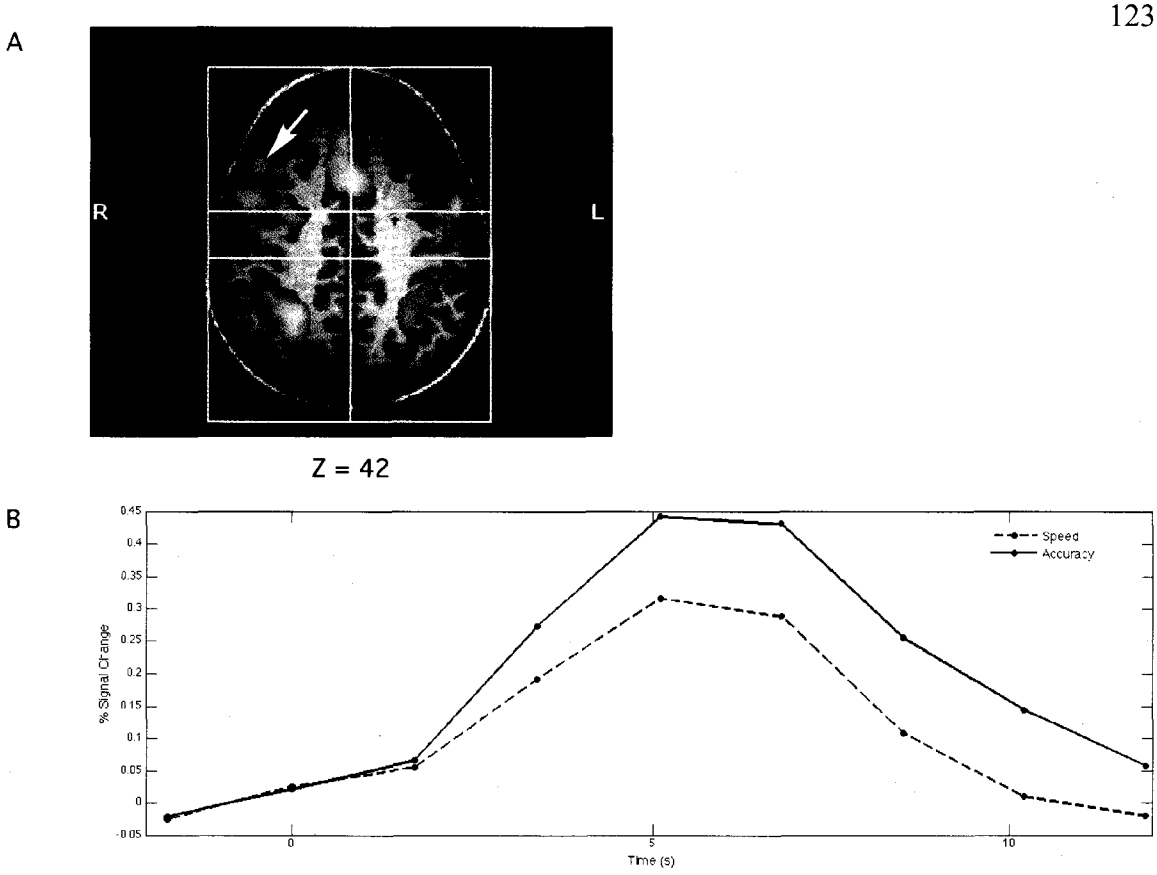
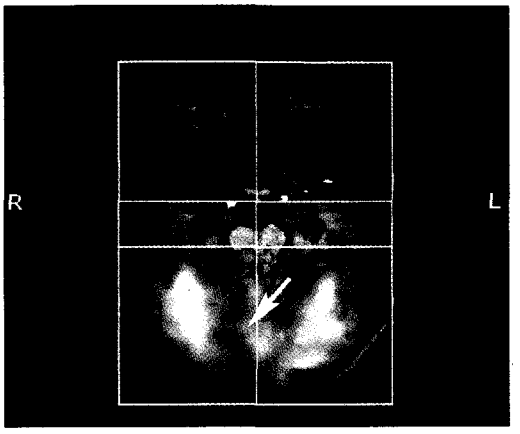


Figure 17. fMRI time-courses for the right middle frontal cortex (BA 8,9) split by speed and accuracy. (A) Axial view of the conjunction SPM from the functional localizer task with the location of the right middle frontal cortex (BA 8,9) indicated by the white arrow. (B) Speed and accuracy time-courses, time-locked to the house cue. Results revealed a main effect of SAT instruction on activation in this region, $F(1,18)=6.19$, $p<.05$, with greater activation following accuracy emphasis.

A



Z = -16

B

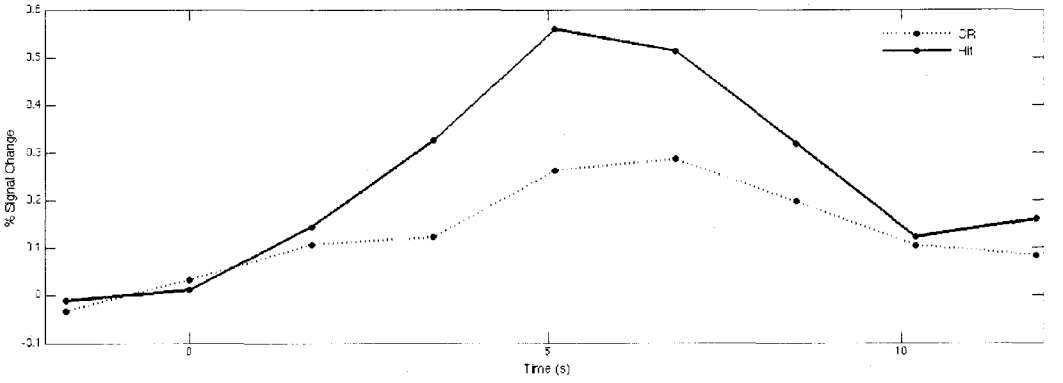


Figure 18. fMRI time-courses for the right cerebellum split by hits and correct rejections. (A) Axial view of the conjunction SPM from the functional localizer task with the location of the right cerebellum indicated by the white arrow. (B) Hit and CR Time-courses, time-locked to the house cue. Activation in this region was greater when making hits relative to CRs, independent of SAT instruction, $F(1,18)=9.64$, $p<.01$.

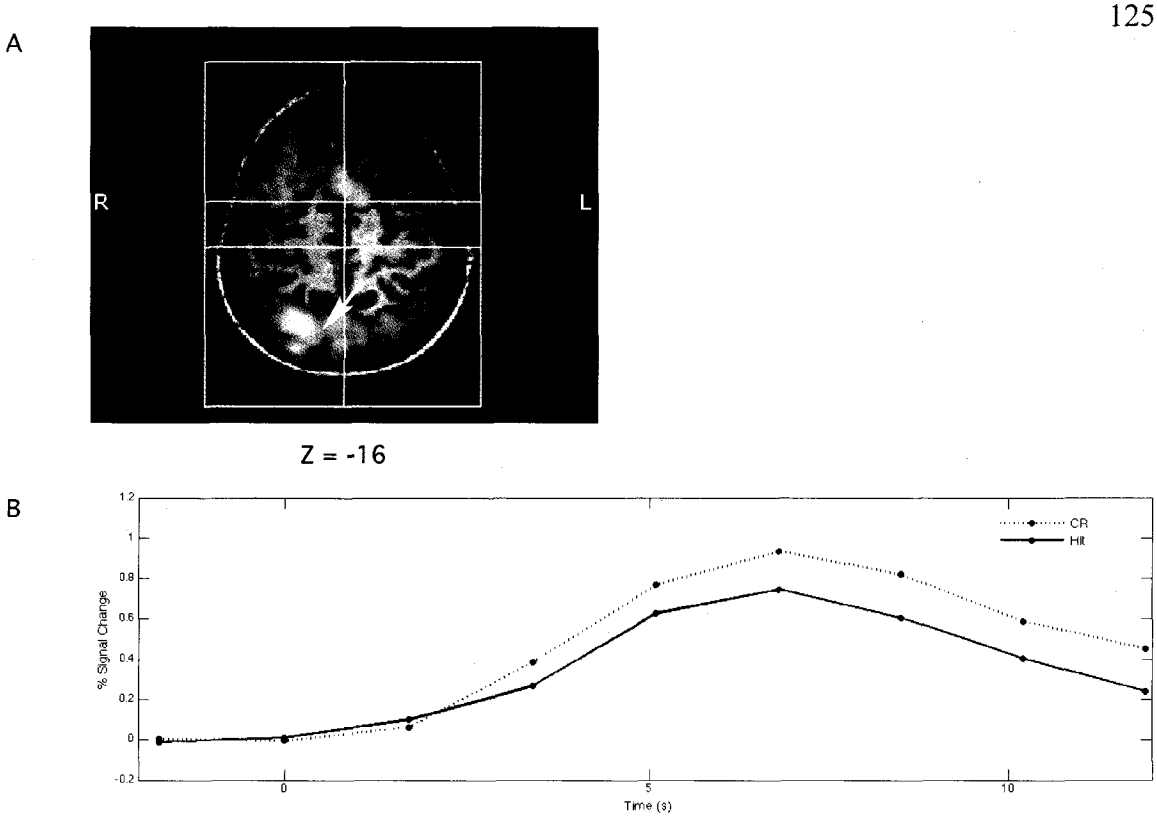


Figure 19. fMRI time-courses for the right SPL/precuneus split by hits and correct rejections. (A) Axial view of the house-fix SPM from the functional localizer task with the location of the right SPL/precuneus indicated by the white arrow. (B) Hit and CR time-courses, time-locked to the house cue. Activation in this region was greater when making CRs relative to hits, indepenendent of SAT instruction, $F(1,18)=5.47$, $p<.05$.

Author Note

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