

**Deficient integration of top-down and bottom-up influences on attention in psychopaths:**

**Potential contribution of the septo-hippocampal system**

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## *Introduction*

There has been an explosion of interest and a great deal of progress in the field of psychopathy since the introduction of the Psychopathy Checklist (Hare, 1980) and Psychopathy Checklist-Revised (Hare, 1991). As noted by Hare (1996) and others (e.g., Harris, Skilling, & Rice, 2001), the development of a reliable method for assessing psychopathy has enabled researchers to demonstrate its outstanding clinical utility in the field of criminal justice. During the past decade investigators have generated a wealth of evidence that psychopathy, as measured by the PCL-R, is a potent predictor of general criminal behavior (Hare, 1996; Hare & McPherson, 1984), instrumental aggression (Cornell, Warren, Hawk, Stafford, et al., 1996), substance abuse (Smith & Newman, 1990), prison adjustment and treatability (Hobson, Shine, & Roberts, 2000; Rice, Harris, & Cormier, 1992), and criminal recidivism (Glover, Nicholson, Hemmati, Bernfeld, & Quinsey, 2002; Hare, Clark, Grann, & Thornton, 2000; Porter, Birt, & Boer, 2001; Salekin, Rogers, & Sewell, 1996; Serin, 1996). Given its outstanding predictive validity, there is strong interest in understanding the psychological and biological processes associated with psychopathic behavior. To the extent that investigators are able to characterize the predisposing factors, it will facilitate the early detection of high risk individuals and the development of interventions to prevent the onset or reduce the severity of the disorder.

Since 1980 (Gorenstein & Newman, 1980), our laboratory has been using a physiological model to generate and test hypotheses concerning the biopsychological processes associated with psychopathy. This model and its associated body of evidence have given rise to the response modulation hypothesis. Response modulation involves a brief and relatively automatic shift of attention from the effortful organization and implementation of goal-directed behavior to its evaluation. According to the response modulation hypothesis, primary psychopaths are deficient

in response modulation and this information processing deficit results in the dysregulated expression of prepotent responses. Originally, the response modulation model generated hypotheses based on the behavioral consequences of septo-hippocampal-orbitofrontal (SHF) system lesions in animals. However, with time, it became possible to use the growing evidence on the performance of psychopathic individuals to generate more theory-based predictions regarding the implications of a response modulation deficit for cognitive (see Patterson & Newman, 1993) and affective (see Newman & Lorenz, 2003) information processing.

Although the experimental methods used to operationalize response modulation have evolved along with the model during the past 20 years, the basic explanatory construct is essentially the same. Specifically, response modulation deficits involve a failure to accommodate information that is not part of a person's primary, prepotent, or dominant response set. In light of the longstanding connection between the response modulation hypothesis and septo-hippocampal system (SHS) and the fact that the SHS has received relatively little attention in the field of psychopathy during the past 20 years, our goal for this chapter is to re-evaluate the connection between the SHS and the psychopath's response modulation deficits. Toward this end, we (1) translate response modulation into neural network terms; (2) clarify our assumptions regarding the nature and assessment of primary psychopathy; (3) outline Gray and McNaughton's (2000) theory of septo-hippocampal functioning; and (4) examine the extent to which psychopaths' deficits in response modulation correspond to the processes that Gray and McNaughton attribute to the SHS.

***Response modulation as the context-appropriate balance  
between top-down and bottom-up influences on behavior***

Gorenstein and Newman's (1980) SHF model was based primarily on the behavioral

consequences of lesioning the septum in rats which they referred to as the “septal syndrome”. Their view of the septal syndrome, in turn, was rooted in McCleary’s (1966) characterization of the “response modulating function of the limbic system” (p. 605). According to McCleary, lesions of the septum reduce an animal’s tendency to suppress certain responses in the face of situational contingencies (i.e., punishment, extinction, contingency reversals) that make continued responding maladaptive. The concept of response perseveration as used in the animal literature highlights the importance of two psychological processes – inflexible approach and inadequate avoidance – both of which have important implications for behavioral regulation. Consider passive avoidance deficits which are the hallmark of both psychopathy and the septal syndrome. Typically, it is assumed that such failures to inhibit prepotent responses reflect inadequate fear and a related lack of motivation to avoid punishment (e.g., Lykken, 1995), but they could just as well reflect exaggerated approach. In this connection, Gorenstein and Newman (1980) noted that rats with septal lesions also perform poorly in DRL (i.e., differential reinforcement for low rates of responding), two-bar shift, and delay of gratification paradigms, all of which require animals to suspend a rewarded response to enact a less prepotent response (i.e., withhold an approach response for a predictable length of time, emit a particular number of responses to a nonrewarded “counting” bar, wait until a more rewarding response becomes available). Thus, paralleling their weak behavioral suppression in the presence of threat cues, rats with septal lesions display weak suppression in the absence of threat (i.e., in reward only contexts). Across diverse paradigms, rats with septal lesions have difficulty suspending a dominant response set for reward in response to peripheral (i.e., nondominant) information that engenders response conflict in normal animals.

In 1993, Patterson and Newman proposed that research on psychopathy and the other

syndromes of disinhibition might progress more efficiently using a theoretical perspective that was less dependent on the literal analogy with the septal syndrome. Toward this end, they (Patterson & Newman, 1993; see also Newman, 1987) outlined a four-stage model of response modulation. At Stage 1, individuals establish a dominant response set for reward. If they experience no difficulty achieving their goal, then the scenario ends. However, when people encounter unexpected events they experience an “automatic call” to process the unexpected information and an increase in nonspecific arousal that constitute Stage 2 of the model. Stage 3 involves “answering the call for processing” which Patterson and Newman referred to as *retrospective reflection*. Whereas the arousal generated at Stage 2 of the model facilitates shifting attention and the processing of unexpected events in retrospective reflection, failure to answer the call for processing at Stage 3 results in *disinhibition* because the arousal generated at Stage 2 serves instead to energize the dominant response set. Answering the call for processing is the normative response, but according to Patterson and Newman psychopaths “less readily switch their attentional focus and motivational set to accommodate feedback” (p. 721). Stage 4 involves the consequences of retrospective reflection or disinhibition for learning and future behavior. Whereas reflection promotes learning associations that afford predictive control (i.e., facilitates the learned modulation of behavior and sound judgment), disinhibition interferes with the formation of causal associations between behaviors and their consequences (p. 722).

The Patterson and Newman model (1993; see also Newman & Lorenz, 2002) is well-suited to re-establishing the link between the psychological model and its neurological underpinnings. To facilitate this link, we will use the language of recent neural network models of cognitive control. Using a neural network approach, cognitions, emotions, and behavioral responses can be represented as networks of co-activated neurons. The network of neurons that

is most activated (i.e., most prepotent) will determine behavior unless the activation level of other nondominant response networks are enhanced by top-down selective attention (e.g., Cohen, Dunbar, & McClelland, 1990, Cohen, Braver, & O'Reilly, 1996). According to proponents of neural network models, the maintenance of prepotent responses, the relatively automatic bottom-up activation of alternative networks by contextual cues, and the use of top-down selective attention to activate alternative goals are fundamental to cognitive control (e.g. Miller & Cohen, 2001). Moreover, these processes are also the focus of intense investigation in the current cognitive and affective neuroscience literatures. The correspondence of these processes to Patterson and Newman's four-stage model are manifest. Stage 1 corresponds to the prepotent top-down focus of selective attention, Stage 2 corresponds to a bottom-up call for processing, Stage 3 corresponds to the reallocation of top-down resources to facilitate activation of sub-dominant networks for the purposes of evaluation and possible substitution as the dominant network, and Stage 4 addresses the importance of this process for ease of network activation in the future (see MacCoon & Newman, in press for elaboration of this analogy). Merging the neural network and response modulation frameworks, MacCoon et al (in press) proposed that psychopaths' poor self-regulation reflects a problem achieving a context appropriate balance between top-down and bottom-up influences on behavior.

### ***The nature and assessment of primary psychopathy***

The suitability of a biopsychological explanation for psychopathy necessarily depends upon one's assumptions regarding the nature of psychopathy and the methods used to identify psychopathic individuals. Our view of psychopathy is based on Cleckley's (1976) classic book, *The Mask of Sanity*. According to Cleckley (1976), the prototypical psychopath is characterized by a severe failure of adjustment that is not easily attributed to disadvantaged social

circumstances, low intelligence, excessive neurotic anxiety, or other psychopathology. Although it is commonplace to emphasize the psychopath's interpersonal callousness and antisocial behavior, Cleckley described the core features of the syndrome as unreliability, untruthfulness and insincerity, lack of remorse or shame, inadequately motivated antisocial behavior, poor judgment and failure to learn by experience, pathologic egocentricity and incapacity for love, general poverty in major affective reactions, and unresponsiveness in general interpersonal relations.

In addition to providing the definitive characterization of psychopathy, Cleckley (1976) attempted to specify a unitary dysfunction that could account for the core features of the disorder. The primary psychopath, he wrote is characterized by "a serious and subtle abnormality or defect at deep levels disturbing the integration and normal appreciation of experience" (p. 388). Similarly, Shapiro (1965) associated psychopathy with "an insufficiency of active integrative processes..." which causes him to remain "oblivious to the drawbacks or complications that would give another person pause and might otherwise give him pause as well." (p. 149).

Cleckley's (1976) characterization of the psychopathic deficit has been criticized for its lack of clarity (e.g., Lykken, 1957, 1995) and even Cleckley noted that "It is easy indeed to become unclear, if not to appear actually ridiculous" (p. 375) "when we say that a disorder at deep levels of personality integration prevents experience from becoming adequately meaningful to the subject" (p. 374). Although the deficit described by Cleckley is both subtle and complex, it seems less abstruse today than it did in 1941 when the first edition of his book was published. Indeed, we believe that the response modulation hypothesis captures the essence of Cleckley's proposal. A problem integrating bottom-up influences (i.e., associated, but secondary neural

networks) by using one's top-down focus of selective attention would quite likely resemble the lack of reflectivity, pathological egocentricity, failure to plan or benefit from experience, and shallow affect described by Cleckley (see Newman, 1998; Newman & Lorenz, 2003).

Regarding the assessment of psychopathy, our laboratory uses the PCL-R (Hare, 1991) with incarcerated offenders to identify extreme groups of psychopathic (PCL-R scores  $\geq 30$ ) and nonpsychopathic controls (PCL-R scores  $\leq 20$ ). However, consistent with Cleckley's emphasis on primary psychopathy, we eliminate psychopathic offenders with inadequate intelligence (i.e., estimated IQ scores  $< 70$ ), excessive neurotic anxiety (i.e., Welsh anxiety scores above the median for the sample), or evidence of psychotic thinking from our primary psychopathy group (see Newman, MacCoon, & Vaughn, 2003 for an empirically-based discussion of primary and secondary psychopathy). To guard against confounding variables, we employ age-matched, incarcerated controls with comparable levels of intelligence, neurotic anxiety, and general psychopathology (see Brinkley, Newman, Widiger & Lynam, in press).

***Gray and McNaughton's (2000) updated theory of septo-hippocampal system function***

For reasons noted below, our re-examination of the association between psychopaths' response modulation deficit and the septo-hippocampal system (SHS) will focus on Gray and McNaughton's (2000) updated theory of SHS function. According to this theory, deficient SHS functioning would likely result in (a) weaker pause and reflect responses to novel or unexpected stimuli; (b) weaker registration of minor discrepancies from expectations associated with stimulus inputs or response consequences (i.e., less hesitation and processing of contextual cues); (c) a reduced likelihood of shifting from automatic to controlled processing and, thus, an associated failure to scrutinize and elaborate stimuli to resolve (SHS-related) conflicts; (d) a reduced tendency to inhibit prepotent responses in situations involving *goal conflicts* (see

below); and (e) less effective tagging of “faulty” responses so that they may be emitted more slowly on future occasions or modified so that more adaptive responses become prepotent. Clearly, this description of SHS dysfunction has much in common with the response modulation model described above. After reviewing the fundamentals of the Gray and McNaughton model, we will examine its correspondence with our laboratory findings.

Before outlining Gray and McNaughton’s (2000) theory of the SHS, it is important to note that the authors used more than 400 pages and 10 substantial appendices to describe and justify their proposals regarding the SHS. Our brief summary can not do justice to the thorough theoretical and empirical analysis that underlies their proposals. In addition, throughout their book Gray and McNaughton are careful to note that their interpretation of the literature on SHS function is not always the most widely accepted one. We focus on the Gray and McNaughton theory in this chapter for two major reasons. First, it provides an efficient means of organizing and summarizing the literature on the SHS. Second, their interpretation of SHS function emphasizes its behavioral and attentional functions as opposed to other aspects of septo-hippocampal functioning (e.g., memory, spatial orientation) that are less relevant to response modulation.

Gray and McNaughton’s (2000) proposal builds on their earlier characterization of the SHS as a comparator that processes expected and observed outcomes. To serve the comparator function, Gray and McNaughton note that the SHS requires access to (1) the current state of the perceptual world (2) an organism’s ongoing motor programs, and (3) “memory stores of past regularities of experience under similar conditions” ( p. 19). As long as events are in line with predictions, the comparator remains in “just checking” mode. However, when the comparator detects a mismatch or threat, it enters “control mode” and initiates processing of additional

information from the environment and/or memory in order to account for the mismatch or avoid the threat (p. 20). In this regard, the comparator contributes to the processing of contextual information that has potential implications for observed discrepancies or avoiding negative outcomes. An especially important consequence of this function is that contextual information becomes linked with responses that engender unexpected outcomes. These associations, in turn, influence the likelihood that the responses will be activated or suppressed within similar contexts in the future.

In their updated theory of SHS function, Gray and McNaughton (2000) outline several modifications of the initial comparator idea that increase the plausibility of their view and enhance its predictive utility. First, the authors expand the structures involved in the SHS to include “the medial septum-diagonal band complex, the dentate gyrus, fields CA1- 4 of the hippocampus proper, the subiculum, the entorhinal cortex, and posterior cingulate cortex” (p. 233). Second, they attribute fewer functions to this elaborated SHS despite assigning it an equally important role in coordinating behavior. This is achieved by assigning to the SHS the relatively global process of monitoring and resolving goal conflicts while allocating the detailed aspects of goal processing to other neural circuitry. To detect goal conflicts “the hippocampus itself need only know that there are a number of goals, not precisely what they are” (Gray & McNaughton, p. 24). A third and related modification involves elevating the unit of processing in the hippocampus to the level of goals. According to Gray and McNaughton, goals conflate stimuli, memories, responses, motor programs, and plans which, according to their perspective, are coded elsewhere in the brain. Thus, the complex functions of checking, comparing, predicting, and responding to mismatches attributed to the SHS in the first edition of their book may be achieved by simply registering the conflict between concurrently active networks of

activation. These first three modifications simplify the processing required by any of the structures within the SHS—a change that makes their proposals more consistent with the actual simplicity of the neuronal structures. A fourth update entails recognition that the hypothesized switch between “just checking” and “control” mode involves a continuum rather than a discrete change of function.

#### ***Four scenarios illustrating the role of the septo-hippocampal system***

To clarify the relevance of the SHS for regulating behavior, Gray and McNaughton (2000) describe four scenarios: (1) exposure to a novel environment, (2) “just checking” mode of the SHS, (3) detection of conflict, and (4) disengagement. After a discussion of these four scenarios, we briefly describe theta rhythm and its implications for hippocampal function.

***Scenario 1: Exposure to a novel environment.*** According to authors “the hippocampus is not directly involved with the construction of predictive models of the stimulus situation, nor directly with production and habituation of the orienting reaction. Rather, it receives subcortical input which reflects the presence of important stimuli (potential goals). If the hippocampus does not at the same time receive a matching cortical input (i.e., the goals are novel), it determines the relative strength of the novel goal and of any prepotent goal and, if there is a significant conflict between these (i.e., neither is significantly greater than the other), then it produces an output which inhibits the prepotent goal and hence permits the orienting and exploratory programs to function properly.” (p. 255-6). As already noted the authors do not view this interruption as dichotomous but assume that there are intermediate cases in which prepotent responses are emitted more slowly with varying degrees of exploration.

***Scenario 2: “Just checking” mode.*** Gray and McNaughton’s (2000) second scenario relates to the “just checking” mode. Here, the hippocampus receives and integrates multiple

sources of information but produces little functional output. In serving the checking function, the hippocampus need only compare the strengths of multiple inputs. As long as there is a clear “winner” in terms of overall activation, then conflict is minimal and the hippocampus will exert little influence. However, in the event that there are two or more sources of nearly equivalent activation, then a conflict is detected. According to Gray and McNaughton, the CA3 comparator plays an important role in determining which stimuli will be gated in to the subicular conflict detector. Stimuli that are judged to be novel or significant by virtue of associated monoamine activity are passed on, whereas stimuli that are judged to be familiar and do not exceed a threshold of activation are gated out. It is worth noting that there may be some output from the SHS even in this relatively inactive mode owing to minor discrepancies in stimulus inputs or response consequences.

*Scenario 3: Detection of conflict.* The third scenario involves the detection of conflict. In general, conflict occurs when a familiar but aversive stimulus co-occurs with approach stimuli or when multiple cortical representations involve incompatible goals. With regard to conflict detection, Gray and McNaughton (2000) suggest that inputs to the hippocampus, mediated by the septum, provide a crude “topographic mapping of response systems” (p. 258). When two concurrently activated goals that involve output from distinct response programming systems are activated, each sends input to the hippocampal formation, which determines by integration and comparison of the level of input whether (a) more than one response tendency (goal) is present and (b) activation of these tendencies is roughly equivalent. If both criteria are met, “the subicular output, then, feeds back the signal of conflict to the relevant motor areas with a recursive reduction of that appetitive response tendency which has the greater negative affective associations” (p. 258). In other words, when two goals achieve about the same level of

activation, the SHS responds to this conflict by acting to reduce the response associated with the most negative outcome.

The SHS is unlikely to be needed in a conflict in which alternatives involve the same response as in simultaneous discrimination tasks when people must select one response from among other simultaneously available responses (e.g., press one button or another). For example, the SHS is unlikely to be involved in a two-choice discrimination task in which participants learn to select the response that is associated with a higher rate of reward or lower probability of punishment (e.g., Newman et al., 1990, Experiment 2). Although such conflicts share features with the conflict scenarios described above, they are unlikely to involve the hippocampal conflict detector. According to Gray and McNaughton (2000, p. 258) such conflicts are resolved primarily by the entorhinal cortex and its connections with polymodal association cortex prior to sending information to the hippocampus.

As already described, when the SHS detects conflict it enters control mode. There are three primary consequences associated with control mode: (1) behavioral inhibition, (2) scrutiny of goals that have gone wrong, and (3) initiation of exploration. We discuss each in turn. According to Gray and McNaughton (2000), the type of behavioral inhibition associated with the SHS is not general inhibition of motor responses, but a more specific type of inhibition that involves the processing of affectively negative associations in conjunction with resolving goal conflicts. More specifically, when the hippocampus receives “concurrent input from two separate and incompatible representations it detects a conflict and proceeds to circulate information between itself and both of the concurrently activated motor representations” (p. 260). One consequence of this process is that an “initially prepotent program is executed with greater restraint (more slowly, more easily interrupted by hesitations for exploratory behaviour)

because of successive interruptions from the hippocampus” (p. 260).

A second consequence of detecting a goal conflict involves the scrutiny of goals that have gone wrong or what Gray and McNaughton (2000) refer to as the ‘faulty, needs checking’ tag. “When conflict is detected, the motor program that has just resulted in conflict and the stimuli associated with it should be ‘replayed’ by the loops which connect the SHS to the areas representing the information. This allows enhanced analysis to commence immediately, essentially re-evaluating any existing affectively negative associations” (p. 262). Moreover, as a result of such processing the goal representation will be altered so that it is activated less strongly in the future. That is, such processing engenders a type of long-term potentiation and long-term depression that Gray and McNaughton relate to metaplasticity. Once it is established, a “tagged stimulus representation is given enhanced attention by the subicular and entorhinal conflict detectors” (p. 261) on future occasions. According to Gray and McNaughton, the increased scrutiny of problematic goals is one of the most important functions that their theory attributes to the SHS. The efficiency of this process of scrutinizing and elaborating stimuli to resolve conflict “depends on the capacity of the septo-hippocampal system to control flexibly the entry of stimuli at the dentate-CA3 gate...By selective, sequential, opening of the dentate gate to different stimuli or stimulus attributes (often originating in the cortex) and to different response attributes (often originating subcortically), the septo-hippocampal system is able successively to examine alternative descriptions of the stimulus situation that has given rise to the conflict and to examine different response alternatives to resolve it” (p. 261).

The third consequence of detecting conflict involves the initiation of exploration to obtain additional information to resolve the conflict. This process is related to the stimulus elaboration function described above, but relates more to the investigation of external stimuli than internal

associations. According to Gray and McNaughton (2000), this process might reflect direct excitation of exploratory systems via projection to the cingulate cortex, but could also occur spontaneously owing to the inhibition of prepotent responses.

***Scenario 4: Disengagement.*** The fourth SHS scenario described by Gray and McNaughton (2000) involves “disengagement” (p. 265) from conflict processing. In all of the conflicts discussed by Gray and McNaughton, “the role of the hippocampus is to inhibit prepotent responses” (p. 265). However, processes associated with inhibition of prepotent responses must also disengage in order for behavior to resume. In some cases, detected conflicts have no important consequences. In such cases, behavior is likely to continue with minimal disruption and there is habituation to the novel / distracting stimulus. In other cases, there is initiation of the “faulty needs checking” routine in the absence of a salient alternative goal. This would occur when the current goal is not being met successfully by current behavior (e.g., a student fails to understand material needed for a test despite attempts at studying) but no readily apparent alternative goal exists. In such cases, the SHS will tend to suppress prepotent behavior and thus increase the likelihood that other responses will be sampled (e.g., the student may take a much needed break or call a classmate for assistance). The SHS control mode disengages when an alternative prepotent response is hit upon or, in the event that no other response becomes prepotent, the organism reverts to unlearned behavior such as sleeping. A third possibility relates to goal conflicts in which the SHS uses associative processes to activate adverse associations to particular goals and thus reduces alternatives until only one goal remains and the system reverts to just checking mode. Finally, Gray and McNaughton note that certain types of conflict, such as those that require continuous updating of the stimulus context to guide the behavior or very fine distinctions, are not compatible with disengagement of the SHS.

### ***Theta rhythm.***

One further aspect of Gray and McNaughton's (2000) theory of SHS function that merits discussion concerns the theta rhythm which modulates and, thus, has the potential to degrade, though not eliminate, hippocampal processing. According to Gray and McNaughton, "the frequency of theta appears to be determined simply by the total sum of inputs to the supramammillary nucleus and the dorsomedial hypothalamic nucleus... (and) control of the frequency appears to be through small numbers of local inhibitory interneurons which regularly clamp the output of much larger numbers of projection neurons" (p. 232). The function of this "phase-locking" activity according to the authors "is to maintain the discreteness of individual cycles of recursive calculation, and thus ensure that the inputs from all the different loops are dealt with by the various hippocampal comparators at essentially the same time on a consistent basis." (p. 271). In other words, if theta rhythm is disrupted, different goals or responses will loop through the SHS at different times, thus disrupting the ability of the SHS to compare these goals or responses. Dysfunction related to theta could have the effects of degrading or even negating the overall functioning of the SHS.

### ***Relation to psychopaths' response modulation deficits***

Response modulation involves a relatively simple process, but it has far reaching implications for self-regulation. In characterizing the process, Patterson and Newman (1993) wrote that unanticipated information generally elicits an "automatic call for processing" and that response modulation pertains to a person's tendency and/or ability "to answer the call". To the extent that individuals answer the call for processing, they are able to analyze the meaning of a stimulus and purposely use that information to improve the quality of immediate and future responses. People with a response modulation deficit are less likely to use contextual cues, past

experience, and controlled processing resources to refine responding.

Gray and McNaughton's (2000) theory of the SHS also involves a rudimentary process with far reaching consequences. The SHS appears to be important for temporarily maintaining the activation of non-dominant networks via recursive loops (i.e., connections with other neural circuitry). By representing concurrently activated neural networks in this way, the SHS facilitates the processing and integration of contextual information, including unanticipated events and competing goals, with a person's dominant response set (i.e., focus of top-down selective attention). Though rudimentary, this function is well suited to effecting significant short-term and long-term modulation of prepotent responses that parallels the consequences of response modulation.

First, each of the conflict scenarios described above involves slowing or temporarily interrupting a prepotent response in response to contextual information (environmental cues or internal associations) that was not anticipated by (i.e., incongruent with) a person's top-down set. This process corresponds to the lack of reflectivity or failure to answer a call for processing that is fundamental to the response modulation hypothesis.

Second, the simultaneous processing of dominant and nondominant networks results appears to alter the structure of particular neural networks and alter the likelihood that particular goals become prepotent in the future. Similar to the consequences of reflection described in Stage 4 of the Patterson and Newman (1993) model, this SHS function represents an important means by which people learn from experience. For example, such learning may lead to refinements in neural networks that distinguish one context from another and thus increase the likelihood that a person's responses will be context appropriate (e.g., respond in context A but not context AB). Similarly, when a dominant response set results in unexpected negative

consequences, the simultaneous activation of the top-down and bottom-up activation essentially causes an inhibitory tag to become part of the dominant network. Such changes reduce the likelihood that the modified dominant network will become dominant under similar conditions in the future. In this regard, Trasler (1978) described socialization as a developmental process that involves considering and rejecting particular responses so that inappropriate, antisocial responses become “unthinkable”. As a result, behaving in a well socialized manner is essentially conditioned (i.e., relatively automatic) and there is a corresponding reduction in the need to use effortful processing to evaluate and inhibit antisocial actions. In other words, the simultaneous activation of competing goals and processing of the goal conflicts (e.g., make an instrumental aggressive response versus avoid the negative consequences of aggressing) will automatically reduce the likelihood of such behavior in the future. According to Trasler, this process is disrupted in psychopathy so that self-serving antisocial behavior remains relatively accessible, and its inhibition is more dependent upon effortful decision making.

Third, in addition to promoting the development of inhibitory tags as noted above, the SHS plays an important part in registering and responding to such information on future occasions. In the event that a particular goal is activated in spite of past negative associations, the SHS is likely to register the competing activation of approach and avoidance goals and slow responding until the simultaneous processing of the activation results in one goal becoming dominant. As in Stage 3 of the response modulation model, this process enables a person to anticipate negative consequences, interrupt anticipated action, and select a more adaptive response.

Fourth, though Gray and McNaughton’s (2000) theory of SHS functioning highlights the processing of threat cues and other negative associations, threat is not the only type of non-

dominant information processed by the SHS. Whenever there is bottom-up activation of sufficient magnitude that is not matched by a corresponding output from cortex or activation by competing goals that involve distinct response programming systems, we assume that the SHS facilitates concurrent processing of these separate networks. Thus, even without a threat of punishment or other negative feedback, the SHS facilitates processing and the integration of top-down/bottom-up networks. Such processing could be very important for directing attention to relatively subtle aspects of experience which, over time, results in better elaboration of associative networks. That is, with multiple experiences involving co-activation of dominant and non-dominant networks, we assume that people become (1) increasingly adept at using subtle contextual cues to distinguish particular situations requiring different responses and (2) more nuanced in their cognitive and affective appraisals of such situations. This view suggests a potential link between the psychopaths' response modulation deficit, SHS functioning, and their relatively superficial processing of events (e.g., lack of affective depth; Cleckley, 1976; Hare, 1991). For a more detailed discussion of the role of hippocampus in processing poly-modal presentations that facilitate subtle context discriminations, see Frankland, Cestari, Filipkowski, McDonald, & Silva (1998).

Fifth, Gray and McNaughton's (2000) model builds a bridge between SHS functioning and the ease with which dominant response sets are modulated. Aside from the role of the SHS in registering goal conflicts and promoting reflectivity in the present, the long-term potentiation or learning associated with such processing means that a person's neural networks will be better elaborated and thus incorporate a larger range of potentially competing considerations. For example, to the extent that a person has resisted an attempt to respond in anger when provoked or to give up in the face of frustration, the neural networks associated with anger and frustration

will be altered so that there are established links to such nondominant reactions. Consequently, when provoked or frustrated on subsequent occasions, these non-dominant responses will be more accessible and more readily compete with the initial, prepotent response.

Though Gray and McNaughton's (2000) theory of SHS functioning is better elaborated than the four-stage model outlined by Patterson and Newman (1993), it overlaps substantially with the essential features of response modulation. One caveat is that the present characterization of SHS functioning may over-attribute complex, far reaching functions to SHS. Though we agree that our assumptions are in need of scrutiny, it is also important to remember that SHS co-opts and/or works in concert with a variety of neural circuitry to achieve these ends. Though there is insufficient space to review this connectivity in detail, the issue is briefly considered toward the end of this chapter.

For present purposes, our central assumption is that the SHS is vitally important for integrating dominant and non-dominant information through the use of pointers that represent activation of simultaneously activated neural networks in a time linked, tightly coordinated fashion. We assume that this function not only facilitates processing of bottom-up information with potential relevance for the top-down set but also enhances a person's ability to suspend a dominant response set and adopt another one when environmental circumstances warrant it. Furthermore, we assume that the ability to maintain and process multiple non-dominant networks facilitates long-term modification of existing networks. Such modification may involve the development of inhibitory tags, refinements that distinguish one response context from others that require alternative responses, and the association of diverse contexts and responses that serve to elaborate (i.e., add depth and perspective to) the existing neural network. Last, but not least, we assume that these functions of the SHS enable it to provide a relatively subtle and

unique conflict detection system that facilitates allocation of top-down selective attention that is at least partially independent of other conflict monitoring systems (e.g., anterior cingulate cortex; Botvinick, Braver, Barch, Carter, & Cohen, 2001; see Bertsch & Newman, 2003).

### ***Psychopaths' response modulation deficits and the SHS: Empirical evidence***

Previous reviews of the SHF and response modulation model have focused on its heuristic value or, in other words, its ability to generate novel and valid predictions regarding the performance of psychopaths and the experimental conditions that reveal their performance deficits (e.g., Newman, 1998; Newman & Wallace, 1993; Newman & Lorenz, 2003). In contrast, the following abbreviated review of research evidence generated by the model addresses the plausibility of regarding the SHS as a neuroanatomical substrate for psychopaths' response modulation deficits. We focus primarily on studies conducted in our lab for two reasons. First, nearly all of the studies conducted in our lab have employed the Welsh anxiety scale (1956) for the purpose of identifying a relatively homogeneous group of primary psychopaths (i.e., screening out secondary or neurotic psychopaths). This is important because the evidence supporting an association between psychopathy and deficient response modulation is relatively specific to primary psychopaths (Brinkley et al., in press). Second, the studies conducted by our lab were designed to evaluate predictions generated by the SHF model or the response modulation hypothesis and are, thus, particularly germane. Given the purpose of this review, we provide minimal details regarding the original rationale for the study and experimental manipulations which, in any case, are provided in the experimental reports. Instead, we describe the studies and their findings as succinctly as possible in order to clarify their compatibility with Gray and McNaughton's (2000) characterization of the SHS.

### ***Approach-avoidance tasks***

***Response perseveration.*** In light of the fact that response perseveration played a prominent role in McCleary's (1966) formulation of the response modulating role of the SHS, Newman, Patterson and Kosson (1987) administered a response perseveration task to psychopathic and nonpsychopathic offenders. Following Siegel (1978), they developed a computerized gambling task in which participants could bet money to "play" a card or quit the game on a trial-by-trial basis (up to 100 cards). At the beginning of each trial, a computer displayed the back of a card with a question mark, and the message "Do you want to play?". If participants pressed the play button, the front of the card was displayed. Participants won money when the card was a jack, queen, king or ace and they lost money when it was a number card (i.e., 2-10). Initially, the probability of reward was high (90%) to establish playing cards as the prepotent response but decreased by 10% with each block of 10 cards played until the probability of reward was 0% and the probability of punishment was 100%. As predicted, psychopathic offenders failed to suppress responding despite the decreasing rate of rewards and increasing rate of punishment (i.e., displayed response perseveration). That is, psychopaths played significantly more cards and earned significantly less money than controls (see also, Fisher & Blair, 1998; O'Brien & Frick, 1996; Siegel, 1978).

Applying Gray and McNaughton's (2000) framework, we assume that the high rate of reward provided early in the task establishes the goal of playing cards to win money as prepotent. As long as responses continue to yield rewards, the SHS would remain in just checking mode. However, when playing a card yields punishment instead of reward, this unexpected result would increase activation of neural networks associated with losing and withdrawal, generate goal conflict, and initiate control mode (shift the focus of top-down selective attention). In other words, the motor program and associated stimuli that resulted in

conflict would be replayed by the loops that connect the SHS to the areas representing the information. In this way, the goal representation (i.e., play cards to win) would be altered so that it is less strongly activated in the future. Moreover, the tagged representation would be given enhanced attention by the subicular and entorhinal conflict detectors and, thus, executed more slowly and with greater ease of interruption on future occasions. Over time, this enhanced behavioral inhibition, tagging of the prepotent response as faulty, and increased attention to contextual information should boost the nondominant goal of avoiding punishment to the point that it overcomes the activation associated with the prepotent approach response. The results of the Newman et al. (1987) study suggest that this process is delayed or effectively absent in psychopaths.

To the extent that psychopaths' failure to alter their dominant response set in the card task reflects a problem elaborating upon and linking bottom-up activation with their dominant response set, then it should be possible to reduce or eliminate their maladaptive reward seeking by providing an external representation of the feedback and interrupting the top-down focus of selective attention. In fact, Newman et al (1987) reported that psychopaths and controls play a comparable and equally adaptive number of cards when participants were forced to wait for five seconds before receiving the cue "Do you want to play" while simultaneously providing them with cumulative feedback (i.e., the letters and numbers representing what cards had appeared in rows of 10 near the top of the computer display). One interpretation of these results is that the enforced delay and cumulative display obviated the need for bottom-up integration of dominant and nondominant networks because the manipulation itself directed top-down attention to the changing probability of winners and losers. More generally, the SHS model predicts that psychopaths' difficulty altering a dominant response set will depend heavily on the extent to

which bottom-up influences are latent, incidental, or otherwise overlap minimally with top-down activation. Conversely, to the extent that an experimental manipulation obviates the need for bottom-up recognition of conflicts (i.e., primes or otherwise increases the likelihood that the to-be-processed information is congruent with their dominant response set), psychopaths may be expected to accommodate the information and make reasonable decisions.

*Passive avoidance tasks.* A major focus of research on response modulation involves passive avoidance learning. Newman and Kosson (1986) assessed passive avoidance using a go/no-go discrimination task that involved presenting a set of eight, two-digit numbers over repeated (i.e., 10) blocks of trials. Stimuli appeared one at a time on a computer monitor and participants were required to learn, by trial-and-error, when to press a button and when to withhold responses. In a reward-punishment version of the task, participants earned money for responding to any of the four “go stimuli” and lost money for responding to any of the four “no-go stimuli”. In a punishment-only version of the task, participants began with a cash stake and lost money whenever they responded to “no-go stimuli” or failed to respond to “go stimuli”. Although both tasks require passive avoidance (i.e., inhibiting responses to no-go stimuli to avoid loss of money) and are virtually identical with regard to their learning and performance requirements, psychopaths committed significantly more passive avoidance errors than controls in the reward-punishment condition but performed as well as controls in the punishment-only condition. In other words, psychopaths displayed a passive avoidance deficit when the task required them to inhibit go responses that sometimes led to reward though they performed as well as controls when there was no opportunity to win rewards (i.e., when responding to go stimuli resulted in active avoidance; see also Hartung, Milich, & Lynam, 2002; Moses, Ratliff, & Ratliff, 1979; Newman & Schmitt, 1998; Thornquist & Zuckerman, 1995 for related findings).

Whereas Newman and Kosson (1986) assessed response modulation indirectly by analyzing passive avoidance errors, Newman, Patterson, Howland, and Nichols (1990) modified the go/no-go passive avoidance task so that they could examine the inhibitory and exploratory components of response modulation more directly. After each response, participants received monetary (i.e., poker chips worth 10 cents were awarded or removed), visual (“Correct! You win 10 cents” or “Wrong. You lose 10 cents”), and auditory (high or low tone) feedback that indicated the success or failure of their response. In addition, the visual feedback remained on the monitor along with the stimulus responded to until participants pressed the response key a second time to advance to the next trial. As predicted by the response modulation hypothesis, psychopaths paused for a significantly shorter period of time than controls in response to negative feedback. In addition, pausing after negative feedback was significantly associated with passive avoidance learning. Those participants who paused for a shorter period of time also displayed weaker passive avoidance learning.

Conceptualized within the Gray and McNaughton (2000) framework, these studies appear to demonstrate the importance of competing or conflicting goals for differentiating the performance of psychopathic and nonpsychopathic offenders. Even though the learning and response requirements of the two experimental conditions were identical, the deficient passive avoidance of psychopaths was specific to the condition involving conflicting reward and punishment contingencies. Thus, it does not appear to be the demands of the task per se but the requirement to suspend one goal (responding for reward) and elevate an alternative goal (avoiding punishment) that differentiates the performance of psychopaths and controls. Relative to controls, psychopaths are less likely to suspend goal-directed behavior, explore the context, and tag faulty responses as in need of checking before being emitted. Remarkably, psychopaths

perform the identical discrimination as well as controls when earning rewards (e.g., Newman, Widom, & Nathan, 1985) or avoiding punishment (Newman & Kosson, 1986) is their only goal. That is, psychopaths have little difficulty on such tasks unless they are required to suspend a prepotent goal and pursue another goal such as accommodating an unexpected event—processes characterized by Gray and McNaughton as central to SHS function.

This interpretation is strengthened by another study reported by Newman et al. (1990). In this study, participants were required to discriminate between good and bad numbers to earn monetary rewards and avoid monetary punishments as in the reward-punishment condition of the passive avoidance task described above. However, the study involved a simultaneous as opposed to a successive go/no-go discrimination task. That is, two numbers were presented on each trial and participants had to choose between responding to the number presented on the left or the right side of the computer monitor. Under these conditions, psychopaths were just as likely as controls to avoid punishment. Furthermore, in contrast to the go/no-go task, psychopaths and controls were equally likely to slow down and process negative feedback following punished errors. Similar findings have been reported by Newman (1979) and Schmitt, Brinkley, and Newman (1999).

This simultaneous discrimination task corresponds to the special case of the conflict scenario (i.e., choosing between alternatives that involve the same response) described by Gray and McNaughton (2000) and, as noted above, there is reason to believe that such conflicts are resolved primarily by the entorhinal cortex and its connections with polymodal association cortex prior to sending information to the hippocampus (Gray & McNaughton, p. 258). One way of understanding this special case is that the prepotent goal of making a response in a simultaneous discrimination is not in conflict with another goal. Thus, the goal does not need to

be compared with any other, although the two response options do. This special case serves to highlight a subtle but important distinction regarding the psychopaths' deficit in response modulation and its potential association with the SHS. It is not the nature of the goals or responses that determines whether psychopaths perform well or display a deficit. Rather, it is the requirement to interrupt one goal (i.e., a particular top-down mediated focus of selective attention) and activate an alternative goal to the point that it competes with a prepotent goal (i.e., switch the focus of selective attention) that is deficient.

A study by Arnett, Smith, and Newman (1997) demonstrates the same pattern of results is obtained when an involuntary measure of emotion reactivity to punishment cues (i.e., electrodermal activity) is used instead of behavioral inhibition. The task involved a desk-top board that had five buttons arranged in a semi-circle. Two small lights – one green and one red – were mounted next to each button in the semi-circle. There was also a centrally located button at the base of the semi-circle and a larger green and red light was mounted above this central button. Each time that participants pressed the center button, a small green light came on. Participants were instructed to press the button associated with the green lights as quickly as possible and to withhold these responses if the small red light came on. Each trial had two, one-minute phases. In phase 1, only the center green light was lit and the peripheral red lights never appeared. In phase 2, both center lights were lit and red lights would occasionally come on between the times that a participant released the center button and began to press a button associated with an illuminated green light.

One study involved a reward-punishment condition in which participants won five cents after every five button presses if they responded quickly enough during phase 1. In phase 2, the task continued but participants lost 50 cents if they pressed a button after a red light came on. A

second study involved punishment only. During phase 1, participants lost five cents after every five presses unless they responded quickly enough (i.e., succeeded at active avoidance). In phase 2, the passive avoidance contingency was superimposed on this active avoidance contingency. For present purposes, the dependent measure of interest is participants' electrodermal responses to the onset of the center red which signaled the onset of the passive avoidance contingency (i.e., an alternative goal requiring inhibition of punishment responses). Consistent with behavioral evidence demonstrating insensitivity to punishment cues among psychopathic offenders, their electrodermal responses to the center red light in the reward-punishment condition were significantly smaller than those of controls. However, paralleling results from the Newman and Kosson (1986) study described above, when the opportunity to earn rewards was eliminated, so was the difference between psychopathic and nonpsychopathic offenders. Psychopaths and controls displayed comparable electrodermal responses to the onset of the center red light in the punishment-only condition (i.e., when it was congruent with their dominant response set).

When the red light associated with the passive avoidance contingency in phase 2 turns on, it signals the need to process a second goal. If psychopaths are deficient in processing goal-conflicts, they should display a weaker reaction to this signal regardless of the experimental conditions. The same argument could be made with respect to the passive avoidance contingency in the punishment-only condition of the Newman and Kosson (1986) study. Nevertheless, psychopaths' performance in these conditions is comparable to that of controls. What is the difference between this type of goal conflict (i.e., between active and passive avoidance) and one that involves suspending a prepotent *approach response* to process cues associated with punishment (approach-avoidance conflicts)? To begin with, it is worth noting

that Gray and McNaughton's (2000) theory of SHS function applies only to conflicts involving the inhibition of approach behavior. In contrast to the amygdala which plays an important role in all avoidance learning, involvement of the SHS is relatively specific to conditions that involve inhibiting approach behavior to reduce threat. It seems likely, therefore, that Gray and McNaughton would not extend their theory of SHS function to the punishment-only tasks used by Newman and Kosson (1986) or Arnett et al., (1997).

Although the presence or absence of an approach response appears to be the critical factor that determines when psychopaths are deficient in response modulation and when SHS dysfunction is most relevant, the predictive utility of this relation may be enhanced by a conceptual understanding of the principle. When concurrent goals compete, we believe that a key factor influencing the necessity for response modulation and SHS involvement is the extent to which neural network activation associated with the competing goals overlap. This is the case for two reasons. First, the more closely two goals overlap the more likely that the neural mechanisms responsible for maintaining the prepotent goal (e.g., the prefrontal cortex) will maintain the second goal as well. In this case, the role of the SHS might be minimized. Second, the SHS increases the relative activation of a nondominant goal through successive loops over time. Thus, how much work it has to do to increase the activation of a nondominant goal depends on the activation level of that goal when a conflict is first detected. To the extent that prepotent and nondominant goals share a number of associations (e.g., negative valence, high arousal), there is likely to be greater bottom-up activation of the nondominant goal.

Though it seems reasonable to conceptualize punishment-only (i.e., active versus passive avoidance) conflicts as representing one goal rather than competing goals as in approach-avoidance conflicts, we propose that these conflicts may be more accurately viewed as on a

continuum. In our view, approach-avoidance and punishment-only tasks differ in their demands for response modulation (i.e., the need to suspend a prepotent goal to allow for activation of an alternative goal). For example, if an individual focuses on reward and approach responses, this network has little overlap with punishment or avoidance responses. Thus, in the combined reward-punishment condition when approach is prepotent, the SHS is required to increase the activation of this response to effectively compete with approach. In contrast, in the punishment-only condition, even if active (but not passive) avoidance is prepotent, punishment cues are associated with both types of responses and thus would activate (bottom-up) passive avoidance responses as well as active avoidance responses. Thus, in our view, the reason psychopaths show deficient passive avoidance in reward-punishment conditions but normal passive avoidance in punishment-only conditions is that there is more overlap between passive and active avoidance than between approach and passive avoidance.

From this perspective, the SHS may be seen as serving a relatively unique role in coordinating bottom-up activation of nondominant goals and the focus of top-down mediated selective attention. To the extent that this characterization of SHS involvement in response modulation is accurate, it follows that SHS dysfunction will become increasingly important as the information indicating a need to revise a prepotent goal becomes increasingly latent or incidental. Moreover, when conceptualizing the saliency of a secondary goal as it relates to septo-hippocampal dysfunction, it is the degree of overlap with a prepotent goal rather than the physical intensity of the eliciting stimulus that appears to be most relevant.

### ***Assessing the generality of psychopaths' deficits integrating top-down and bottom-up networks***

According to the theory of SHS presented in this chapter, SHS dysfunction is associated with impairment in the ability to detect conflicts that involve bottom-up activation of neural

networks, especially those that are nondominant and incongruent with the top-down focus of selective attention. Psychopaths' insensitivity to punishment cues appears to conform to this pattern. However, if psychopaths are characterized by a more general deficit in the integration of bottom-up activation, it should be possible to observe the same pattern of results with other types of bottom-up activation.

### ***Evidence from Stroop tasks***

To evaluate this prediction, our lab has employed a variety of Stroop-like tasks. In the standard, color-word Stroop task (Stroop, 1935), participants are instructed to name the color of a word while ignoring its meaning. Owing to the well learned practice of reading words, it is difficult for people to ignore the bottom-up activation associated with a word's meaning and maintain the top-down focus of attention on the color of the stimuli. Thus, the well replicated finding is that participants are slower to name the color of letter strings when they spell incongruent color names (e.g., the word BLUE written in red) compared to control trials in which participants must name the color of color patches or the color of nonword letter strings (e.g., XXXX). In addition to the standard version, it is possible to pair incongruent pictures and words (e.g., the word "dog" superimposed on a picture of a pig). As in the standard Stroop task, participants are slower to name pictures paired with incongruent words than they are to name pictures with superimposed non-word letter strings. Both color-word and picture-word Stroop tasks represent common methods for assessing the effects of bottom-up processing on the top-down focus of selective attention.

Results from four separate studies involving four different versions of the color-word Stroop task conducted by our lab provide convincing evidence that psychopaths and controls display comparable interference on common versions of the color-word Stroop task (Bertsch &

Newman, 2003; Brinkley, Schmitt & Newman, 2003; Hiatt, Schmitt & Newman, in press; Smith, Arnett & Newman, 1992). Conversely, results from two separate studies demonstrate that psychopaths display significantly less interference than controls on picture-word Stroop tasks (Hiatt et al., in press; Newman, Schmitt & Voss, 1997) and this finding has been replicated in psychopathic women as well as psychopathic adolescents (Vitale, Brinkley, & Newman, 2003; Vitale, Newman, Bates, Goodnight, Dodge, & Petit, 2003).

Clearly some difference between color-word and picture-word Stroop tasks plays an important role in determining when psychopaths will or will not differ from controls. One salient difference between these tasks concerns the fact that the incongruent information in the color-word task is usually spatially-integrated whereas the incongruent information in the picture-word task, of necessity, is spatially-separated (i.e., pictures and words have different shapes and occupy different space). Although our lab has also investigated other task-related differences (e.g., Brinkley et al., 2003), Hiatt et al. (in press) demonstrated the importance of the spatial dimension by examining color-word interference within a spatially-separated format. Using a computerized administration, color words or non-word letter strings (i.e., iiiii) appeared in white font inside yellow, green, red, or blue rectangles. Thus, the task maintains the simple content (i.e., four colors) of the color-word task while incorporating the spatial separation that characterizes picture-word tasks. Consistent with results for the picture-word tasks and demonstrating the importance of the spatial dimension, psychopaths displayed significantly less interference than controls on this task.

***Relation to SHS dysfunction.*** The above findings demonstrate that psychopaths are relatively insensitive to incongruent, bottom-up information when it is spatially distinct from their top-down focus of selective attention. Conversely, they display normal sensitivity to

incongruent information when it spatially overlaps their top-down focus of selective attention. Thus, as with psychopaths' reaction to punishment stimuli, it is not the quality or content of the bottom-up activation but its degree of overlap with the dominant response set that determines its effect on psychopathic individuals.

We have proposed that the SHS is especially important in detecting conflict when there is a dominant response set combined with bottom-up activation that is incongruent with (i.e., not already activated by) that set. An important distinction between spatially-integrated and spatially-separated Stroop tasks is that participants must first attend to and disentangle the incongruent elements in spatially integrated Stroop tasks whereas this is not necessary in spatially separated versions of the Stroop task (i.e., overcome integration; see McLeod, 1998). Given this perspective, it follows that both elements of the spatially integrated stimulus receive top-down attention and activate competing responses before one color network becomes dominant. Indeed, if anything, it is generally assumed that reading the word is prepotent. Under such circumstances, interference is unlikely to reflect the type of bottom-up activation of non-dominant networks attributed to the SHS. Indeed, to the extent that the spatially-integrated color information activates competing top-down responses it would correspond to the special conflict scenario described by Gray and McNaughton (2000) in connection with simultaneous discrimination tasks. As noted earlier, registration and resolution of such conflicts has little to do with the SHS because it is difficult to establish a dominant response set without first adjudicating (i.e., using top-down attention to resolve) the conflict. That such conflicts do not rely on SHS processing or differentiate the performance of psychopaths and controls has been a consistent theme of this chapter.

Although highly speculative, especially given the lack of imaging data for spatially

separated Stroop tasks, psychopaths' situation-specific lack of Stroop interference is consistent with our proposal regarding SHS dysfunction. An alternative explanation for the pattern of results, however, is that psychopaths are characterized by a narrow focus of attention that reduces the processing of peripheral stimuli regardless of SHS functioning. If this alternative is correct, psychopaths would be less affected by spatially separated cues regardless of whether they are compatible or incompatible with their dominant response set. Notably, results from the rectangle Stroop task employed by Hiatt et al (in press) do not support this alternative interpretation.

On one-third of the trials in the rectangle task, the color words (e.g., BLUE) are congruent with the color of the rectangles. Thus, one can assess the extent to which congruent color words facilitate color naming relative to trials involving non-word letter strings. To the extent that psychopaths are oblivious to all spatially separated information, they should display less facilitation in addition to less interference than controls. However, if psychopaths' deficit involves a failure to activate bottom-up information when it has minimal overlap with a top-down set as predicted by the SHS theory, then psychopaths should display normal Stroop facilitation. In other words, to the extent that the color of a congruent word is activated by the top-down focus of attention because it is consistent with the color of the rectangle, its activation will have little to do with the SHS which registers and juxtaposes competing neural networks. In light of the fact that psychopaths displayed at least as much facilitation as controls on congruent trials, the results are consistent with an interpretation of the psychopathic deficit that highlights a specific deficit in the processing of incongruent, bottom-up activation – a deficit that is also predicted by the theory of SHS functioning presented in this chapter.

***Summary.*** Paralleling results from laboratory studies of passive avoidance learning,

psychopaths' insensitivity to bottom-up, affectively-neutral stimuli appears to be situation specific. Furthermore, the emergence of group differences appears to reflect the degree of overlap between bottom-up stimuli and a person's top-down focus of selective attention. More specifically, psychopaths are relatively insensitive to conflicting information that relies on the bottom-up activation of non-dominant neural networks—a function that we have ascribed to the SHS.

### ***The SHS and top-down / bottom-up integration of affective cues***

There is increasing recognition that the SHS plays an important role in emotion as well as other types of information processing (Wall & Messier, 2001). This is especially important when considering the potential relevance of the SHS for psychopathy because psychopaths are notorious for their insensitivity to affective information (see Newman & Lorenz, 2003). In our analysis of psychopaths' performance in passive avoidance and Stroop-like tasks, we emphasized the importance of conflicting or incongruent information as the type of bottom-up information that psychopaths fail to process. That is, we portrayed the SHS as registering and juxtaposing neural networks associated with alternative or competing goals and responses. However, consideration of the SHS functions presented earlier in this chapter suggests that the SHS is also involved in micro-shifts of attention that facilitate the integration of novel or unanticipated contextual information with a person's dominant response set. Such information may be thought of as activating a competing goal of exploring the significance of the unanticipated information.

As described in our review of the Gray and McNaughton (2000) theory, when there is subcortical input that reflects the presence of important stimuli (i.e., potential goals) and the hippocampus does not at the same time receive a matching cortical input (i.e., the goals are novel), it produces an output which inhibits the prepotent goal and hence permits the orienting

and exploratory programs to function properly.” (p. 255-6). Although this response is clearest when the novel (i.e., unanticipated) input conflicts with the dominant response set, the authors describe this interruption as a continuum that includes intermediate cases in which prepotent responses are emitted more slowly with varying degrees of exploration. Thus, even without clear registration of “conflict” and a shift to “control mode”, the SHS will tend to compare, and thus link, bottom-up, nondominant activation with an ongoing dominant response set. Whenever the nondominant information is affective, an association between one’s dominant response set and affective experience may be established. This link, in turn, increases a person’s ability to access “the affective accompaniments of experience” (Cleckley, 1976; p. 6) which is often cited as the primary deficit in psychopathy.

This routine function of the SHS is what enables a person to use a wide array of contextual information to distinguish one episodic memory from another, acquire knowledge about the circumstances that predict particular threats or rewards, and use bottom-up information to distinguish between circumstances in which reinforcers will or will not occur. Beyond these functions commonly attributed to the SHS, we speculate that the same processes that subserve these functions (i.e., the simultaneous processing of dominant and non-dominant networks) produce the type of long-term potentiation that integrates networks that are frequently co-activated (see also O’Reilly & Rudy, 2001). Although individuals are capable of using top-down, PFC resources to achieve the same integration effected by the SHS, this means of achieving the same end is generally slower and more effortful (e.g., Rudy and O’Reilly, ). To the extent that psychopathy is associated with SHS dysfunction, their ability to use polymodal representations (including affective associations) to discriminate between related contexts is likely to be more effortful and less efficient than for nonpsychopaths (see Frankland et al., 1998).

To the extent that our characterization of SHS dysfunction is accurate and applies to psychopathy, then psychopaths' processing of affective information should also be moderated by their top-down focus of selective attention. Cleckley's (1976) characterization of the psychopaths' emotion processing appears consistent with this possibility. He wrote: "All judgments of value and emotional appraisals are sane and appropriate when the psychopath is tested in verbal examinations" (p. 369)...though these capabilities do "not significantly or consistently influence his behavior" (p. 385). Moreover, laboratory studies provide considerable evidence that psychopaths and controls make comparable appraisals of affective stimuli and even display comparable psychophysiological reactions when task instructions focus attention on the affective stimuli even though affective information has minimal impact on their dominant responses, especially when the affective information is incidental to performance (Blair, 1997, Levenston, et al, 2000, Lorenz & Newman, 2002, Patrick, Bradley, & Lang, 1993, Williamson, Harpur & Hare, 1991, see Newman & Lorenz, 2003 for a review).

Lorenz and Newman (2002) have referred to this discrepancy between psychopaths' ability to appraise versus use emotion stimuli while pursuing other goals as the emotion paradox. Based on earlier findings by Williamson et al. (1991; see also Patrick et al., 1993), whose research served to highlight this issue, Lorenz and Newman (2002) evaluated the emotion paradox using a lexical decision task with emotional and neutral words. Participants were shown a letter string for 100 ms and instructed to press one key with their index finger if the string was a word or another key with their middle finger if it was not a word. Half of the letter strings were neutral words and half of the words had affective significance (i.e., high arousal in addition to positive or negative valence). Previous research demonstrates that normal participants identify words with affective significance more quickly and accurately than neutral words -- an

effect that has been labeled emotion facilitation. Demonstrating the emotion paradox and replicating the earlier research of Williamson et al. (1991), psychopaths displayed significantly less emotion facilitation than nonpsychopathic controls though their ratings of the words' affective valence were nearly identical to those of controls.

As with the investigation of interference using the Stroop-related tasks, there is a lack of direct evidence regarding the link between the use of contextual affective information (i.e., emotion facilitation) and the SHS. Nevertheless, the circumstances that differentiate the passive avoidance, Stroop performance, and emotion processing of psychopaths and controls appear to be related. Specifically, psychopaths typically perform like controls when the relevant information is part of their top-down focus of selective attention. Conversely, they are relatively unresponsive to information that does not receive top-down activation and is thus dependent on bottom-up activation of non-dominant neural networks.

Although the potential relevance of the SHS for the psychopaths' processing of bottom-up inhibitory, spatially incongruent, and affective information is undermined by the lack of imaging data addressing this question directly, when imaging studies are conducted they appear as likely to identify structural (e.g., Laasko et al. 2001; Raine et al., in press; Soderstrom et al., 2002) and functional (e.g., Kiehl et al., 2001) differences in the SHS as in other brain regions. Moreover, given the general dearth of imaging data on psychopaths, it would be unwise to dismiss potential neural models for this reason.

On the other hand, there is considerable behavioral evidence demonstrating that psychopathy is associated with a relatively distinctive information processing deficit. Across multiple domains, psychopaths appear oblivious to nondominant information that is not congruent with their dominant response set, though they are adept at processing the same

information when it is the focus of top-down attention (see Newman & Lorenz, 2003 for review). This deficit is not specific to particular types of bottom up information or to particular response requirements. Thus, it is more general than would be expected on the basis of a deficit in fear processing or even a more general deficit in emotion processing. Similarly, the fact that psychopaths often perform as well as controls in processing inhibitory, incongruent, and affective information when doing so is consistent with their top-down focus of selective attention (see Newman & Lorenz, 2003), is also inconsistent with postulating a specific content related deficit. For this reason, we believe that a primary task for neuroscientists wishing to clarify the nature of psychopathy is to understand their deficiency in the integration of top-down and bottom-up information.

### *The SHS placed in context*

It was not our intention in this chapter to argue that there is better support for the etiological significance of the SHS than for other brain systems that have been associated with psychopathy. Our decision to focus on the potential relevance of the SHS in this chapter was influenced by (a) the fact that the response modulation hypothesis was originally based on this system (including its connectivity with the orbito-frontal cortex); (b) our view that the potential relevance of the SHS has been relatively neglected owing to the field's preoccupation with psychopaths' deficient fear processing; and (c) our data emphasizing the situation-specific nature of psychopaths' information processing deficits.

Because we have focused our attention on the SHS, it is critical to emphasize the fact that the SHS is part of a complex circuitry, with connections to many areas of the brain, including various regions of the prefrontal cortex (PFC), the amygdaloid complex, the cingulate cortex, and others. Indeed, the functionality of the SHS is fundamentally a property of its connectivity

with these other neural systems. To illustrate the importance of this connectivity, we discuss the orbitomedial-prefrontal cortex (OMPFC) and the amygdaloid complex.

The OMPFC, which in humans includes Brodmann areas 10, 11, 47/12, 13, 14, 25, and 32 (Ongur & Price, 2002), is a polymodal association and integration system implicated in diverse learning and memory processes, involving emotional processing (Bechara, Damasio & Damasio, 2000), operant conditioning (Rolls, 2000), decision making (Bechara & Damasio, 2002) and reversal learning (Dias et al, 1996), among others. The OMPFC has connections with unimodal sensory areas (e.g. primary visual, auditory, gustatory, olfactory and somatosensory processing areas; Carmichael & Price, 1995), polymodal limbic association centers (e.g. the amygdala and hippocampus; Price, Carmichael & Drevets, 1996), and brainstem visceral-autonomic effectors (e.g. the hypothalamus, periaqueductal gray; Groenewegen & Uylings, 2000).

By virtue of these connections, the OMPFC can act as a working memory system capable of integrating complex internal and external representations along with cognitive and emotional aspects of current (or recent) stimuli and associated behaviors (Wall & Messier, 2001). Neurons in the OMPFC are thought to be involved in decoding the reinforcement value of sensory stimuli according to the cognitive-behavioral context in which they occur (Rolls, 2000). This includes learning the association between a UCS, a primary reinforcer, and the behavior necessary to obtain the reinforcer. The OMPFC is also important in the rapid relearning of stimulus-reinforcer associations when reinforcement contingencies change. For example, if a monkey is trained to press a bar for food reward at the onset of a light, the OMPFC uses the learned association between light and reward to bias the active response (i.e., bar press) in favor of the most rewarding option. If contingencies change such that a bar press after light no longer

delivers food, the OMPFC assists in the rapid relearning of the new stimulus-reinforcement contingency, so that when the light appears again the animal is able to use this newly updated contingency information to override the prepotent response, i.e. bar pressing (Rolls, 2000; O'Doherty et al, 2001; Shultz, Tremblay & Hollerman, 2000). In other words, the OMPFC appears to act as a working memory structure for holding current or very recent cognitive/emotional/motor associations of motivational significance. In this way, representations in the OMPFC provide a context to guide the planning and execution of ongoing behavior (Gallagher, McMahon & Schoenbaum, 1999).

These rich representations encoded by the OMPFC are made available to the hippocampus through reciprocal connections between the OMPFC and the hippocampus (Barbas & Blatt, 1995), including several parallel channels (Ongur & Price, 2000; Cavada et al., 2000), and particularly dense reciprocal connections between the OMPFC and parahippocampal gyrus structures (entorhinal and perirhinal cortices; Frey & Petrides, 2000). Additionally, the hippocampus projects directly to the OMPFC, primarily from the CA1 and CA1' fields and the adjacent subiculum region (Cavada et al., 2000).

This connectivity scheme has intriguing implications for SHS-OMPFC interactivity. As part of its checking function, the hippocampus receives information from and recirculates information to the OMPFC regarding the animal's current cognitive-emotional-behavioral set (goal state; Gray & McNaughton, 2000; Wall & Messier, 2002). Thus, the hippocampus is able to compare current and recent stimulus-emotion-response representations held in the OMPFC (Wall & Messier, 2002). If the SHS detects a conflict between these representations (e.g., if bar pressing in the presence of a light is no longer associated with food), such a conflict indicates a deviation from the expected outcome and the SHS enters “control mode” by signaling the need

(presumably through the direct CA1/subicular projection) to modify the attentional resources allocated to whatever prefrontal set is active at the instant conflict is detected. Specifically, if conflict is detected, the SHS tags the currently active set, which is then looped and re-looped through the OMPFC-entorhinal-hippocampus circuit, allowing for increased scrutiny of the specific variables responsible for the current conflict. The hippocampus may help resolve a current conflict by signaling a decrease in the activation of the OMPFC network dominant when the conflict occurred. If an alternative response is enacted without further conflict, the SHS would return to "just-checking" mode. This is in line with Wall and Messier's (2002) proposal that the hippocampus-OFC circuit "activates, maintains, monitors and modifies current and recent past cognitive/emotional/motor set representations... [allowing for] the continuous updating and integration of internal and external associative emotional representations" (p. 110).

There is also rich interconnectivity between the SHS and amygdala. Indeed, investigators commonly refer to an amygdala-hippocampal complex. According to cytoarchitectonic and functional research, the amygdala, or more specifically, the amygdaloid complex, located in the medial temporal region of the human brain, consists of several groups of cells or nuclei. The nuclei comprising the amygdaloid complex have been subdivided into two distinct regions, the ventral region, or 'basolateral amygdala', and the dorsal region, or 'extended amygdala'. This subdivision of the amygdaloid complex is justified by significant differences in cell structure, content, and connectivity (Davis & Whalen, 2001).

The basolateral amygdala receives information about sensory inputs from the thalamus, and highly processed information from the hippocampus and cortex, and in turn modulates neural activity in several target areas appropriate for pairing sensory stimuli with unconditioned stimuli (i.e. Pavlovian conditioning: Kapp et al., 1984; LeDoux et al., 1988; Davis, 1997, 1998;

Davis & Whalen, 2001). With regard to fear conditioning, for instance, a tone paired with shock will alter the neural activity within the basolateral amygdala and its target areas, allowing a previously neutral cue (CS) to be paired with an unconditioned fear stimulus (UCS). Moreover, connectivity between the basolateral amygdala and the central nucleus (CeA) of the amygdala, allows for a previously neutral stimulus to elicit the same 'fear expression' as the unconditioned stimulus (LeDoux, 2000). The dorsal, or 'extended amygdala', consists of the central, medial and cortical nuclei, and receives the majority of its input via afferent connections from the basolateral amygdala. By virtue of its connectivity with hypothalamus and brain stem regions, this region of the amygdala is important for mediating the autonomic and endocrine aspects of fear expression as well as increases in attention to fear stimuli (Davis & Whalen, 2001).

The amygdala plays a fundamental and crucial role in fear conditioning. Selective lesions of the BLA severely attenuate the acquisition of fear conditioning to both contextual and discrete CSs when made before training. The CeA, by contrast, is primarily involved in expressing CS-US associations (Maren, 2001, p. 904). Whereas information pertaining to discrete CSs appears to reach the amygdala via direct projections from primary sensory areas, the hippocampal formation plays a key role in "assembling contextual representations and transmitting these representations to the amygdala for association with USs" (Maren, 2001, p. 908). Thus, the role of the hippocampal formation in fear conditioning is often crucial but it is also much more specific than that of the amygdaloid complex.

The amygdala-hippocampal complex is also implicated in trace conditioning. In contrast to simple fear conditioning, trace conditioning involves a delay between presentation of a CS and delivery of a US and depends upon the hippocampus as well as the amygdala presumably because the hippocampus is essential for maintaining the representation of the CS during the

temporal delay (e.g., Buchel et al., 1999; LeDoux, 2000). Similarly, amygdala and hippocampus both play a key role in the formation and context relevant retrieval of affective memories. In this regard, we assume that the SHS is important for incorporating the affective elements into a polymodal representation that enhances memory and facilitates attention to such representations in the future (McGaugh, Introini-Collison, & Cahill, 1992; Packard & Teather, 1998).

With regard to instrumental learning, Gray and McNaughton (2000) ascribe to the amygdala a fundamental and general role in defensive avoidance. According to these authors, the amygdala is crucial for active avoidance as well as for passive avoidance whereas the SHS is important for defensive approach which involves interrupting approach behavior that may result in punishment (i.e., passive avoidance). Thus, paralleling their involvement in fear conditioning, the amygdaloid complex plays a fundamental role in mediating instrumental avoidance whereas the role of the SHS in avoidance learning is more circumscribed. However, as with fear conditioning, instrumental learning is likely to depend upon the interaction of the amygdala and SHS whenever instrumental learning requires an individual to discriminate between polymodal or partially overlapping contexts. In such cases, the SHS will play an important role in facilitating context appropriate responding.

Thus, with regard to emotion processing and avoidance learning, the functions of the amygdala and hippocampus appear to be closely intertwined. Whereas the amygdala complex plays a fundamental role in establishing affective associations and in emotional expression, the hippocampus is important for modulating these functions, particularly when the acquisition of conditioned responses involves temporal delays and configural (i.e., polymodal) representations as opposed to rudimentary stimuli.

With regard to response modulation, it seems likely that amygdala activation is important

for increasing arousal when an individual encounters stimuli that have been associated with affective consequences (i.e., Stage 2 of the response modulation model). It may be speculated that such information would be transmitted to the SHS and signal a goal conflict when it is incongruent with the dominant response set. However, the CeA may also indirectly influence widespread cortical activation via dopaminergic projections to cholinergic nuclei in the basal forebrain (e.g., nucleus basalis) which, in turn, project to cortex (Davis & Whalen, 2001) and modulate attention (e.g., Kilgard & Merzenich, 1998). Thus, especially in response to salient conditioned stimuli, the amygdaloid complex may influence a person's ability to modulate attention (i.e., answer a call for processing at Stage 3 of the response modulation model). Moreover, to the extent that a stimulus interrupts a person's dominant response set and redirects top-down attention, it is likely to influence learning and subsequent behavior. Thus, although we elected to focus on the SHS in this chapter, it is also possible to construct an explanation for psychopaths' response modulation deficits that depends primarily on amygdala dysfunction.

In contrast to the amygdala, which we assume responds to emotionally salient stimuli by simultaneously increasing arousal and preempting attention (e.g., Davis & Whalen, 2001), the SHS appears to be especially important for modulating as opposed to overtly interrupting ongoing approach behavior. To the extent that stimulus circumstances include unexpected aspects, the SHS will either engage in pattern completion and register a match or engage in pattern differentiation and register a competing goal. Though small departures from expectations are unlikely to initiate goal conflict immediately, their registration and representation makes it more likely that a goal conflict will be registered if the discrepancy persists or grows in magnitude. In this manner, we assume that the SHS issues a more subtle call for processing and only gradually interrupts top-down attention as activation associated with an alternative goal

increases (perhaps via the SHS-OMPFC circuitry discussed earlier). In other words, rather than disrupting top-down attention in an immediate way, we assume that activation associated with a dominant response set will gradually decrease as activation associated with a competing goal increases.

By facilitating the activation of competing goals, we assume that the SHS enhances the ease with which a person may shift behavioral strategies when a stimulus array suggests that punishment is more likely than reward (i.e., passive avoidance), one's approach behavior is no longer likely to achieve a desired end (i.e., extinction), or an alternative approach is more appropriate (i.e., reversal). Moreover, we believe that the simultaneous activation of competing goals facilitates (a) identification of features that distinguish one context from another (i.e., often aids discrimination learning) and (b) modification of polymodal representations that were dominant when alternative goals became salient. Although such discriminations and learning will often reflect top-down processing or the deliberate allocation of cortical resources, we assume that the SHS provides a more rapid and less capacity-demanding means of processing circumstances that modulate goal-directed behavior (see also O'Reilly & Rudy, 2001).

### *Summary and implications of the SHS for psychopaths'*

#### *deficient integration / bottom-up information*

The goal of this chapter was to re-establish a link between the response modulation hypothesis and the neuroscience literature. Toward this end, we have translated the response modulation hypothesis into neural network language (see also MacCoon et al., in press) and used this framework to consider the role of the SHS for the integration of top-down and bottom-up neural networks. According to the response modulation hypothesis, psychopaths' difficulty using

non-dominant information to modify their prepotent goal or response set is a crucial factor underlying their self-regulatory deficits. From its inception the response modulation hypothesis has focused on the SHS as a possible mechanism for this psychopathic deficit. Based on our interpretation of Gray and McNaughton's (2000) synthesis, we have proposed that the SHS facilitates the bottom-up activation of contextually important (but non-dominant) networks so they can compete effectively with a prepotent goal or response set. According to this perspective, the SHS will be important when bottom-up influences are relatively unexpected (a cue is unexpected to the extent it is not activated by top-down selective attention). Conversely, the SHS will be relatively unimportant for modulating bottom-up activation when top-down attentional resources are available and directed appropriately. This would occur when a current goal does not demand full capacity, when a competing goal is already represented in the PFC, when competing responses are salient enough to require adjudication and thus activate other conflict monitoring systems that gate bottom-up information into the PFC (e.g., the anterior cingulate), or when the characteristics of unexpected stimuli are so intense or meaningful that they are able to interrupt goal-directed behavior more directly (e.g., when delivery of an electric shock activates the primary defense system and interrupts the top-down focus of attention).

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