

# The Conscious Control of Behavior: Revisiting Gray's Comparator Model

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This chapter was spurred into existence by the admiration that the authors have for Jeffrey A. Gray (1934-2004), a scientist who contributed much to our understanding of the mind/brain, including the study of the elusive relationship between consciousness<sup>1</sup> and behavioral control, which is the focus of this chapter. One of us (PC) had the good fortune of being the protégé of Gray; the other (EM) had the great pleasure, not only of reading and benefiting from Gray's theorizing, but from having once met him in New York City to discuss his ideas for several hours, thanks to John Bargh, who generously arranged the meeting. During this wonderful conversation, taking place more than a decade ago, it became apparent to both the distinguished scientist and the recently PhD-minted young scientist that Gray's (1995) *Comparator Model* of conscious processing (presented in *Behavioral and Brain Sciences*) could explain more about consciousness and behavioral control than even envisioned by its author, which was already quite a bit including disparate phenomena such as the contents of consciousness (Gray, 1995), the neuropsychology of anxiety (Gray, 1982a, 1982b; Gray & McNaughton, 2000), and the positive symptoms of acute schizophrenia (Gray, Feldon, Rawlins, Hemsley, & Smith, 1991; Gray, 1998). These extensions of Gray's BIS theory are the focus of this chapter.

## *Gray's Comparator Model*

To appreciate the insights discussed on that day, now many years ago, it is important to understand Gray's comparator model of consciousness. The model explains, among other things, the lateness of conscious processing (Gray, 2004; Libet, 2004; Velmans, 1991, 2000), error detection in behavioral control, and, importantly, how some contents, but not others, are selected to enter consciousness.

Perhaps no one can explain the model better than Gray himself:

The essential computational function discharged by the

comparator is to compare, non-consciously and quite generally, information currently received via all thalamocortical sensory pathways (up to the level of neocortical analysis) with a prediction as to what that information should be. The prediction is based jointly upon previous stimulus-stimulus and response-stimulus regularities (stored as memories) under circumstances similar to those operating now; the circumstances ‘operating now’ are themselves defined by the output of the comparator at the preceding comparison process. In addition, the comparator takes account of the subject’s ongoing motor program, as what the world will be like in the next moment depends upon what the subject is doing in this one. These processes occur on a time base of the order of 100 ms from the termination of one process of comparison to termination of the next. The output from the comparison process selects a series of items in the neocortical description of the sensory world in the light of their novelty/familiarity and predictedness/unpredictedness (these concepts are not identical to one another)... The selection is biased towards items which are novel, either because they occur despite not being expected or because they fail to occur despite being expected; and towards items which are goals or sub-goals for an ongoing motor program. The selected items are reactivated by feedback from the comparator system to those areas of the sensory neocortex (visual, auditory, somatosensory etc) in which they have just been non-consciously analysed. It is this reactivation by feedback from the comparator that selects these items for entry into consciousness (Gray, 2002, p. 4).

As Gray himself noted, similar ideas had been proposed before (e.g., by Jackendoff, 1987; Miller, Galanter, & Pribram, 1960; Neisser, 1967). However, until Gray’s own model, no ‘nuts and bolts’ theory existed that contained as much specificity regarding both the component processes of consciousness (e.g., detecting, comparing, and matching) and its neuroanatomical substrates (see Gray, 1995, for hypotheses about the hippocampus and neocortex in conscious processing).

According to the model, unconscious motor programs (discussed below) lead to expressed action, which then leads to action effects (which are perceptual in nature) that are, then, compared to the anticipated action effects, which themselves are perceptual-like memories based on previous experience (Gray, 1995). The stages of processing in situations in which the comparator detects a mismatch could be conceptualized as follows. *Unconscious motor programs* (Stage 1) → *perceptual-like action effects* (Stage 2) → *comparator process* (Stage 3) → *mismatch detection* (Stage 4) → *entry into consciousness of mismatched, perceptual-like information and error signals (along with other goal-relevant information)* (Stage 5). As is clear in this sequence,

consciousness occurs late, as when one withdraws one's hand reflexively from a hot pot. In this case, consciousness regarding the action is experienced only *after* the, in this case, the pain withdrawal action is already mediated successfully, albeit unconsciously, by the nervous system (Gray, 2004). According to Gray (2002), the pain (the quale that is a consequence of late error detection) influences, not so much the nature of ongoing action at the moment (for the appropriate action to the situation already took place in an unconsciously mediated manner), but future actions transpiring in a similar context. In this way, entry into consciousness influences future behavior, in a manner that is not well understood (see treatment in Corr, 2011).

In this comparator framework, when outcomes from actions do not match expected outcomes, representations of the salient features about these unexpected outcomes enter consciousness -- as, for example, when we learn that the pot was hotter than expected. This representation occurs also for actions that do not involve pain: any outcome mismatch has the potential to have its salient features represented in the contents of conscious awareness. For example, just imagine the case in which a child intended saying something but then, unexpectedly and for the first time in her life, found herself coughing. The child becomes very much aware of this cough experience, long after the motor plans engendering the cough behavior transpires.

It was while discussing mechanisms such as these that, during that conversation more than a decade ago, something became clear: When the sequence of the comparator is reversed, such that the stages flow from 5 to 1 rather than from 1 to 5, the model resembles *ideomotor theory* (Greenwald, 1970; Harleß, 1861; Hommel, 2009; Hommel, Müsseler, Aschersleben, Prinz, 2001; James, 1890; Lotze, 1852): A historic approach illuminating how behavior can be controlled voluntarily. Interestingly, the ideomotor approach developed independently of comparator frameworks, but the two have much in common, as we will now discuss.

### *Ideomotor Approaches to Behavioral Control*

In ideomotor approaches, one's conscious knowledge regarding action production and control is limited to the perceptual consequences of expressed action (or 'action effects'). From this standpoint, motor control—that which specifies which muscles should be activated at a given time in order to express an action (e.g., flexing a finger)—is largely unconscious (see evidence in Fecteau, Chua, Franks, & Enns, 2001; Grossberg, 1999; Goodale & Milner, 2004; Heath, Neely,

Yakimishyn, & Binsted, 2008; Jeannerod, 2006; Liu, Chua, & Enns, 2008; Rosenbaum, 2002; Rossetti, 2001). As William James stated, during action control, one's consciousness is occupied only by the perceptual consequences of action: "In perfectly simple voluntary acts there is nothing else in the mind but the kinesthetic idea... of what the act is to be" (James, 1890, p. 771). These action-generated perceptual effects include bodily states (e.g., a flexed finger) or 'remote' effects in the external world, such as the change in position of a lever (Hommel, 1998; Hommel & Elsner, 2009; Jordan, 2009). Harleß (1861) referred to these perceptual consequences of a given action as the 'Effektbild' (i.e., the picture of the effect).

From this standpoint, one is unconscious of efference generation to the muscles. According to a minority of theorists (see list of the names of four 'dissenters' in James, 1890, p. 772), one is conscious of the efference to the muscles (what Wundt called the *feeling of innervation*; see James, 1890, p. 771). This efference was believed to be responsible for action outcomes (see review in Sheerer, 1984). (Wundt himself later abandoned the feeling-of-innervation hypothesis; Klein, 1970.) Following the controversy, James (1890) concluded, "There is no introspective evidence of the feeling of innervation" (p. 775).

Ideomotor theory then goes on to propose that, when these perceptual-like representations are activated in the future, they automatically activate the unconscious motor programs responsible for enacting the action that led to them. For example, when holding the image in mind of one's finger flexing, the image of the action activates the motor programs that would give rise to the action. In short, activation of the (perceptual-like) representation of action effects leads to the automatic expression of the associated action. According to James (1890), this form of ideomotor action must always take place, unless, that is, one simultaneously has activated in mind the perceptual consequences of an incompatible action. From this standpoint, mere thoughts of action effects produce impulses that, if not curbed or controlled by "acts of express fiat" (i.e., the representation of incompatible action effects) result in the performance of those actions (James, 1890/1950, pp. 520-524). Thus, James emphasized the image of the sensorial effects of an action leads to the corresponding action. Of important in this framework is that there is no central homunculus, preferring to realize one action effect over another: The process is effortless, automatic, and without any knowledge of the motor programs involved. Rather, activation of the representations of action effects lead to those actions, unless there is also the activation of representations of incompatible action effects. To take one example, when one imagines one's

finger moving but decides not to move the finger, it is only because, when imaging the former, one also had activated the idea of not moving the finger, which is an incompatible idea.

In this way, voluntary action can be guided by the activation of the perceptual-like representations of action effects. In some situations, this guidance is intentional and is accompanied by the sense of agency (Moore, Wegner, & Haggard, 2009), especially when action outcomes match one's action goals. According to the ideomotor theory, voluntary action control requires memory of previous action effects. The process unfolds as follows. *Activation of conscious, perceptual-like representations of action effects (Stage 1) → activation of unconscious motor programs (Stage 2) → perceptual action effects (Stage 3) → comparator process (Stage 4) → entry into consciousness of, say, mismatching perceptual consequences.* One can appreciate that this resembles the reversed sequence of Gray's comparator model, which begins, not with the conscious action effects, but with the unconscious motor program. (For treatments of how these ideas are related to social cognition, see Johnson & Shiffrar, 2013; Jordan, 2009.) It was always implicit in Gray's model that (always automatic) actions were elicited, or afforded, by stimuli; however, it was never made explicit how such stimuli trigger these actions. Ideomotor theory provides an account of this process, and highlights the recursive interplay of automatic processes and controlled (often conscious) processes – neither one nor the other is in exclusive control of behavior, but rather they are joint causal partners in an experience-action system of coordination.

### *Ideomotor Theory and Mirror Neuron Approaches*

In line with ideomotor accounts, contemporary research on 'mirror neurons' (see review in Rizzolatti, Sinigaglia, & Anderson, 2008) suggests that there is overlap in the neural networks involved in (a) the perception of actions (e.g., the perception of actions by others) and (b) the execution of one's own actions. It is through such overlap that one can learn to perform actions based on imitation (Rizzolatti et al., 2008). From the perspective on research on mirror neurons, perceptual processing is an inextricable part of action control (Iacoboni, 2005; Jordan, 2009; Miall, 2003). (It is worth mentioning that this is consistent with the aforementioned ideomotor models which propose that perceptual action effects and action codes share the same representational format, hence the description of some ideomotor accounts as 'common code' theories of perception-and-action; Hommel, 2009.) From this standpoint, voluntary action can be guided by

the perceptual representations not only of the behaviors performed by one but by the observed behaviors of others. Consistent with both ideomotor and mirror neuron accounts, Desmurget et al. (2009) concluded in their brain stimulation study (on awake patients undergoing brain surgery for the treatment of epilepsy) that action intentions in perceptual regions may be processed in terms of the perceptual consequences of the intended action (see review of convergent evidence in Jordan, 2009; Miall, 2003). Complementing these findings is research on the role of reafference in action control, which reveals that essential to the control of intentional action is reafference to perceptual areas of the brain, such as parietal cortex (Berti & Pia, 2006; Chambon et al., in press; Iacoboni, 2005; Miall, 2003).

In summary, theorizing falling under the rubrics of ideomotor, common code, or mirror neuron research reveal the counter-intuitive hypothesis that the perceptual representations about the external world, including those about the behaviors of others, can be a major influence of behavioral control (see discussion in Jordan, 2009). As such, mirror neuron research supplies theoretically important empirical support for the ideomotor theories advanced by William James and others. It is, now, intriguing to see how they can easily be incorporated in to Gray's neuropsychological model of behavioral control and consciousness.

### *Subjective Aspects of Skinner's Three-Term Contingency*

Ideomotor theory, Gray's neuropsychological work, and more recent insights from mirror neuron research highlights the importance of the stimulus-response processes favoured by Skinner and the other radical behaviorists – their work can now be extended to understanding the machinery hidden in their black boxes. Neglected in traditional ideomotor accounts is the mechanism by which currently-experienced favorable outcomes from action production increase the likelihood that only some behaviors are expressed in the future. As far as we know, and in accordance with Loewenstein (1996),<sup>2</sup> operant conditioning remains the best mechanistic model to explain this phenomenon, especially when considering Skinner's (1953) three-term contingency description of operant learning. From this point of view, the traditional circumstance under which operant conditioning takes place involves three different terms. The first term involves the discriminative stimulus ( $S_D$ ), which is the stimulus the signifies the appropriate context for expressing the operant. In a standard operant conditioning experiment, a lever may be the

discriminative stimulus. In everyday life, a traffic light signaling green may be a discriminative stimulus. The  $S_D$  is considered the first term of the three-term contingency.

Faced with this  $S_D$ , the organism issues the operant behavior, or response ( $R$ ). It is important to note that, in this framework, the operant is not a simple response. When a rat depresses a lever, the action can be accomplished by the leg or the snout. Similarly, the operant may be getting the soccer ball into the goal, one way or another, as in a game of soccer. This can be accomplished through several means (e.g., pushing the ball in the goal with the left leg, the right leg, or, instead, by a header). That the same action goal can be accomplished through several motoric means is called ‘motor equivalence’ (Lashley, 1942). (Gray referred to such action goals as ‘goals’.) The operant ( $R$ ), learned through trial and error, is the second term of the three-term contingency.

The third and last term of the three-term contingency is the most relevant to our question regarding how behavioral outcomes could reinforce (i.e., increase the likelihood of) some behaviors over others in a specific context (i.e., when faced with a particular  $S_D$ ). This is the outcome variable, or  $O$ . The outcome is either a *reinforcer*, which increases the likelihood of a certain operant in the presence of a given  $S_D$  (e.g., the presentation of something positive or removal of something negative) or a *punisher*, which decreases the likelihood of a certain operant in the presence of a given  $S_D$  (e.g., the presentation of something negative or removal of something positive). Skinner (1953) explains that, in the three-term contingency ( $S_D \rightarrow R \rightarrow O$ ), it is the outcome term,  $O$ , that determines the strength of the association between  $S_D$  and  $R$ . If the outcome is a reinforcer, then the association is strengthened, making  $R$  more likely in the presence of  $S_D$ . If the outcome is a punisher, then the association between  $S_D$  and  $R$  is weakened, such that  $R$  is now less likely to occur when  $S_D$  is presented.

According to Gray, because the  $S_D$  is part of the perceptual world, it is a conscious representation, as is, importantly, the action effect and outcome term ( $O$ ). However, the motor aspects of  $R$  are unconscious. This is consistent with both Gray (1995, 2004) and ideomotor theory. Figure 1 reveals schematically that which is conscious and unconscious in the three-term contingency. Figure 1 reveals that, for that which falls within consciousness, it could be described, in terms of its neural processing, as *afference* or *reafference* (Sherrington, 1906).

### *Neural Correlates of the Subjective Aspects of the Three-Term Contingency*

Gray (1995, 2004) was more concerned with the nature of the different component processes of the comparator model than with the actual neural substrates of these processes. Speaking of alternative models, Gray (2002) concludes, “Where I stress the hippocampal system, more recent views tend to emphasise the prefrontal, anterior cingulate and/or parietal cortex. The precise anatomical localisation of the computations, however, does not bear upon the issues raised... What does bear upon these issues is the emphasis in all these models upon the interaction of top-down (contextual) and bottom-up (perceptual) processing as giving rise to the contents of consciousness” (p. 6).

Regarding the conscious aspects of behavioral control in the three-term contingency, it seems that much of the *control-related* processing in frontal cortex may be unconscious. Consistent with this view and with ideomotor frameworks, it seems that, as mentioned above, one does not have direct, conscious access to motor programs or other kinds of ‘efference generators’ (Grossberg, 1999; Morsella & Bargh, 2010; Rosenbaum, 2002), including those for language (Levelt, 1989), emotional systems (e.g., the amygdala; Anderson, & Phelps, 2002; Öhman, Carlsson, Lundqvist, & Ingvar, 2007), or executive control (Crick, 1995; Suhler & Churchland, 2009). The notion that efference generation is largely unconscious illuminates why, when speaking, one does not always know exactly which words one will utter next (Levelt, 1989; Slevc & Ferreira, 2006).

Regarding conscious awareness of action effects, there is evidence implicating, not frontal areas, but posterior perceptual regions (e.g., parietal areas) as being the key regions responsible for conscious states (see review in Godwin et al., in press). (Relevant to this hypothesis is research on the phenomenon of *sensory neglect*; cf., Graziano, 2001; Heilman, Watson, & Valenstein, 2003.) In addition, in a study with seven patients undergoing awake brain surgery, direct electrical stimulation of parietal areas of the brain gave rise to the subjectively-experienced will (an ‘urge’) to perform an action. Interestingly, increased activation made subjects believe that they actually executed the corresponding action (e.g., flexing a finger), even though no action was performed (Desmurget et al., 2009; Desmurget & Sirigu, 2010). Activating frontal motor areas (e.g., in premotor areas) resulted in the performance of the actual action, but, surprisingly, subjects believed that they did not perform any action (see also Fried et al., 1991): “Stimulation of the



premotor region triggered overt mouth and contralateral limb movements. Yet, patients firmly denied that they had moved” (Desmurget et al., 2009, p. 811).

These observations are consistent with the age-old *Sensorium Hypothesis* first proposed by the great Johannes Müller and then proposed, in one fashion or another, by others (Gray, 2004; Godwin et al., in press; James, 1890; Müller, 1843). The Sensorium Hypothesis is that action/motor processes are largely unconscious (Gray, 2004; Goodale & Milner, 2004; Grossberg, 1999) and that the contents of consciousness are influenced primarily by perceptual-based (and not action-based) events and processes, which is in direct agreement with Gray (1995) and ideomotor theory. Consistent with these perspectives, Desmurget et al. (2009) concluded in their brain stimulation study that action intentions in perceptual regions may be processed in terms of the perceptual consequences of the intended action (see review of convergent evidence in Jordan, 2009; Miall, 2003). Complementing these findings is research on the role of refference in action control. This research reveals that a key component of the control of intentional action is refference to perceptual areas of the brain, such as parietal cortex (Berti & Pia, 2006; Chambon et al., in press; Iacoboni, 2005; Miall, 2003). Accordingly, it has been proposed that, in terms of neural processing, that which characterizes conscious content is the notion of *perceptual afference* (information arising from the world that affects sensory-perceptual systems) or *perceptual re-fference*, such as the proprioceptive information generated during action production.<sup>3</sup>

Last, consistent with Gray (1995), the conscious contents (e.g., urges and perceptual representations) of behavioral control are similar to (or perhaps one and the same with) the contents occupying the ‘buffers’ in working memory (WM), a large scale mechanism that is used to sustain the activation of content-based representations in mind (e.g., for information manipulation) and is intimately related to both consciousness and action production (Baddeley, 2007; Fuster, 2003). Recent developments reveal that WM is intimately related to both action control and consciousness (LeDoux, 2008), as is evident in the title and contents of a treatise on WM—*Working Memory, Thought, and Action* (Baddeley, 2007). Indeed, perhaps no mental operation is as consistently coupled with conscious processing as is WM (LeDoux, 2008). When trying to hold in mind action-related information, a person’s consciousness is consumed by this goal (James, 1890). For instance, when holding a to-be-dialed telephone number in mind (or when gargling with mouthwash for 30 sec), action-related mental imagery occupies one’s consciousness during the delayed action phase. Similarly, before making an important toast (or, more

dramatically, making the toast in an un-mastered language), a person has conscious imagery regarding the words to be uttered, much as when an actor rehearses lines for an upcoming scene. In this way, before an act, the mind is occupied with perception-like representations of what that act is to be, as James (1890) stated above: “In perfectly simple voluntary acts there is nothing else in the mind but the kinesthetic idea... of what the act is to be” (James, 1890, p. 771). Thus, voluntary action control often occupies both WM and perceptual consciousness.

In conclusion, it is clear that there are several contemporary accounts that are consistent with Gray (1995) and with the age-old hypothesis that the urges associated with intentional action should involve regions of the brain that have historically been associated with perceptual processing.

### *What Is It about the Sensorium?*

Proposals have been made regarding why consciousness is associated with Müller’s sensorium but not with his *motorium*. For example, according to one framework about the micro-architecture of cognition (Grossberg, 1999), motor programming involves a neural process called ‘inhibitory matching,’ which is unconscious and does not involve ‘resonant states’ (according to Grossberg, 1999, all conscious states are resonant states, but not all resonant states are conscious states) whereas perceptual detection often involves ‘excitatory matching,’ which can be conscious, for reasons too complicated to explain here (see Grossberg, 1999).

According to several frameworks the primary function of conscious processing is to integrate processes that would be un-integrated otherwise (Baars, 1988, 2002; Boly et al., 2011; Clark, 2002; Damasio, 1989; Dehaene & Naccache, 2001; Del Cul, Baillet, & Dehaene, 2007; Doesburg et al., 2009; Freeman, 1991; Koch, 2004; Llinás & Ribary, 2001; Ortinski & Meador, 2004; Sergent & Dehaene, 2004; Tononi & Edelman, 1988; Ulhaas et al., 2009; Varela, Lachaux, Rodriguez, & Martinerie, 2001; Zeki & Bartels, 1999). These accounts have fallen under the *integration consensus* (Morsella, 2005). Germane to Gray (1995), conscious contents are available to various systems, as if the contents were somehow ‘broadcasted.’ It has been proposed that, for contents to have such communicability, then the contents of consciousness must be communicable (Fodor, 1983).

For communicability to occur successfully, representations must be in a format that is

understood by multiple systems, especially systems involved in behavioral control. Some theorists have proposed that this format must be perceptual in nature, as most brain systems evolved to be sensitive to perceptual-like representations (Morsella, Lanska, Berger, & Gazzaley, 2009b). These representations provide information about what Gestalt psychologists described as the ‘distal’ object (Koffka, 1922). (See research on how perceptual analysis reaches the stage of processing known as ‘objecthood’ in Goodhew, Dux, Lipp, & Visser, 2012.) In terms of neural processing, the representations rely on afference from the external world as well as on perceptuo-semantic knowledge (Most, Scholl, Clifford, & Simons, 2005).

Regarding this perceptual-like representations, one must consider that multiple systems in the brain respond in various ways to the same perceptual stimulus. In the processing of emotion-related stimuli, for example, LeDoux (1996) proposes that the same perceptual afference is processed by a ‘quick and dirty’ subcortical pathway and by a slower, more accurate cortical pathway. In either case, it is perceptual afference that is capable of activating analysis by systems that, most likely, evolved at different times and follow distinct operating principles. Independent of these considerations, Fodor (1983) proposed that the most ‘communicable’ kind of representation in the brain is that of the perceptual kind. Figuratively speaking, the perceptual-like information is the common-currency or lingua-franca of the brain.

The idea that consciousness represents a model of the external world, and one’s place and inclinations within that world, is not new and has become uncontroversial (Hesslow, 2002; Merker, 2007; Yates, 1985). However, it should be noted that the representations making up this simulacrum represent a small subset of what is really ‘out there.’ This subset includes objects and other physical information that are of ‘concern’ (Frijda, 1986) to the organism. We humans, for example, do not represent in our conscious simulacrum ultraviolet radiation. This is of little consequence because such energies are not of terrible concern to human welfare, though detection of such energies is essential for other species. It is also important to add that this simulacrum serves to afford adaptive action (Morsella, Montemayor, Hubbard, & Zarolia, 2010) and is not in the business of representing the external world accurately.

Such an evolutionary-based perspective on the nature of the conscious simulacrum begins with the assumption that most mental phenomena are primarily concerned with how the organism should behave at one moment in time. (This was the ‘functionalist’ approach adopted by William James and others.) As beautifully explained in Gray (2004), the nature of the

isomorphism to the world remains unclear with respect to many ‘representational’ processes. What of the outside world represented by a ‘mood’? What does the aversive feeling of holding one’s breath represent? What does the pungent flavor of hydrogen peroxide represent? This nasty chemical differs molecularly from water only by the addition of a single oxygen atom, but few would perceive it as ‘water with a little too much oxygen.’ Instead, the toxic chemical is perceived (or ‘represented’) as something that ‘tastes bad’ and should be violently expelled from the body. Similarly, in the real (physical) world out there, the color blue and red are just the same thing (electromagnetic frequencies) occurring at different speeds, but no one perceives the color red as a slower version of the color blue. Rather, color perception is intimately associated to action (and not the way the world *is*): It evolved for selecting fruits and detecting camouflaged prey (Morsella et al., 2010).

Some representations in vision (e.g., the spatial layout of a garden) do seem isomorphic to what is out there in the real world. In such cases, it just so happens that representing space as accurately as possible does lead to the most adaptive response. But representing how things are is not the primary goal of the conscious simulacrum. Thus, ‘representational accuracy’ is secondary to the adaptive guidance of a response.

In short, there are several independent accounts, based on different considerations, which propose that conscious representations should be of a perceptual-like nature, which is in complete accord with Gray (1995, 2004).

Returning to our three-term contingency, that which enters consciousness (the  $S_D$  and outcome) is not the kind of nervous event that is directly associated with efference generation; instead, it is the kind of event that resembles perceptual processing. Gray (1995, 2004) argues that which conscious awareness comprises what, in everyday life, we refer to as ‘perception.’ Regarding why this kind of processing can be associated with consciousness, whereas so many other kinds of processes cannot, Gray (2002) states, “I have no serious idea how such an ‘entry into consciousness’ actually occurs, but then neither does anyone else; this is the nub of the Hard Problem” (p. 5). Here Gray is referring to the Hard Problem of Consciousness: How does consciousness arise from physical, brain processes? It remains a mystery why this form of perception-related processing in the brain can bring with it ‘subjectivity.’ Explaining why this is so is one of the greatest puzzles in science, one that has been tackled by the some of the greatest

scientific minds, including Nobel Laureates Leon Cooper, Francis Crick, Gerald Edelman, Eric Kandel, and Charles Sherrington. At this stage of understanding, the field possesses not even an inkling regarding how physical events in the brain (or anywhere else) can give rise to a subjectivity of any kind (Godwin et al., in press) – as philosophers such as Karl Popper long ago noted, physical-objective systems are closed, neither needing nor able to accommodate the subjective material of the mind, especially the contents of the conscious mind that is so central to psychology. The type of approach epitomized by Gray's (2004), as well as other theorists noted above, of creeping up on this Hard Problem, may be starting to bear fruit as there does seem a convergence of theory and data, of which the mirror neuron work is one recent example, that can trace its origins back to, at least, the ideomotor theory of William James. More creeping will be needed, but our prey -- the understanding of the function and form of the conscious sensorium -- may well be within, albeit indistinct sight if not immediate grasp. This is especially the case regarding the outcome term of the three-term contingency, to which we now turn.

Although Behaviorism avoided mention of mentalistic variables, consciousness is inevitably stumbled upon when examining the three-term contingency. The outcome term, for example, is said to be a reinforcer if it increases the future likelihood of a behavior. This definition was criticized for being circular: That which renders something a reinforcer is that it increases the likelihood of a behavior. Then one asks, "Why does a reinforcer increase the likelihood of behavior?" The answer is, "Because it is a reinforcer." When one then asks, "Why is it a reinforcer?," the answer is, "Because it increases the likelihood of a behavior. As is clear, this line of reasoning is circular." It seems that there must be something else at play for something to be a reinforcer. In everyday life, one would argue that this extra something may be pleasure, joy, relief, or some other kind of positive feeling. It is this kind of mentalistic variable that may play a role in operant conditioning and even in decision making (Loewenstein, 1996). Consider, for example, Hull's (1943) 'law of least work' (or 'law of least effort') which states that, given two means to reach some end, an organism tends to select the means associated with the least effort/aversiveness (see recent treatments in Botvinick, 2007). In this case, the negative affect associated with effort (Morsella, Feinberg, Cigarchi, Newton, & Williams, 2011) is one of the variables in the calculation regarding which course of action to take, as Loewenstein (2007) states:

Humans have the capacity, perhaps uniquely, to deliberate about their own behavior and to make trade-offs between near-term and

long-term rewards. Such deliberations require consciousness, but consciousness is not enough. To make trade-offs between rewards at different points in time, there has to be *something* to trade off. The subjective sensations of affective states provide that thing; they allow us to make conscious trade-offs between, for example, the immediate pleasure of indulging in dessert and being thin, or between smoking a cigarette and enjoying better health. We may not make such trade-offs optimally, but were it not for the subjective feelings associated with affective states, we would have no basis for making them at all (p. 409).

As Loewenstein (2007) notes, it is undeniable aspect of conscious life that some states are preferred over others. The pleasure of drinking when thirsty is more positive than enduring pain. As quotidian as these examples are, they remains mysterious. Indeed, this is the very basis of the reinforcement-based theory of personality for which Gray is perhaps most famed (for the review of this literature, see Corr, 2008; Corr & McNaughton, 2012). But how can a physical system *prefer* some states over others? That is, how can something be an ‘affinity-based system,’ in which the system prefers, and strives to be in, some states over others. One may say that the northern pole of magnet A prefers to be adjacent to the southern pole of another magnet, but few would propose that magnet A ‘prefers’ subjectively such a situation. That some physical system, such as the nervous system, have inclinations of this kind remains outside of our current explanatory scope (Shallice, 1972). Chomsky (1988) adds that, unlike machines, which are compelled to act in one way or another, we humans can also be *inclined* to act in a certain way. It is this peculiar state of being inclined to act one way, but to not act overtly, that currently remains unexplained from a mechanistic point of view. Gray (2005; Gray, Williams, Nunn, & Baron-Cohen, 1997) astutely points out that, because of such undeniable mentalistic variables (positive and negative subjective states), a strict functionalistic account of nervous function in which understanding is based solely on the association between objective variables (e.g., neural activity and behavior) without invoking the physical processes underlying consciousness (e.g., Dennett, 1991) does not provide a complete picture of nervous function.

To make this argument, Gray (2005) entertains the phenomenon of synesthesia. In this phenomenon, sensory qualities from one modality (e.g., color) are experienced when perceiving stimuli from another modality (sound). For example, a synesthete may reliably experience the color red when hearing a high pitched sound or when seeing the letter A (Gray et al., 1997). In synesthesia, two people may experience different quale toward the same object, even though the

overt behavior of both people may be the same toward the object. For example, when perceiving an apple, John may have the experience of Rachel's *blue*, and Rachel may experience what John experiences as *red*. Yet, both Rachel and John refer to the apple as 'red.' According to Gray et al. (1997), this provides evidence against a strict interpretation of functionalism (e.g., Dennett, 1991) in which consciousness is directly tied to overt behavior.

Regarding the mystery of consciousness, one may argue that the real mystery is not such much the existence of an affinity-based system, but, rather, the subjectivity that is associated with the inclinations of such a system. From this standpoint, *subjectivity* is the unsolved puzzle regarding, not only inclinations, but all brain processing, including color perception, music perception, and other conscious states – the very states that make human life worthwhile. As mentioned in Footnote 1, an organism possesses subjectivity (or basic consciousness) if there is *something it is like* to be that organism. One may argue that the real puzzle is not how a physical thing could prefer to be in one state versus another but how such a preference could be experienced subjectively, which is part of a larger question: How could anything ever have a subjective experience of any kind?

Nevertheless, it seems that the three-term contingency—our best conceptual account explaining how favorable outcomes can increase the likelihood of a given  $R$  in the presence of a given  $S_D$ —requires mention of mentalistic states in order to explain everyday operant conditioning in humans. Why should there be any central states in operant conditioning when all that needs to occur for instrumental learning is for the connection between  $S_D$  and  $R$  to be strengthened?

### *Function of Central States and of Consciousness*

The case for central states was made long ago by Neal Miller (1959), who claimed that central states render the nervous system more efficient in terms of its many connectivities. This proposal is obvious in the following scenario. Imagine a simplified nervous system that only experiences two inclinations: to approach and to avoid. Now consider that, in the simplified environment of this organism, there are eight discriminative stimuli, four of which should be approached, such as food, and four of which should be avoided, such as noxious stimuli (Figure 2, top left). In addition to these eight discriminative stimuli, there are several different potential motor responses, some for approach and some for avoidance (Figure 2, top right). Miller reasoned

that it would be inefficient in terms of processing speed and wiring for there to be direct connections between all  $S_D$ s and all potential  $R$ s. Instead, Miller proposed that it would be more efficient for the inputs and outputs to be connected to a central state (Figure 2, bottom), one for the state of ‘approach’ and one for the state for ‘avoid.’ These two states obviously resemble positive and negative affect, respectively (Frijda, 1986). This would be even more true in an actual nervous system, in which there is a larger set of discriminative stimuli and potential responses. Which particular  $R$  is selected may depend on contextual details (e.g., a rat freezing, fleeing, or attacking, depending on the context).

Once the central states are established, then, depending on context, the appropriate action can be selected. In some contexts, an organism should freeze when under threat; in other circumstances, an organism should flee (Corr, 2011, 2013).

The view that central states may serve such a functional role in the nervous system, and that these states may involve consciousness, whose contents are often ‘projected’ on to an apparently external world (Merker, 2007). This is consistent with the aforementioned integration consensus about the function of consciousness. According to the consensus, conscious states integrate information processes that would otherwise be independent. The consensus is consistent with evidence from neurology, neuroscience, and psychology (see Chapter X in this volume) showing: (a) consciously mediated actions involve more information integration than unconsciously mediated actions; (b) conscious states involve a wider network of brain activations than unconscious states; and (c) conscious perceptual information processing involves the integrating, or ‘binding,’ of more kinds of information than unconscious perceptual processing (see review in Godwin et al., in press). The information involved in the conscious state is available to multiple systems, much as information broadcasted on television is available to many viewers who can act toward the information as they like, depending on their interests. In other words, the systems that have access to the information must evaluate the information and respond to it according to their ‘concerns’ (Frijda, 1986; Morsella, 2005). Sometimes, conscious content can cause systems to provide additional content (which can then, too, become conscious) or to generate action plans, which can influence behavior directly or indirectly, as in consciously experienced inclinations.

Interestingly, it has been proposed that the integration involving consciousness is intimately related to the skeletal muscle effector system (Morsella, 2005), which, by no accident,



has been called ‘voluntary’ muscle. Interestingly, this effector has been associated with operant conditioning more than any other effector system. (Many kinds of information in the nervous system can be integrated unconsciously.<sup>4</sup> It appears that the information which requires conscious integration is intimately related to skeletal muscle action, or ‘skeletomotor’ control; Morsella, J. R. Gray, Krieger, & Bargh, 2009a; Morsella et al., 2009c.)

With all this in mind, we will attempt to synthesize the various frameworks we discussed—Gray’s comparator model, ideomotor theory, the three-term contingency, Miller’s central states, and the integration consensus about conscious processing. In doing so, it is clear that these frameworks have much in common.

### *A New Synthesis*

It is a fairly straightforward process to integrate all frameworks into one overarching framework. Let us begin by revisiting the sequence of stages outlined in the comparator model. As mentioned above, in some ways, the sequence is the mirror image of that of ideomotor models. In this framework, the sequence is as follows. *Unconscious motor programs* (Stage 1) → *conscious action effects* (Stage 2), which are perceptual-like and can include both afference and re-afference → *comparator process* (Stage 3) → *entry into consciousness of, say, mismatching perceptual consequences or an error signal, as seen in the experience of pain* (Stage 4). We will present the sequence again, but combine it with the sequence of ideomotor models, such that the actor can willfully repeat an expressed action intentionally. This would occur, for example, if, while dancing or playing the drums, one exhibited a strange and unintentional move that led to a favorable outcome, an outcome that should be repeated. (The added elements of the sequence is presented in presented bold font.) In addition, we will add elements of the three-term contingency, specifically, the outcome variable. The resultant sequence is as follows.

Unconscious motor programs (Stage 1) → conscious action effects (Stage 2) → comparator process (Stage 3) → entry into consciousness of, say, positive affect (outcome) (Stage 4) → **activation of representation of conscious action effects (Stage 5)** → **unconscious motor programs (Stage 6)** → **conscious action effects (Stage 7)** → **comparator process (Stage 8)** → **entry into consciousness of, say, positive affect (outcome) from repeating**

**action successfully (Stage 9).**

There are several features in the model that are worthy of some reflection. First, it is no accident that Stages 2, 4, 5, 7, and 9—stages in which information must be evaluated by diverse systems in the brain—involve consciousness, which is consistent with the integration consensus. Second, the conscious states of these stages resemble the central states to which Miller (1959) alluded, especially the outcome variables (e.g., positive or negative affect). Third, consistent with Morsella (2005), the action-related conscious states in stages 5 through 9 influence behavior only through skeletal muscle. Fourth, one can appreciate that efference generation is unconscious and that the actor only has conscious access to the representations of action effects, which are perceptual-like (Gray, 2004) and are experienced after action production (as in the comparator model) and can be experienced before action production (as in ideomotor control).

Regarding the limited information to which the actor has access, James (1890) proposes that, in behavioral control, all *the will* can do is pay attention to the representation of one action effect versus another. It is by this allotment of attention that the actor can, through ideomotor mechanisms, influence behavior intentionally: Activation (through attention) to the representation of a given action effect will lead to the expression of that action, through unconscious motor control. This, of course, fails to occur if there is simultaneously the activation of a representation of an incompatible action effect (James, 1890; Lotze, 1852). In this way, *behavioral control* is only through *mental control*, involving perceptual-like representations (Gray, 1995). As a pleasing by-product of this analysis, our model assigns a causal role to attention: viz., to recruit processing resources towards salient areas of the phenomenal field and by so doing appropriate affording automatic actions. It is perhaps no surprise that we ‘pay attention’ to what we consider to be important.

*Conclusion*

In this chapter, we revisited Gray’s (1995) pioneering comparator model of consciousness, which focuses on the control of behavior and the contents of consciousness. We then combined this model with that of ideomotor theory, which complements the comparator model in several respects. For instance, it explains how the architecture of something like the comparator model could illuminate the mechanisms underlying the intentional control of behavior. We also revisited

the integration consensus and approaches in operant conditioning, which explain the function of consciousness and how outcomes can influence future behaviors, respectively. Both the comparator model and ideomotor theory posit that it is perceptual-like content that is conscious. The integration consensus explains why this is so: It is because this is the content that is the most communicable, the most capable of being detected and processed by multiple systems (Bargh & Morsella, 2010; Fodor, 1983).

What no account to date has been able to explain is why subjectivity must be part of this process. At this stage of understanding, we propose that more knowledge about the limitations of the hardware of the nervous function may reveal why something as strange as consciousness was selected in evolution to perform an integrative, albeit circumscribed, role. From this viewpoint, just as intrapsychic conflict is not something that an engineer would ever program into a von Neumann computer, but, in the course of evolution, natural selection may have selected it as a solution for biological systems having slow processing units (i.e., neurons; Livnat & Pippenger, 2006), perhaps, given the constraints and limits of biological function, consciousness is actually a clever solution challenges faced by the nervous system.

## References

- Anderson, A. K., & Phelps, E. A. (2002). Is the human amygdala critical for the subjective experience of emotion? Evidence of intact dispositional affect in patients with amygdala lesions. *Journal of Cognitive Neuroscience*, *14*, 709–720.
- Baars, B. J. (1988). *A cognitive theory of consciousness*. Cambridge, England: Cambridge University Press.
- Baars, B. J. (2002). The conscious access hypothesis: Origins and recent evidence. *Trends in Cognitive Sciences*, *6*, 47–52.
- Baddeley, A. D. (2007). *Working memory, thought, and action*. Oxford, UK: Oxford University Press.
- Bargh, J. A., & Morsella, E. (2010). Unconscious behavioral guidance systems. In Agnew, C. R., Carlston, D. E., Graziano, W. G., & Kelly, J. R. (Eds.), *Then a miracle occurs: Focusing on behavior in social psychological theory and research* (pp. 89–118). New York: Oxford University Press.
- Berti, A., & Pia, L. (2006). Understanding motor awareness through normal and pathological behavior. *Current Directions in Psychological Science*, *15*, 245–250.
- Block, N. (1995). On a confusion about a function of consciousness. *Behavioral and Brain Sciences*, *18*, 227–287.
- Boly, M., Garrido, M. I., Gosseries, O., Bruno, M-A., Boveroux, P., Schnakers, C., Massimini, M., Litvak, V., Laureys, S., Friston, K. (2011). Preserved feedforward but impaired top-down processes in the vegetative state. *Science*, *332*, 858–862.
- Botvinick, M. (2007). Conflict monitoring and decision making: Reconciling two perspectives on anterior cingulate function. *Cognitive, Affective and Behavioral Neuroscience*, *7*,

356–366.

Chambon, V., Wenke, D., Fleming, S. M., Prinz, W., & Haggard, P. (in press). An online neural substrate for sense of agency. *Cerebral Cortex*.

Chomsky, N. (1988). *Language and problems of knowledge: The Managua lectures*. Cambridge, MA: MIT Press.

Christensen, M. S., Lundbye-Jensen, J., Geertsen, S. S., Petersen, T. H., Paulson, O. B., & Nielsen, J. B. (2007). Premotor cortex modulates somatosensory cortex during voluntary movements without proprioceptive feedback. *Nature Neuroscience*, *10*, 417-419

Clark, A. (2002). Is seeing all it seems? Action, reason and the grand illusion. *Journal of Consciousness Studies*, *9*, 181–202.

Corr, P. J. (2008). Reinforcement sensitivity theory (RST): Introduction. In P. J. Corr (ed), *The reinforcement sensitivity theory of personality* (pp.1-43). Cambridge: Cambridge University Press.

Corr, P. J. (2011). Anxiety: Splitting the phenomenological atom. *Personality and Individual Differences* (Special Issue: Anxiety), *50*, 889-897.

Corr, P. J. (2013). Approach and avoidance behavior: Multiple systems and their interactions. *Emotion Review*, in press.

Corr, P. J., & McNaughton, N. (2012). Neuroscience and approach/avoidance personality traits: A two stage (valuation–motivation) approach. *Neuroscience and Biobehavioral Reviews*, *36*, 2339–2354.

Crick, F. (1995). *The astonishing hypothesis: The scientific search for the soul*. New York: Touchstone.

Damasio, A. R. (1989). Time-locked multiregional retroactivation: A systems-level proposal for

- the neural substrates of recall and recognition. *Cognition*, 33, 25–62.
- Dehaene, S., & Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: Basic evidence and a workspace framework. *Cognition*, 79, 1–37.
- Del Cul, A., Baillet, S., & Dehaene, S. (2007). Brain dynamics underlying the nonlinear threshold for access to consciousness. *PLoS Biology*, 5, e260.
- Dennett, D. C. (1991). *Consciousness explained*. Boston: Little, Brown.
- Desmurget, M., Reilly, K. T., Richard, N., Szathmari, A., Mottolese, C., & Sirigu, A. (2009). Movement intention after parietal cortex stimulation in humans. *Science*, May 8th, 324 (5928), 811–813.
- Desmurget, M., & Sirigu, A. (2010). A parietal-premotor network for movement intention and motor awareness. *Trends in cognitive sciences*, 13, 411-419.
- Doesburg, S. M., Green, J. L., McDonald, J. J., & Ward, L. M. (2009). Rhythms of consciousness: Binocular rivalry reveals large-scale oscillatory network dynamics mediating visual perception. *PLoS*, 4, 1–14.
- Fecteau, J. H., Chua, R., Franks, I., & Enns, J. T. (2001). Visual awareness and the online modification of action. *Canadian Journal of Experimental Psychology*, 55, 104-110.
- Fodor, J. A. (1983). *Modularity of mind: An essay on faculty psychology*. Cambridge, MA: MIT press.
- Freeman, W. J. (1991). The physiology of perception. *Scientific American*, 264, 78 – 85.
- Fried, I., Katz, A., McCarthy, G., Sass, K. J., Williamson, P., Spencer, S. S., & Spencer, D. D. (1991). Functional organization of human supplementary motor cortex studied by electrical stimulation. *Journal of Neuroscience*, 11, 3656–3666.
- Frijda, N. H. (1986). *The emotions*. Cambridge, England: Cambridge University Press.

- Fuster, J. M. (2003). *Cortex and mind: Unifying cognition*. New York: Oxford University Press.
- Godwin, C. A., Gazzaley, A., & Morsella, E. (in press). Homing in on the brain mechanisms linked to consciousness: Buffer of the perception-and-action interface. In A. Pereira and D. Lehmann's (Eds.), *The unity of mind, brain and world: Current perspectives on a science of consciousness*. Cambridge, UK: Cambridge University Press.
- Goodale, M., & Milner, D. (2004). *Sight unseen: An exploration of conscious and unconscious vision*. New York: Oxford University Press.
- Goodhew, S. C., Dux, P. E., Lipp, O. V., & Visser, T. A. W. (2012). Understanding recovery from object substitution masking. *Cognition*, 122, 405-415.
- Gray, J. A. (1982a). *The neuropsychology of anxiety: An enquiry into the functions of the septo-hippocampal system, first edition*. Oxford, UK: Oxford University Press.
- Gray, J. A. (1982b). Précis of 'The neuropsychology of anxiety: an enquiry into the functions of the septo-hippocampal system'. *Behavioral and Brain Sciences*, 5, 469-484.
- Gray, J. A. (1995). The contents of consciousness: A neuropsychological conjecture. *Behavioral and Brain Sciences*, 18, 659-676.
- Gray, J. A. (1998). Integrating schizophrenia. *Schizophrenia Bulletin*, 24, 249-266.
- Gray, J. A. (2002). The sound of one hand clapping. *Psyche*, 8.  
<http://psyche.cs.monash.edu.au/v8/psyche-8-11-gray.html>
- Gray, J. A. (2004). *Consciousness: Creeping up on the hard problem*. New York: Oxford University Press.
- Gray, J. A. (2005). Synesthesia: A window on the hard problem of consciousness. In L. C. Robertson & N. Sagiv (Eds.), *Synesthesia: Perspectives from cognitive neuroscience*. New York: Oxford University Press.

- Gray, J. A., & McNaughton, N. (2000). *The neuropsychology of anxiety: An enquiry into the functions of the septo-hippocampal system, second edition*. Oxford, UK: Oxford University Press.
- Gray, J. A., Feldon, J., Rawlins, J. N. P., Hemsley, D. R., & Smith, A. D. (1991). The neuropsychology of schizophrenia. *Behavioral and Brain Sciences*, *14*, 1-20.
- Gray, J. A., Williams, S. C. R., Nunn, J., & Baron-Cohen, S. (1997). Possible implications of synaesthesia for the hard question of consciousness. In S. Baron-Cohen & J. E. Harrison (Eds.), *Synaesthesia: Classic and contemporary readings*. Oxford, UK: Blackwell.
- Graziano, M. S. A. (2001). Awareness of space. *Nature*, *411*, 903-904.
- Greenwald, A. G. (1970). Sensory feedback mechanisms in performance control: With special reference to the ideomotor mechanism. *Psychological Review*, *77*, 73–99.
- Grossberg, S. (1999). The link between brain learning, attention, and consciousness. *Consciousness and Cognition*, *8*, 1–44.
- Harleß, E. (1861). Der apparat des willens [The apparatus of the will]. *Zeitschrift für Philosophie und philosophische Kritik*, *38*, 499 – 507.
- Heath, M., Neely, K. A., Yakimishyn, J., & Binsted, G. (2008). Visuomotor memory is independent of conscious awareness of target features. *Experimental Brain Research*, *188*, 517-527.
- Heilman, K. M., Watson, R. T., & Valenstein, E. (2003). Neglect: Clinical and anatomic issues. In T. E. Feinberg & M. J. Farah (Eds.), *Behavioral neurology and neuropsychology, second edition* (pp. 303 – 311). New York: The McGraw-Hill Companies.
- Hesslow, G. (2002). Conscious thought as simulation of behavior and perception. *Trends in Cognitive Sciences*, *6*, 242–247.



- Hommel, B. (1998). Perceiving one's own actions—and what it leads to. In J. S. Jordan (Ed.), *Systems theories and a priori aspects of perception* (pp. 143-179). Amsterdam: North-Holland/ Elsevier.
- Hommel, B. (2009). Action control according to TEC (theory of event coding). *Psychological Research, 73*, 512-526.
- Hommel, B., & Elsner, B. (2009). Acquisition, representation, and control of action. In E. Morsella, J. A. Bargh, & P. M. Gollwitzer (eds.), *Oxford handbook of human action* (pp. 371 – 398). New York: Oxford University Press.
- Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding: A framework for perception and action planning. *Behavioral and Brain Sciences, 24*, 849–937.
- Hull, C. L. (1943). *Principles of behavior*. New York: Appleton-Century.
- Iacoboni, M. (2005). Understanding others: Imitation, language and empathy. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From mirror neurons to memes*. Cambridge, MA: MIT Press, pp 77-99.
- James, W. (1890). *The principles of psychology*. New York: Dover.
- Jackendoff, R. (1987). *Consciousness and the computational mind*. Cambridge, MA: MIT Press.
- Jeannerod, M. (2006). *Motor cognition: What action tells the self*. New York: Oxford University Press.
- Johnson, K. L., & Shiffrar, M. (2013). *People watching: Social, perceptual, and neurophysiological studies of body perception*. New York: Oxford University Press.
- Jordan, J. S. (2009). Forward-looking aspects of perception-action coupling as a basis for embodied communication. *Discourse Processes, 46*, 127-144.

- Klein, D. B. (1970). *A history of scientific psychology: Its origins and philosophical backgrounds*. New York: Basic Books.
- Koch, C. (2004). *The quest for consciousness: A neurobiological approach*. Englewood, CO: Roberts and Company Publishers.
- Koffka, K. (1922). Perception: and introduction to the Gestalt-theories. *Psychological Bulletin*, 19, 531–585.
- Lashley, K. S. (1942). The problem of cerebral organization in vision. In H. Kluver (Ed.), *Visual mechanisms. Biological symposia*, 7 (pp. 301–322). Lancaster, PA: Cattell Press.
- LeDoux, J. E. (1996). *The emotional brain: The mysterious underpinnings of emotional life*. New York: Simon and Schuster.
- LeDoux, J. E. (2008). Emotional colouration of consciousness: How feelings come about. In Weiskrantz LW, Davies M (eds), *Frontiers of consciousness*. Oxford, UK: Oxford University Press, pp 69-130.
- Levelt, W. J. M. (1989). *Speaking: From intention to articulation*. Cambridge, MA: The MIT Press.
- Libet, B. (2004). *Mind time: The temporal factor in consciousness*. Cambridge, MA: Harvard University Press.
- Liu, G., Chua, R., & Enns, J. T. (2008). Attention for perception and action: Task interference for action planning, but not for online control. *Experimental Brain Research*, 185, 709 – 717.
- Livnat, A. & Pippenger, N. (2006). An optimal brain can be composed of conflicting agents. *Proceeding of the National Academy of Sciences, USA*, 103, 3198–3202.
- Llinás, R. R., & Ribary, U. (2001). Consciousness and the brain: The thalamocortical dialogue in health and disease. *Annals of the New York Academy of Sciences*, 929, 166–175.

- Loewenstein, G. (1996). Out of control: visceral influences on behavior. *Organizational Behavior and Human Decision Processes*, 65, 272-292.
- Loewenstein, G. (2007). Defining affect. *Social Science Information*, 46, 405-410.
- Lotze, R. H. (1852). *Medizinische Psychologie oder Physiologie der Seele*. Leipzig: Weidmann'sche Buchhandlung.
- Merker, B. (2007). Consciousness without a cerebral cortex: A challenge for neuroscience and medicine. *Behavioral and Brain Sciences*, 30, 63-134.
- McGurk, H., & MacDonald, J. (1976). Hearing lips and seeing voices. *Nature*, 264, 746-748.
- Merker, B. (2007). Consciousness without a cerebral cortex: A challenge for neuroscience and medicine. *Behavioral and Brain Sciences*, 30, 63-134.
- Miall, R. C. (2003). Connecting mirror neuron and forward models. *Neuroreport*, 14, 1-3.
- Miller, N. E. (1959). Liberalization of basic S-R concepts: Extensions to conflict behavior, motivation, and social learning. In S. Koch (Ed.), *Psychology: A study of science, Study 1, Vol 2* (pp. 196-292). New York: McGraw-Hill.
- Miller, G. A., Galanter, E., & Pribram, K. H. (1960). *Plans and the structure of behavior*. New York: Henry Holt & Co.
- Moore, J. W., Wegner, D. M., & Haggard, P. (2009). Modulating the sense of agency with external cues. *Consciousness and Cognition*, 18, 1056-1064.
- Morsella, E. (2005). The function of phenomenal states: Supramodular interaction theory. *Psychological Review*, 112, 1000-1021.
- Morsella, E., & Bargh, J. A. (2010). What is an output? *Psychological Inquiry*, 21, 354-370.
- Morsella, E., Feinberg, G. H., Cigarchi, S., Newton, J. W., & Williams, L. E. (2011). Sources of avoidance motivation: Valence effects from physical effort and mental rotation.

- Motivation and Emotion, 35, 296–305.
- Morsella, E., Gray, J. R., Krieger, S. C., & Bargh, J. A. (2009a). The essence of conscious conflict: Subjective effects of sustaining incompatible intentions. *Emotion, 9*, 717–728.
- Morsella, E., Lanska, M., Berger, C. C., & Gazzaley, A. (2009b). Indirect cognitive control through top-down activation of perceptual symbols. *European Journal of Social Psychology, 39*, 1173-1177.
- Morsella, E., Montemayor, C., Hubbard, J., & Zarolia, P. (2010). Conceptual knowledge: Grounded in sensorimotor states, or a disembodied deus ex machina? *Behavioral and Brain Sciences, 33*, 455-456.
- Morsella, E., Wilson, L. E., Berger, C. C., Honhongva, M., Gazzaley, A., & Bargh, J. A. (2009c). Subjective aspects of cognitive control at different stages of processing. *Attention, Perception, & Psychophysics, 71*, 1807 – 1824.
- Most, S. B., Scholl, B. J., Clifford, E., & Simons, D. J. (2005). What you see is what you set: Sustained inattentive blindness and the capture of awareness. *Psychological Review, 112*, 217-242.
- Müller, J. (1843). *Elements of physiology*. Philadelphia: Lea and Blanchard.
- Nagel, T. (1974). What is it like to be a bat? *Philosophical Review, 83*, 435–450.
- Neisser, U. (1967). *Cognitive psychology*. New York: Apple-Century-Crofts.
- Obhi, S., Planetta, P., & Scantlebury, J. (2009). On the signals underlying conscious awareness of action. *Cognition, 110*, 65–73.
- Öhman, A., Carlsson, K., Lundqvist, D., & Ingvar, M. (2007). On the unconscious subcortical origin of human fear. *Physiology & Behavior, 92*, 180–185.
- Ortinski, P., & Meador, K. J. (2004). Neuronal mechanisms of conscious awareness. *Archives of*

- Neurology*, 61, 1017–1020.
- Pinker, S. (1997). *How the mind works*. New York: W. W. Norton & Co.
- Rizzolatti, G., Sinigaglia, C., & Anderson, F. (2008). *Mirrors in the brain: How our minds share actions, emotions, and experience*. New York: Oxford University Press.
- Rosenbaum, D. A. (2002). Motor control. In H. Pashler (Series Ed.) & S. Yantis (Vol. Ed.), *Stevens' handbook of experimental psychology: Vol. 1. Sensation and perception* (3rd ed., pp. 315–339). New York: Wiley.
- Rossetti, Y. (2001). Implicit perception in action: Short-lived motor representation of space. In P. G. Grossenbacher (Ed.), *Finding consciousness in the brain: A neurocognitive approach* (pp. 133–181). Netherlands: John Benjamins Publishing.
- Sergent, C., & Dohaene, S. (2004). Is consciousness a gradual phenomenon? Evidence for an all-or-none bifurcation during the attentional blink. *Psychological Science*, 15, 720–728.
- Shallice, T. (1972). Dual functions of consciousness. *Psychological Review*, 79, 383–393.
- Sheerer, E. (1984). Motor theories of cognitive structure: A historical review. In W. Prinz & A. F. Sanders (Eds.), *Cognition and motor processes*. Berlin: Springer-Verlag.
- Sherrington, C. S. (1906). *The integrative action of the nervous system*. New Haven, CT: Yale University Press.
- Skinner, B. F. (1953). *Science and human behavior*. New York: Macmillan.
- Slevc, L. R., & Ferreira, V. S. (2006). Halting in single word production: A test of the perceptual loop theory of speech monitoring. *Journal of Memory and Language*, 54, 515–540.
- Suhler, C. L., & Churchland, P. S. (2009). Control: Conscious and otherwise. *Trends in Cognitive Sciences*, 13, 341–347.
- Tononi, G., & Edelman, G. M. (1988). Consciousness and complexity. *Science*, 282, 1846–1851.

- Tye, M. (1999). Phenomenal consciousness: The explanatory gap as cognitive illusion. *Mind*, *108*, 705-725.
- Ulhaas, P. J., Pipa, G., Lima, B., Melloni, L., Neuenschwander, S., Nikolic, D., & Singer, W. (2009). Neural synchrony in cortical networks: History, concept and current status. *Frontiers in Integrative Neuroscience*, *3*, 17.
- Varela, F., Lachaux, J. P., Rodriguez, E., & Martinerie, J. (2001). The brainweb: Phase synchronization and large-scale integration. *National Review of Neuroscience*, *2*, 229–239.
- Velmans, M. (1991). Is human information processing conscious? *Behavioral and Brain Sciences*, *14*, 651-669.
- Velmans, M. (2000). *Understanding consciousness*. London: Routledge.
- Vroomen, J., & de Gelder, B. (2003). Visual motion influences the contingent auditory motion aftereffect. *Psychological Science*, *14*, 357-361.
- Yates, J. (1985). The content of awareness is a model of the world. *Psychological Review*, *92*, 249–284.
- Zeki, S., & Bartels, A. (1999). Toward a theory of visual consciousness. *Consciousness and Cognition*, *8*, 225–259.

### Figure Captions

*Figure 1.* Conscious and unconscious aspects of Skinner's three-term contingency.

*Figure 2.* Schematic of Neal Miller's theorizing that direct connections between discriminative stimuli and responses (top) yield a framework that is less efficient than one invoking central states (bottom).

Figure 1

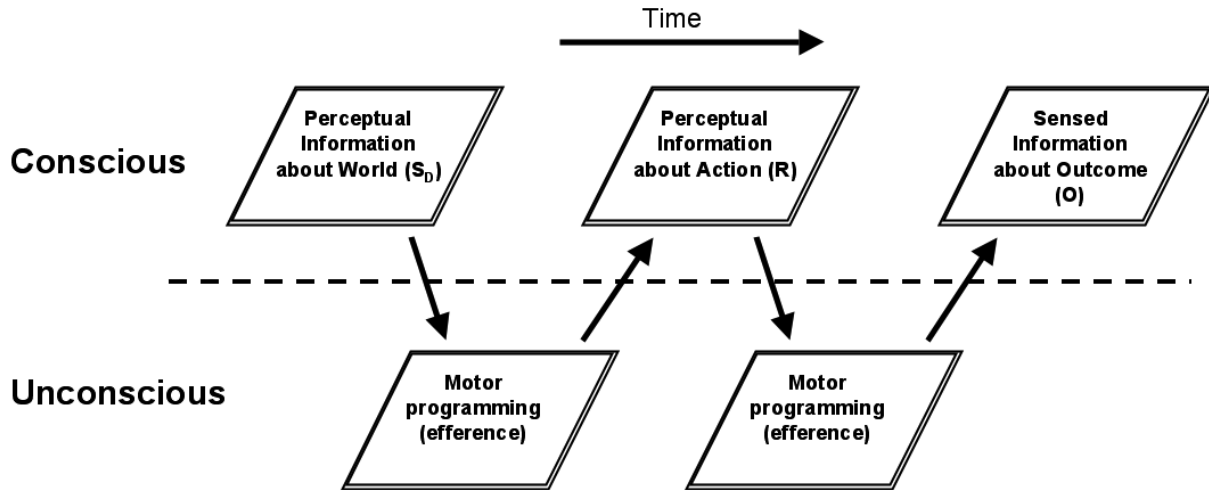
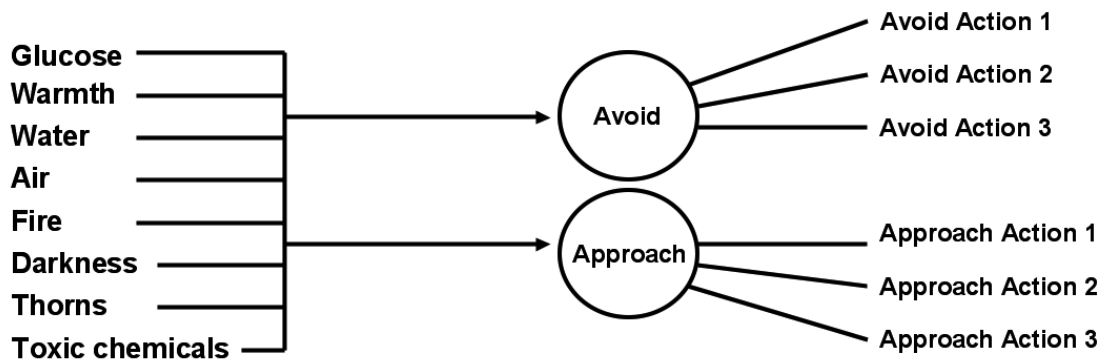
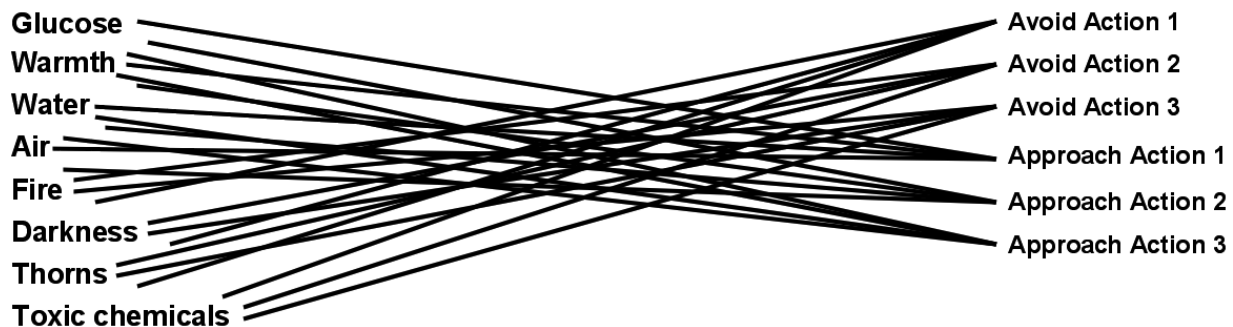




Figure 2



### Footnotes

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<sup>1</sup> Here we are speaking of the most basic kind of consciousness. This kind of consciousness, also referred to as ‘sentience’ (Pinker, 1997), ‘phenomenal state’ (Tye, 1999), ‘qualia’ (Gray, 2004), and subjective experience, has perhaps been best defined by the philosopher Thomas Nagel (1974), who proposed that an organism possesses subjective experiences if there is *something it is like* to be that organism—something it is like, for example, to be human and experience pain, love, or breathlessness. Similarly, Block (1995) claimed, “the phenomenally conscious aspect of a state is what it is like to be in that state” (p. 227).

<sup>2</sup> Why one choice of action over another is selected in the future remains mysterious. It seems that, regardless of mentalistic or decision-making dynamics, past behavior is still the most reliable predictor of future behavior. Speaking of decision-making approaches following the cognitive revolution, Loewenstein (1996) concludes, “Another area in which the decision making perspective falls short is its treatment of motivation and effort. In the decision paradigm there is no qualitative distinction between choosing, say one car over another, or ‘deciding’ to pick up one’s pace in the last mile of a marathon; both are simply decisions. Years after the decline of behaviorism, behaviorists still offer the most coherent theoretical perspective on motivation and the most sophisticated and comprehensive program of research” (p. 287).

<sup>3</sup> Sherrington (1906) aptly referred to these two, similar kinds of information as *exafference*, when the source of information stems from the external world, and *reafference*, when the source is feedback from overt actions. There is also similar feedback from the activation of internal, action plans (e.g., information arising from ‘corollary discharges’ or ‘efference copies’ of our own action plans; Chambon, Wenke, Fleming, Prinz, & Haggard, in press; Christensen et al., 2007; Jordan, 2009; Miall, 2003; Obhi, Planetta, & Scantlebury, 2009).

<sup>4</sup> Unconscious integrations can involve smooth muscle, such as in the papillary reflex (see evidence in Morsella et al., 2009a), and intersensory processing. For example, the McGurk effect involves unconscious interactions between visual and auditory processes: An observer views a speaker mouthing “ba” while presented with the sound “ga.” Surprisingly, the observer is unaware of any intersensory interaction, perceiving only “da.” Similar consciously impenetrable

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interactions are exemplified in countless other intersensory phenomena (see Morsella, 2005, Appendix A), including the popular ventriloquism effect, in which visual and auditory inputs regarding the source of a sound interact unconsciously (cf., Vroomen & de Gelder, 2003).