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Evaluating Theories of Consciousness Using the
Autonomic Nervous System for Comparison

by

Thomas Daniel Ryder

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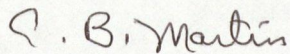
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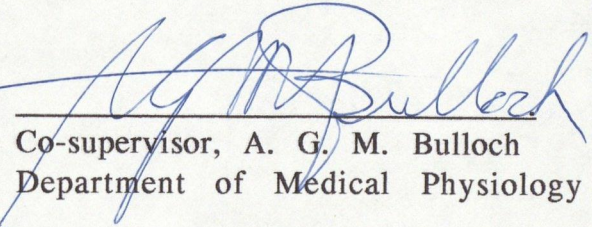
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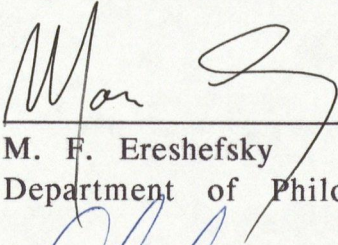
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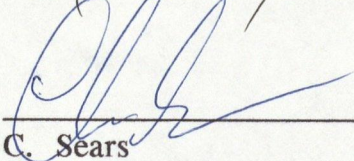
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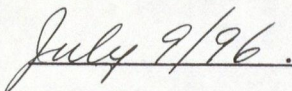Co-supervisor, A. G. M. Bulloch
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Abstract

A common strategy in studying conscious states is to compare them with non-conscious states. The thesis extends C. B. Martin's novel instance of this strategy, using the autonomic nervous system (ANS) as the non-conscious partner in the juxtaposition. It is argued that the ANS has the capacity to represent stimulus qualities in a spatial context, to misrepresent, to learn, and to engage in true goal-directed behaviour. Any theory which defines a conscious system as one uniquely possessing these characteristics is therefore inadequate. Evidence is also provided that the ANS exhibits functionally relevant synchrony achieved through oscillatory mechanisms, has an analogue to attentional processes, and may generate signals internally which are for primarily internal use. It is concluded that the ANS comparison strategy is a valuable tool for evaluating theories of consciousness, and that further studies may intimate the demise of functionalism.

Acknowledgements

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CHAPTER 1
Introduction

1.1   General strategy

It is a common procedure in studies of consciousness to compare conscious with non-conscious states (see especially Baars 1988), for any property or process present in the former but not the latter is potentially necessary for consciousness. This strategy has a venerable history, beginning with William James in 1890. More recently, the anaesthetized brain (Penrose 1995), the sleeping, non-dreaming brain (Llinás and Paré 1991), and so-called "pre-conscious" processes and implicit memory (Baars 1988) have all occupied the non-conscious space in the juxtaposition, but there is one conspicuous pairing which has been entirely ignored - that with the autonomic nervous system (ANS). That situation has recently been rectified by C. B. Martin (unpublished 1991; ms), and it is my intention to illustrate, explain, and extend his project by using his comparison to evaluate particular philosophical and neuroscientific theories of consciousness.

The neglect of this particular strategy is likely due to a history of prejudice against the ANS, such that comparing it with a conscious system would seem equivalent to comparing an apple, not with an orange, but with an ecosystem. Traditionally, the ANS has been regarded as a set of relatively simple reflex mechanisms based upon the antagonistic sympathetic and parasympathetic divisions. It is becoming increasingly obvious, however, that this conception is

naïve. At its most sophisticated, autonomic function involves complex central integration of a large quantity of peripheral and central input, followed by output involving a large array of effector mechanisms. The complexity of this coordination rivals that found in conscious, voluntary systems, as the following neuroscientists attest:

> There is a growing appreciation that many of the older ideas concerning the structure and control of the autonomic nervous sytem are either wrong, or relevant to only conditions of life or death. We now realize that the autonomic nervous system is active on a continual basis to give second by second control thoughout normal life. This is brought about through a complexity of control mechanisms that parallels that of the somatic motor system. (Sharkey and Pittman 1996.)

Sir Roger Bannister and C. J. Mathias (1992, p.1) agree that the ANS "has as complex a neural organization in the brain, spinal cord, and periphery as the somatic nervous system." Autonomic control is thus a worthy component of the comparison.[1]

1.2   Phenomenal consciousness

It is often said that "consciousness" is a mongrel concept (Wilkes 1984; Lycan 1987 (preface); Allport 1988; Güzeldere 1995). It is thus necessary for anyone who purports to shed light on consciousness to explain what is meant by the term. Ned Block, in a very recent but already widely influential article (1995), has differentiated between two meanings of "consciousness." He calls the first "access consciousness" (AC), and the second "phenomenal

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[1] Please refer to the Glossary (Appendix B) for definitions of unfamiliar terms, both philosophical and neuroscientific.

consciousness" (PC). While I think that Block has put his finger on an important distinction, I have some difficulties with his characterization of it. Consequently, I will attempt to give my own account of the difference.

The type of consciousness that I mean is something like Block's PC. Its characterizing feature is the referent of the philosophical term "qualia." Qualia are the "raw feels" of experience, the sensations which form a part of perception, and the sensation-like components of imagery in all modalities. They are what you get when you abstract away all of the conceptual content of one's experience, as Thomas Reid tried to do in his *Inquiry into the Human Mind on the Principles of Common Sense* (1764/1983). This is quite easy to accomplish in the case of pain, says Reid, where the sensation itself is attended to independently of a concept of its cause, but for the submodality of touch, the abstraction becomes more difficult. When a man strikes his head against a pillar (p. 38),

> [t]he attention of the mind is here entirely turned towards the painful feeling; and, to speak in the common language of mankind, he feels nothing in the stone, but feels a violent pain in his head. It is quite otherwise when he leans his head gently against the pillar; for then he will tell you that he feels nothing in his head, but feels hardness in the stone. Hath he not a sensation in this case as well as in the other? Undoubtedly he hath; but it is a sensation which nature intended only as a sign of something in the stone; and, accordingly, he instantly fixes his attention upon the thing signified; and cannot, without great difficulty, attend so much to the sensation as to be persuaded that there is any such thing distinct from the hardness it signifies.

The sensation is there nevertheless, and it is not the same as the concept of hardness or resistance to pressure.

All of the modalities of sensation are qualitative. Other examples of qualia are the redness occupying a portion of the visual field when looking at an apple (or experiencing the afterimage of a blue billiard ball), the olfactory sensation caused by hot buttered toast, or the auditory sensation brought about by rolling waves. The concept of PC is the concept of a state possessing qualia as constituents or as properties. Qualia characterize both wakefulness (in perception and imagery) and dreaming, so the latter is considered a conscious state on this definition.

1.3 Other concepts of consciousness

1.3.1 Voluntarity and the Common-Sense explanation of PC

The concept of PC differs from a number of other concepts, which are linked to Block's AC. First, PC differs from the concept of voluntarity. To perform an act involuntarily is not necessarily to perform it without PC. The typical example is driving a car - one might be performing this act in a series of automatic responses to sensory input, but it is counter-intuitive to suggest that these sensory inputs are not phenomenal, that they have no raw feels. Typically one can recall sensations from a few seconds before, if a passenger asks, for instance, "Wasn't that light back there red?" Another example is when the doctor tests one's reflexes. One feels the entire motion that ensues, but it is certainly not voluntary.

There is an even simpler way to draw the distinction, however. Voluntarity refers to behaviour, whereas PC refers to something on the perceptual side. One can have a pain, a paradigm quale, with no co-occurrent action, voluntary or otherwise. This does suggest an *explanation* of our possession of PC, however. The identification of PC with a *disposition* to act voluntarily is an interesting position, which I will examine in Chapter 4. But the two concepts - "disposition for voluntary action" and "phenomenality" - certainly differ, whether or not it turns out that they pick out the same thing in the world.

So what I am attempting to evaluate using the autonomic comparison strategy are *explanations* of PC. Thomas Reid accepted a "folk-psychological" explanation of PC and qualia, or what I will call the "common sense explanation" (after the school of philosophy to which Reid belonged.) The common sense explanation of PC is that qualia are the intrinsic qualities of subpersonal states - they are not relational properties, and not dispositions (whether intrinsic or not.)[2] So dispositions for voluntary action are an alternative explanation of PC to the common-sense explanation. I will go on to explain some other differences between concepts of consciousness, and along the way point out those which suggest candidates for alternatives to the common-sense explanation of PC.

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[2] I would favour the somewhat controversial view that this "common sense explanation" is also an analysis of the concept of PC, but this claim is not crucial to my project. My general aim is concerned with explanation, not conceptual analysis, so I adopt the minimalist conception of qualia as phenomenal individuals (see section 1.3.2).

1.3.2 Concepts related to "subjectivity"

PC does not imply a capacity for complex thought. Many organisms (e.g. human infants) are unable to perform abstract logical operations or even simple generalizations; this does not mean that they are phenomenally non-conscious. Neither does this seem to lead to a plausible explanation of PC, since it seems that PC is present even in the absence of *dispositions* for complex thought. Similarly, self-awareness is not necessary for PC. Possessing the capacity to represent oneself as such is a sophisticated ability, which goes far beyond an organism's capacity for PC.

Related to this is the idea that consciousness implies a point of view, or that the mental is necessarily subjective. Often qualia are explained as "what it is like *for* the organism" to have a particular experience (Nagel 1974; Searle 1992). I think that this is at best a rather unfortunate way of putting it, and at worst just mistaken, if intended as a synonym for PC.

The terms "subjective" and "what it is like *for*" suggest that when one is introspecting, qualia are presented in some Cartesian Theatre for the benefit of some observer, the "self." Independently of the truth or falsity of the position, the concept of PC is different from the concept of subjectivity. The concept of qualia as originally conceived (e.g. Lewis 1929) is of phenomenal individuals *simpliciter*[3], explained in common sense by the attribution of

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[3] Phenomenal individuals are normally taken to be anti-materialist, but I think it makes more sense to regard them as topic-neutral. This allows, for example, Sellars's (1971) solution to the "grain problem" (see section 1.3.4) by countenancing *physical* phenomenal individuals called "sensa."

intrinsic qualities to some subpersonal state, qualities which are relevant to the identity of the mental state. The concept of PC carries no implication of the *presentation* of the relevant qualities in the Cartesian Theatre.

The Cartesian Theatre might be part of "folk psychology", but it is *not* an element of the common-sense explanation of PC, even going back to Reid. Reid is at pains to demonstrate that though we may conceive of objects *via* imagery and perception, images and percepts (and thus the qualia that compose them) are not *objects* of thought, as in the Cartesian theatre. "Thus [when] *I feel a pain...* the distinction between the act and the object is not real but grammatical" (Reid 1764/1983 p. 42).

But does the Cartesian theatre offer a plausible alternative explanation of PC? Daniel Dennett (1991) argues vehemently against this, and most theorists have at least accepted that part of his conclusion. It is simply not the case that there is some place in the brain, at the end of the hierarchy, where "it all comes together," (Dennett 1991, p. 107.) In fact, evidence is mounting that even the term "hierarchy" is misapplied to the brain, because so-called "early processes" and "late processes" act in parallel, with significant interactions between the two (Churchland et al. 1994; Bullier and Nowak 1995). So it seems that the Cartesian Theatre is not a neurophysiologically plausible alternative to explain PC, at least until some progress is made towards naturalizing "the self." And it seems likely that this further project will yield a result inconsistent with the Cartesian Theatre.

There is a related theory that is worth consideration, however. It is possible that being conscious consists in having a "higher-order thought" (HOT) about some sensation or image.[4] This HOT is not itself conscious, unless there is another higher-order thought about it, an introspection perhaps leading to the conclusion that one is phenomenally conscious. The concept of HOT and PC are obviously not the same. The suggestion takes the sense of consciousness in "conscious of" and uses it to explain PC, for HOT theorists, led by David Rosenthal (1986), suggest that the sensation itself has no phenomenal character. The apparent phenomenal character is in fact just the content of the HOT, and is thus to be explained by a theory of intentionality. (Note that a HOT theorist is not commited to the Cartesian Theatre, or "the self", since there is no need for the HOT to occur in some central Place of Meaning.)

If a HOT is taken in a very robust sense, i.e. something like fully propositional belief about sensory states, then it seems to imply the absurd dilemma that either human infants are not conscious, or that they have propositional attitudes. On the other hand, if the "thought" in a higher order thought is taken in a deflationary sense, where any old *representation* will do, there is only a small twist to differentiate HOT theories from the representational theory (see the next section). Furthermore, it is difficult to see what sort of evolutionary value these higher order representations would have. As the objections I think are most successful against HOT theories are

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4 This is a variety of representation of a representation *qua* representation, discussed by C. B.₁ Martin in the unpublished manuscript listed in the references as Martin (ms).

unrelated to the autonomic juxtaposition (see e.g. Dretske 1993), a discussion of them is beyond the scope of this thesis.

Attention and awareness are more varieties in the same vein. The word "conscious" is often used synonymously with "attention" or "awareness." For example, instead of saying that I am attending to my stereo playing Beethoven's ninth, I might say that I am conscious of it. Again, this is not the same concept as being phenomenally conscious, which one might apply to the sensations caused by the stereo though I am attending to the telephone conversation I am having with my mother. However, some theorists try to *explain* PC in terms of something like attention, or "dominant focus" (Kinsbourne 1993). I will consider such theories in Chapter 5.

1.3.3   The representational theory

According to the representational theory of PC, phenomenality just *is* representation. Thus to have a sensation of red occupying a particular region of the visual field would be to represent that a particular region of space out in the world is red. Representational theories of PC run into the greatest difficulties when attempting to account for sensations which seem to be practically devoid of representational content, like pain or orgasm. (For example, in the commentary section on Block [1995], Michael Tye claims that orgasm is merely a representation "that something very pleasing is happening down *there*," [p. 269]. Even disregarding the difficulties with naturalizing "pleasing," many would take this to be a *reductio* of the view, including Block [1995, author's reply].) Again, the concept

of representation is different from the the concept of phenomenality, but it may turn out that the former explains the latter. The difficult part is naturalizing representation, and I will consider two complex theories of those who do in chapters 2 and 3. Also, Fred Dretske's (1995) representational theory of phenomenal consciousness relies upon the capacity of the system to *learn*. This capacity will be taken up in detail in Chapter 4.

1.3.4   Binding

Binding is a feature of conscious experience which in some of its guises is closely related to phenomenality. The forming of an experiential unit from seemingly or theoretically disparate constituents is generally referred to as "perceptual binding," though it is present in imagery and other perception-like states. There are three kinds of binding, where the results are qualia, object-percepts, and experience. Binding into qualia further subdivides into two categories: quality characteristic binding and the "grain" problem.

This last is perhaps the most closely related to phenomenality. Wilfrid Sellars (e.g. 1971) wrestled with the difficulties of the homogeneity or grainlessness of colour qualia, due to the apparent irreconcilability of homogeneity with the complexes of colourless particles which compose our brains (according to the scientific image.) Analogous problems arise for other modalities. The details of Sellars's argument are complex and controversial,[5] but the grain problem is plausibly one of the most troublesome intuitions

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[5] See Lycan (1987), chapter 8, for a good discussion and further references.

underlying the mind-body problem. Perhaps it is the same as the "hard problem" of consciousness (Chalmers 1995), i.e. qualia or phenomenal consciousness, since it is hard to imagine what one could mean by non-homogeneous qualia. Even if our colour experience were particulate and "spotty", presumably the regions between the spots would be qualitative, just qualitatively different. How could they form part of the experience otherwise? Moreover, they must be qualitatively homogeneous, barring an infinite regress. So homogeneity seems to be an inalienable feature of phenomenal experience, and grainlessness may have a connection with the concept of PC.

The second version of the binding problem where qualia are the product is the unification of quality features. Some examples are the combination of hue, saturation, and brightness into a single colour, or tone, loudness, and pitch into a sound. This is probably not fundamental to PC, since there are arguably sensory qualities which can be unitary, such as touch, or the visual sensation of movement.

The next order of binding is that which takes features to objects. How is it that the brain obtains a *gestalt* representation of an apple from a size, shape, and colour? The last stage is the one at which a unitary consciousness is obtained. It is questionable whether consciousness is always unitary, not only on the basis of split-brain experiments (Gazzaniga 1995b), but also the demonstration that it is possible to dissociate linguistic and eye blink responses to discrimination tasks which would be expected to require conscious involvement (Marcel 1993). However, even if

conscious processes can sometimes be dissociated, there is certainly a level of binding beyond object binding, to form a "whole" experience.

A representational theory of PC is, in a way, an explanation of binding. A quality may be represented as homogeneous without the medium of representation being grainless, and representation *as* an object could take care of object binding. As mentioned above, representational theories will be addressed in Chapters 2 and 3. There are a group of neurobiological theories of binding, perhaps intended to explain all varieties, though the experiments are directed towards a limited version of object binding. These theories make use of neuronal oscillations and synchrony, and will be discussed in Chapter 5, since it is possible that lower level binding could explain PC.

1.3.5   Summary

To recapitulate, the essential feature of the concept of consciousness which I wish to examine is phenomenality. This phenomenality gets a common sense explanation in terms of intrinsic qualities of phenomenal individuals, but there are a number of alternative possible explanations of phenomenality. These alternative explanations include representationalism (and higher order thoughts), dispositions for voluntary action, attention, plus binding consisting in synchrony and oscillations. It is these alternative explanations whose viability I wish to evaluate in comparing them with the autonomic nervous system.

Many features of adult human consciousness ought to and will be ignored in the comparison. These include the items discussed above which were rejected as conceptually distinct from PC and also implausible as explanations of PC, such as voluntary action and the Cartesian Theatre. *All* conscious modalities will be considered in the comparison; gustation is simpler but no less conscious than the mechanisms which mediate vision. Consciousness pared down to its essentials is all that need be demonstratively paralleled.

1.4   Functionalism

Most theories of consciousness are functional theories, as functionalism is something of a "received view" among materialists. In particular, the majority of the theories of consciousness which are objects of study in this paper are functional theories, broadly construed. That is, they are explanations which appeal to specified sets of causal powers, rather than any intrinsic properties.[6] Mental properties are identified with functions from input (including internal input) to output. It should be noted that this functional strategy contradicts the common-sense explanation of PC, and that is why they are *alternative* explanations of PC. Representation is cashed out by Dennett (1992) and Dretske (1995)[7] in terms of function, dispositions for voluntary action and learning are functional

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[6] For the functionalist, these are manifestation-bound causal powers, not the rather open-ended dispositionality espoused by C. B. Martin, which is only for a particular manifestation *with* particular reciprocal partners (Armstrong et al. 1996, Martin (ms).)

[7] Confusingly, though Dretske relies heavily on the notion of function, strictly speaking his theory is not purely functionalist since he partly cashes out function in terms of evolutionary history.

notions, and synchrony and oscillations offer what might be called a microfunctional account.

My strategy of paralleling mostly functional characteristics should not be taken as an endorsement of functionalism. On the contrary, one of my tentative conclusions shall be that functionalism may not be able to account for phenomenal consciousness, and that there may be something right about the common-sense explanation after all.

1.5 Introspection vs. observation

There are two vastly different general methods to study consciousness, and neither can be successful in the absence of the other. First (quite literally) comes introspection, carried to its extreme in the hands of the twentieth century phenomenologists, who were at least partially engaged "in an analysis and description of consciousness" (Kockelmans 1995). We certainly have some kind of access to our own minds, even if not incorrigible access as Descartes suggested (1641/1980; see discussion in Churchland 1988, pp. 73-81). We might build models of sensation, perception, and cognition based upon our own introspection. Alternatively we might build models based upon introspective reports, verbal or otherwise[8], from other people. All of these procedures are derived ultimately from introspection.

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[8] For an example of a nonverbal introspective report, see the study of monkey blindsight by Cowey and Stoerig (1995).

The other method is the "scientifically reputable" one. That is to decipher the brain's functional characteristics from the bottom up (neurophysiologically) or the top down (behaviourally). With luck, one might be able to establish correspondences between the results of the introspective and scientific methods. However, the only method available to study the ANS is of course the scientific one, and this limits the field of comparison between conscious systems and the ANS.

Often there will be some characteristic of consciousness, as determined by introspection, for which there is no proposed neuro-functional basis. Obviously it will be impossible to demonstrate a parallel in the ANS for such features, since no-one has any idea what it is that is to be paralleled. The only task that I can reasonably set for myself is a comparison of the central autonomic network with the thalamocortical system in virtue of neurophysiological and behavioural considerations. Features of consciousness determined by introspection must first be theoretically formulated in neurofunctional terms. It is thus attempts to *naturalize* the mind which shall be evaluated.

One resultant difficulty of using the ANS as a basis for comparison is that the system's use of stimuli can *only* be evaluated insofar as they affect behaviour, and it is possible that "perceptual" differences will not make for behavioural differences. The ultimate goals of autonomic investigation are predominantly therapeutic, and for medical purposes, it is the behaviour of the system which ultimately matters most, e.g. to reduce hypertension. The further

removed a neuron is from the motor side of things, the more difficult it is to interpret its activity in the framework of the whole system, and thus most studies tend to focus on output.[9] This problem of bias hinders the project of paralleling PC, which is primarily on the perceptual side. Some degree of incompleteness and speculation is the unfortunate result, though my conclusions will be as definite as I can make them.

1.6 Basic outline of the ANS

Having now made the autonomic comparison strategy clear by defining my terms and describing its weaknesses, it is almost time to actually embark upon the project. But first, some background is needed in the form of a general description of the central autonomic control of vegetative functions.

The primarily regulatory nature of autonomic operation has led to the use of the term "reflex" in describing it. This term should not invite analogies to the simple spinal reflexes found in the somatic motor system.[10] Autonomic equivalents of somatic spinal reflexes are to be found, but a greater understanding of the central control of autonomic systems has reduced the meaning of the term "reflex" in this context to synonymy with "non-conscious and non-voluntary."

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[9] Also, the ANS has been traditionally regarded as a motor system only - see section 1.6.2.

[10] The simplest example of a reflex is the stretch reflex, which is the tendency of a muscle to contract in order to resist lengthening. This particular example involves only monosynaptic (single) connections, though spinal reflexes are in general oligosynaptic (several connections.)

Complexity is not precluded, and is in fact the norm rather than the exception.

1.6.1 Central structures

Autonomic complexity is due to central control, accomplished by many regions in the lower brainstem, midbrain, and forebrain. The lower brainstem regions include the nucleus of the tractus solitarius (NTS), the parabrachial nucleus, the rostral and caudal ventrolateral medulla (RVLM and CVLM), the nucleus ambiguus, the dorsal vagal nucleus, the caudal medullary raphe, the Kölliker-Fuse nucleus, the brainstem reticular formation, the dorsal medullary pressor region, the locus coeruleus, and the area postrema. The main relevant midbrain structures are the periaqueductal grey matter, ventral tegmental area, and the subfornical organ. In the forebrain, important autonomic areas include the central nucleus of the amygdala, the anterior periventricular region, the bed nucleus of the stria terminalis, and several regions of the hypothalamus including the lateral hypothalamic area, the paraventricular nucleus, the preoptic nucleus, anterior hypothalamus, and the posterior hypothalamus. There is also some cortical involvement, especially in the insular cortex (Cechetto and Saper 1990), which seems to be the locus for much visceral sensation (Penfield and Faulk 1955). This list, which is far from complete, gives some indication of the complexity of central autonomic control. Expanding upon Loewy (1990), I will call the regions of the CNS relevant to autonomic control "the central autonomic network" (CAN). (Please refer to

Appendix A for detailed anatomical information on the CAN structures mentioned here and throughout the thesis. Appendix A includes diagrams of brain sections and a chart of the connections between the main CAN nuclei.)

The partition of the ANS into sympathetic and parasympathetic divisions tends to be absent or invisible in most central nuclei, other than output nuclei in the lower brainstem and spinal cord. Nuclei whose functions lie primarily on the afferent and lower reflex side of autonomic function (e.g. NTS, parabrachial) and highly integrative nuclei (e.g. in the hypothalamic complex) play a major role in determining both sympathetic and parasympathetic output. The relevance of a particular central neuron to the sympathetic division of outflow may sometimes be determined by mathematical analysis of the neuron's firing profile. Barman et al. (1995) have claimed that any brainstem neuron which exhibits the 10-Hz rhythm, one of two centrally generated rhythms which characterize sympathetic nerve discharge, may be reasonably assumed to form part of the sympathetic network. Anatomical considerations alone are rather indeterminate unless specific pathways are labeled using careful tracing studies (e.g. retrogradely migrating viruses [Jansen et al. 1995]).

1.6.2 Afferent input

The ANS has been traditionally viewed as a purely efferent system, which is odd since its homeostatic functions could hardly be carried out in the absence of afferent information and feedback.

Afferents which feed into the CAN travel in sympathetic nerves, parasympathetic nerves, or somatic nerves. The main afferent target nucleus in the CAN is the NTS, which receives inputs from all of the major organs of the body (Loewy 1990b). (Many other nuclei receive autonomic afferent projections, e.g. the parabrachial nucleus, medial reticular formation, and PAG, but pathways through the NTS seem to be the most important for non-conscious function [Cervero and Foreman 1990]).

A problem is encountered in classifying autonomic afferents, since some never evoke a conscious sensation (e.g. baroreceptor afferents), others may subserve a non-conscious function at all times but may evoke conscious sensation (especially pain) with sufficient stimulation or in summation with other inputs, and certain others may always cause a conscious sensation if stimulated (Cervero and Foreman 1990). To what extent each of these classes of receptors are present is controversial. My concern is with those afferents relevant to the function of the non-cortical CAN, and I can be quite confident that the functional characteristics of the systems I will describe do not involve the cortex since versions of virtually all of the experiments I cite have been performed on anaesthetized animals, and most on decerebrate animals. For more arguments as to the irrelevance of conscious systems to ANS function, see Martin (ms).

In the cat, approximately 20% of all fibres coursing through sympathetic nerves are afferent; in the parasympathetic division, that number increases to 80% for the abdominal vagus nerve (Jänig and Morrison 1986; Andrews 1986). In short, there is a large

amount of afferent input to the CAN, even ignoring the relevance of somatic input. Receptors whose stimulation never results in conscious sensation include baroreceptors (for blood pressure), chemoreceptors (e.g. for detecting levels of CO_2 in the blood), lung inflation and deflation receptors, and atrial volume receptors (Cervero and Foreman, 1990). To make assurance double sure, whenever possible I will use examples which rely exclusively upon these types of receptors, and thus avoid begging any questions about conscious involvement.

The NTS is organized into two different types of subnuclei, organ specific and general. Most autonomic afferents, perhaps after synapsing in the spinal cord, project to other NTS subnuclei besides their organ specific one, and the general subnucleus (the commissural NTS) receives inputs from all visceral systems except those related to the pelvic organs (Loewy 1990b). It is the pathway through the commissural NTS which seems to give rise to the most elaborate responses, but no part of the NTS is merely a relay station. Rather, the lack of pure summation of independent inputs, time dependent inhibition effects, and other factors indicate that some integration occurs within this structure (Mifflin and Felder 1988). In the rostral NTS, gustatory afferents terminate, which are relevant to both conscious sensation (presumably via the connections to the thalamus and thence cortex) and such automatic functions as swallowing (Loewy 1990b). Other somatic inputs also target the NTS, from both cutaneous and skeletal muscle sites. These inputs may be

relevant to both autonomic and conscious functions as well (Toney and Mifflin 1994).

1.6.3 Efferent projections

Efferent autonomic projections have a somewhat more complicated organization than their consciousness related somatomotor counterparts, due to the parasympathetic/sympathetic division and the presence of ganglia. When they project to the same organ, the sympathetic and parasympathetic fibres tend to have opposite effects, and use different neurotransmitters.

The main output nuclei of the parasympathetic division are the dorsal vagal nucleus, which gives rise to the cholinergic parasympathetic preganglionic fibres of the vagus nerve, and the nucleus ambiguus, which also gives rise to efferent vagal fibres in addition to projecting to the cervical and thoracic intermediate gray matter and ventral horn (Loewy and Spyer 1990b). (There is also a source of parasympathetic fibres in the sacral spinal cord.) Vagal efferent fibres are called "preganglionic" because they project to integrative way-stations, collections of cell bodies called ganglia. The parasympathetic ganglia lie within or near the organ that they innervate. The cholinergic "postganglionic" neurons (more appropriately called "ganglionic" since their cell bodies are located within the ganglia) are the last in the chain, and they are the actual effector neurons. Autonomic afferents, ganglia, and postganglionic neurons are part of the peripheral nervous system (PNS); all other

neural constituents of the ANS are considered part of the central nervous system (CNS).

There are several nuclei in the brainstem which contain *pre-sympathetic* (i.e. earlier in the chain than preganglionic) motor neurons (e.g. the RVLM), but the vast majority of the pre-ganglionic fibres originate in the intermediolateral cell column of the thoracic and upper lumbar spinal cord. Most sympathetic ganglia are located near the spinal cord in the paravertebral chain at the thoracic and lumbar levels. The other sympathetic ganglia, which lie beyond the paravertebral chain and are reached via the splanchnic nerve, are called prevertebral ganglia. They supply the the gastrointestinal system. Synapses within the ganglia are cholinergic, and postganglionic sympathetic neurons are noradrenergic, except for the cholinergic sudomotor neurons. This description is rather simplified; for example, other transmitters may be colocalized with acetylcholine or noradrenaline.

The effectors which are under the control of the ANS are too numerous to list. The types of muscle which are innervated are almost exclusively smooth and cardiac (as opposed to striate skeletal muscle.) Cardiac muscle is of course found in the heart, and some examples of smooth muscle structures under ANS control are the walls of arteries and arterioles, muscles in the eye controlling pupillary dilation and contraction, the diaphragm, and sphincters in the bladder and gastrointestinal tract. Other effector organs include sweat glands, lacrimal and salivary glands, islet cells in the pancreas, the adrenal medulla, and the liver.

1.6.4   Enteric division

There is another division of the ANS which can operate independently of the CAN, though it receives inputs and sends afferents to both parasympathetic and sympathetic divisions. This is the enteric nervous system (ENS), whose complex integratory functions are performed by the submucosal plexus and the myenteric plexus, both located in the wall of the gastrointestinal tract. Their ultrastructural organization resembles that of the CNS (Gabella 1987) and "terms such as 'minibrain' have been used to describe the gut's intrinsic innervation." (Aber-Bishop and Polak 1992.) I will largely ignore the ENS because its plexus structure stands in contrast to the modular, nuclear structure of the CAN. This is not to say that its function may not, in some ways, parallel that of conscious systems.

1.6.5   Parallel and hierarchical organization

As in conscious systems, the ANS operates in both a parallel and an hierarchical manner, with modules specialized for different "perceptual" and motor tasks. Some parts of the central autonomic network are modality or sub-modality specific, while other parts are more integrative. Many of these areas sport reciprocal interconnections, and it is likely that feedback exists between almost all levels within the network (Loewy 1990b; see also Appendix A). To the extent that a modular organizational description applies to conscious systems it also applies to the ANS.

Hierarchical organization of modules is being de-emphasized in both the visual system (the conscious modality in which it is most apparent - see Churchland et al. 1994; Bullier and Nowak 1995) and the ANS. The importance of parallel function is becoming increasingly apparent, and one result of such an organization is that if one subsystem designed to perform a specific task is damaged, another subsystem may take over, an aspect of conscious systems emphasized in Edelman (1989). This is exemplified throughout the ANS. One example is in the regulation of blood pressure, where excitation associated with the defense reaction is achieved by parallel mechanisms. One involves inhibition at the level of the NTS, removing inhibitory control over medullary premotor sympathetic vasoconstrictor neurons, and the other consists in a direct excitation of these neurons thus facilitating the baroreceptor reflex. Both are expressed simultaneously, to varying degrees in different species and perhaps individuals (Spyer 1990, 1992.)

There is still something of a module hierarchy however, at least in function if not in temporal order of operation. The ANS includes central supervisory control systems, just as it appears conscious systems do. A few modules are high level integratory centres, processing combined inputs from many parts of the CAN and giving rise to complex global outputs. For example the hypothalamus, which contains several interacting nuclei, receives somatosensory, olfactory, visual, limbic, humoral, thermal, pressor, fluid volume, and various chemical inputs to coordinate global cardiovascular and

thermoregulatory behaviour (Pittman 1991).[11] An example of a highly elaborate autonomic behaviour elicited by "top modules" is the defense reaction (Jansen et al. 1995).

1.6.6 Summary

The central autonomic network receives input from throughout the body, engages in complex integratory processing involving a very large number of CNS structures, and in response controls a vast array of effector mechanisms. It operates twenty four hours per day over an entire lifetime, and survival depends upon it. This general outline has obviously glossed over many interesting details and complexities, and it is in these that we will find our parallels to conscious systems. Throughout this thesis, only a small number of examples of the capabilities of the ANS will be shown, but that small number shall prove instructive. In the next chapter, I turn to philosophical theories of representation which are touted as explanations of phenomenal consciousness.

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[11] The complexity and importance of the hypothalamus make it a prime candidate for conscious vs. autonomic comparisons. However, its complexity also confounds theorists in developing a detailed model of its functioning. As a result, most of the examples I use in the rest of the thesis are based upon better understood anatomical sites in the brainstem; this is not to deny that in the future, the autonomic comparison strategy featuring the hypothalamus could be an especially fruitful one.

CHAPTER 2
Spatially Represented Qualities

2.1   Representation

There is a growing literature in the philosophy of mind devoted to the naturalization of internal representation.   It seems that one thing of which a mind is capable is the *representation* of its environment, thus enabling the organism of which the mind forms a part to *interact* with its environment.   The modern development of this framework (for the basis of multifarious theories cannot itself be called a theory) occurred in response to behaviourism.   Philip Johnson-Laird summarizes the position of what he reports to be the first modern exponent of representationalism, Kenneth Craik (1943):

> ... human beings translate external events into internal models and reason by manipulating these symbolic representations.   They can translate the resulting symbols back into actions or recognize a correspondence between them and external events.

These internal representations run the gamut from representing a series of dots as a straight line, to representing the sound of a predator as coming from the right, to representing a spider as an arachnid.

What counts as evidence for internal representations is controversial.   One might take internal representations and their true nature to be immediately accessible.   Adopting this theory would place one firmly within the tradition of Cartesian incorrigibility.   Alternatively, one might take representations be true *objects* of

introspection, and thus mediately accessible in a manner akin to perception. Further alternative positions are that internal representations are veridical theoretical constructs (Stich 1978), falsidical theoretical constructs (Churchland 1981), or mere instruments for the prediction of behaviour (Dennett 1987). Probably the most popular position among cognitive scientists and philosophers is that the evidence for internal representations consists in a mixture of introspection and theoretical construction. I would (at least) include Fodor (1975, 1990), Lycan (1988), Jackendoff (1987), Block (1986), and Dretske (1988, 1995) in this group.

Not all of the authors cited above are pursuing a naturalistic program, and fewer still wish to reduce consciousness to their version of representation. I will take two very different examples of philosophers who *do* wish to reduce consciousness to what they take representation to be. Daniel Dennett is an instrumentalist, and Fred Dretske offers a causal theory of representation. My goal is to show that their models of representation, and thus their models of consciousness, apply to the ANS.

2.2 Daniel Dennett's theory of consciousness

2.2.1 The intentional stance

Dennett's instrumentalism makes it relatively easy, in a certain sense, to apply his model of "representation" to the ANS. He claims that consciousness is a continuum, where the robustness of conscious experience depends upon the complexity of the entity's behavioural

dispositions. If the behavioural dispositions are complex enough, one might postulate internal representations, but Dennett emphasizes that this is merely an heuristic, the adoption of an "intentional stance" towards the system being described (see "True Believers" in Dennett 1987.)

Dennett's other stances are the physical stance and the design stance. The physical stance is just a description of the physical constituents of the system, upon the basis of which one might predict anything the system might do in any circumstance, if one knew enough. Practically, though, the physical stance is often inaccessible. Normally most of us adopt the design stance towards our thermostats for instance - we move the needle up or down because we believe that the thermostat was designed to make the room warmer or colder. We usually do not spare a thought for the bending of the bimetallic strip and the flow of electric current. The design stance is also appropriate when talking about some functions, for example the functions of bodily organs. An understanding of the heart is aided by considering it as an item evolutionarily "designed" to pump blood.

The next step is to adopt the intentional stance.

> Here is how it works: first you decide to treat the object whose behavior is to be predicted as a rational agent; then you figure out what beliefs that agent ought to have, given its place in the world and its purpose. Then you figure out what desires it ought to have, on the same considerations, and finally you predict that this rational agent will act to further its goals in the light of its beliefs (Dennett 1987, p. 17).

Adopting this stance towards the thermostat, one might say it will turn off the furnace when it *believes* the room is at the *desired* temperature. Or we might say when Phil *desires* to quench his thirst, and *believes* that the water from the water fountain will do so, he will take a drink. The intentional stance has yielded both of these good predictions.

As applied to a particular system, the predictive success of the intentional stance in comparison with the physical or design stances determines its appropriateness. For the thermostat, the intentional stance is no more useful to us than the physical stance. Given an ambient temperature, the properties of the bimetallic strip, and the location of the connection which will complete the circuit, we can predict the behaviour of the thermostat. We could also predict its behaviour by attributing to it beliefs and desires, as outlined above, but this gives us no prognostic advantage.

On the other hand, Dennett argues, when predicting the behaviour of a person, certain generalizations are available using the intentional stance which are not available on the physical stance. Suppose, just before she leaves on a trip, you ask a friend to send you a postcard from Brazil. Consider a prediction of the goings on following the asking of the question. Taking the intentional stance, one might predict that in about a week's time, your friend will remember your question, wish to satisfy your request, and, according to certain beliefs she has about how to do so, go to the stationer's and buy a postcard and a stamp, write "Wish you were here!" and your address, drop it in a mailbox, and eventually, with the help of others

who have a certain set of reliable beliefs and desires, you would receive the postcard in your mailbox at home. Such a prediction is quite easy and fairly reliable (though not infallible.)

But consider the prediction involved when taking the physical stance. Each step of the way would have to be calculated according to the laws of physics, from the vibratory effect of your larynx on the air, to the effect on your friend's ear and brain, to your friend's movements from boarding a plane to licking a stamp, the ghastly events in the post office, etc. etc., all described at the microphysical or at least molecular level. The mishaps avoided along the way would have to be carefully calculated, for example narrowly missing the flames from a garbage can carelessly set on fire by a smoking postal worker. The intentional stance prediction is compatible with an indefinite number of microphysical stories between the beginning and the end, *and yet correctly describes a pattern common to all of these possibilities.* Dennett claims that this pattern is invisible from the physical stance, such that the purely physical predictor would be nonplussed by the success of the intentional predictor. So in this case, the intentional stance gives a predictive advantage, and one is justified in using internal representations - of the belief and desire type - as instruments for prediction.[1]

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[1] I find myself unpersuaded by Dennett's argument, though here I just present it in order to explain the intentional stance. Dennett assumes that the pattern is invisible from the physical stance, but this is not obvious. The most complex and restrictive dispositions here belong to the agents involved, thus the causal story depends mostly on them. For example, a desire to mail a postcard has a very limited set of physical circumstances under which the desire would be satisfied. Assuming eliminativism is not obviously true, it may make sense from the physical stance to identify and make law-like generalizations over similar structures, which happen to be characteristic of beliefs and desires.

2.2.2 Heterophenomenology, or "the conscious stance"

What does the intentional stance have to do with consciousness? In Dennett's *Consciousness Explained* (1991), the intentional stance appears as "heterophenomenology," where one attributes conscious experience to a system, and draws conclusions as to the nature of this experience based on the system's behaviour. Heterophenomenology seems like taking a "conscious stance," but by the end of the book one comes to realize there is little to distinguish between the conscious and intentional stances. This becomes even clearer in Dennett's discussion of Ned Block's article, "On a confusion about a function of consciousness" (1995). Dennett claims the difference between phenomenal consciousness (relevant to heterophenomenology) and access consciousness (relevant to belief, rationality, and the intentional stance) is merely one of degree. Access consciousness has a higher degree of influence on behaviour, while phenomenal consciousness is richer in content.

In discussing consciousness, Dennett talks less of beliefs than of judgements. "Judgement," he explains, is to be taken in a minimal sense (generally supported by the text of 1991 and explicitly in1993), which seems to be any sub-systemic state or process of an

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Surely the physical stance does not require working at the microphysical level when useful generalizations may be made at higher structural levels. Molecular geneticists, for example, generalize over complex DNA structures to predict the role of these structures in the economy of the cell. Some repeating properties of brain structures may define a certain set of causal chain possibilities which mirror the generalizations obtained from the intentional stance. What I am suggesting, then, is that it is far from obvious that beliefs and desires do not form physical kinds.

intentional system which can be interpreted, from the intentional or conscious stance, as contentful. Despite his misleading use of the term "narrative," (1991, e.g. p. 135-6) "the content of the judgements doesn't have to be expressible in propositional form" (1991, p. 365). If belief is propositional, it seems that Dennett's judgements are merely a more inclusive category of contentful states than beliefs. Given Dennett's deflationary position on propositions and belief ("Beyond Belief" in 1987), little should hinge on this difference, and I will treat the conscious and intentional stances as essentially identical.

Both stances are adopted with respect to a whole system, but throughout *Consciousness Explained* sub-systemic modules are postulated as the only structures which will support them, as opposed to a look-up table for instance (p. 437). Judgements are made by modules ("homunculi" or "demons", 1991 p. 261), which "are just units with particular circumscribed competences" (pp. 261-20). Each module is equipped to discriminate a particular feature of a stimulus, e.g. its pitch (for an auditory stimulus) or its colour (for a visual stimulus.) Modules further up the hierarchy might be responsible for object recognition, or determining spatial location. What Dennett is at pains to demonstrate is that there is no single place where "it all comes together" to form conscious experience - all that happens is the simultaneous operation of the various modules. The modules go into discriminatory states, and singly or together underwrite the organism's behavioural dispositions, which Dennett wants to characterize with as fine a grain as possible.

If you wish to discover the nature of a creature's phenomenal consciousness, you test to see what discriminatory powers it has. One might ask a person if she can tell the difference between two similar shades of blue. If an organism's capacities do not include language, one might use a forced choice/reward test, to determine whether a bat can tell the difference between a large disk and a small disk by echolocation, for example. If it can *distinguish* objects based on size, then Dennett claims it *experiences* size.

I intend to show that the types of discriminations that Dennett would identify with qualia are present in the ANS. Moreover, I will characterize them through their dispositions to affect behaviour, the only legitimate method in Dennett's view and the only one available for autonomic functions. Basically, what must be demonstrated is that the ANS is composed of modules which make feature discriminations, and in cooperation cause the system's behaviour.

2.3   Characteristics of sensation

From Dennett's discussion, one can see that his champion modality of the mind is vision. The low-level features and sub-features which are visually discriminated include the following: spatial characteristics (shape, size, location, depth), colour (hue, saturation, and intensity), and motion. These features summarize the characteristics of visual sensation. As far as its stimulus parameters go, vision is certainly one of the most complex of conscious

modalities, but it is only one of six.[2] C. B. Martin (ms) has argued convincingly that it is not even the most important modality to the organism, even for humans. So it would be acceptable to find an ANS parallel in another modality (see Chapter 1). Audition, for example, is characterized by frequency, loudness (amplitude), and, at a more complex level, tone. As in the case of vision, spatial location also plays a role here. Somatosensation is characterized by temperature, pain (nociception), or touch (mechanosensation), again each in some spatial location, in this case on the body surface or interior.

The presence of some spatial characteristic to each of these types of sensation may have some significance. C. B. Martin (ms) has argued that each modality possesses a sensory "field," in which percepts (and images, hallucinations etc.) must be formed. The field "provides a kind of *matrix* for the different qualities of the sense modalities." This is certainly true of somatosensation, which exhibits the closest parallels with the ANS in terms of its functional environment, i.e. the body. Martin is careful to differentiate between the spatial properties of the stimulus and the sensory field. In vision, for instance, the same object will subtend different amounts of the visual field depending upon its distance from the retina. But this is because visual stimuli are distant from the relevant receptors; in the case of somatosensation, stimuli and receptors abut, and stimulus spatial relations correspond to sensory field relations.

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[2] Or possibly seven, depending upon how one divides up somatosensation, proprioception, and vestibular related sensation.

Therefore if it can be shown that for some of its modalities, the ANS represents stimuli *spatially*, i.e. somehow according to the spatial properties of the stimuli to which it responds, an important characteristic of phenomenal experience will have been paralleled. If this representation is not *only* spatial, i.e. if feature discrimination takes place and some *property* of the stimulus is represented in a spatial context, then the essential features of phenomenal experience will have been paralleled. Since, for Dennett, phenomenality is nothing more than the reactive dispositions implied by sensation, he would have to accept the phenomenality of these ANS modalities. Of course, he does not really accept phenomenality at all, in the usual sense of the word, so what he would be accepting would be that there is no difference in kind between sensation in conscious systems and sensation in the ANS, surely an absurd conclusion.

2.4 Spatial representation

Martin (ms) has given a complex account of representational use (a notion he considers prior to representation) which has as one of its components spatial representational use. Without delving too deeply into Martin's framework, I intend to present what I take to be sufficient for a central controller ("integrative control area" [Martin]) to spatially represent distal stimuli. This will essentially be a slightly simplified, concrete explanation of Martin's account.

First, a somatotopic or viscerotopic organization of input is an indicator of, but does not imply spatial representation. It is an indicator of spatial representation because without topographical

arrangement, it is difficult for the correct organization of connections required for spatial representation to develop. But to take a blatant example of its fallibility as an indicator, the reflexes in the spinal cord involving two or three synapses could be considered to have a topographically organized central component, since the interneurons in the spinal cord are rostrocaudally arranged in correspondence with the muscles to which they are relevant. (There is also a mediolateral somatotopy [Kelly 1991].) However, these interneurons do not have any intercourse; each reflex occurs independently of the others. Likewise, in the brain, the pattern of input cannot simply be piped up to another centre, neuron to neuron (or small neuronal group to neuronal group) so that each cell's response in the higher centre is determined only by the single cell (group) which provides it with input.

In order for there to be true spatial *representation*, the pattern of inputs from the area represented must be reacted to as a whole. This means that variations in the input pattern must result in variations in the output pattern *such that variation in one part of the input cannot be systematically related to variation in any one part of the output pattern.* This obviously requires connections, possibly indirect, *between* topographically organized interneurons, so that they can influence one another's activity. In terms of prediction, it means that besides the central structure, the *entire* input pattern must be known in order to predict the output. It must also be the case that under certain circumstances, parts of the pattern may segregate. They are parts, after all - just not completely independent

parts. Therefore variably composed parts of the input, central controller, and output may segregate from the rest, such that they operate together as their own whole. Under other conditions, this segregated representational system may be re-integrated into the larger one.

How does this play itself out in the conscious, somatic nervous system, the kind of spatial representation being paralleled? Both the primary somatosensory cortex and the primary motor cortex (on either side of the central sulcus) are topographically organized - the "homunculi." More sensitive areas have larger receptive fields in the primary somatosensory cortex, and the topography of motor intensive body parts occupy larger portions of the primary motor cortex. The hands, for instance, occupy disproportionately large regions of each, and the back a disproportionately small area (Kandel and Jessell 1991a). (There are extensive interconnections between the sensory and motor strips - in fact, they are not even distinct areas in more primitive mammals such as hedgehogs [Ghez 1991].)

Central topography is an indicator of spatial representation, though not, of course, an infallible one. Representation comes into the relations the basic topography has with higher centres. On the motor side, various higher areas (e.g. the premotor cortex and frontal lobes) project to the primary motor cortex and can elicit a number of different behaviours involving coordinated flexion and relaxation of different sets of muscles. They can activate the motor topography variably, recruiting different combinations of muscles, and they can activate it differentially, with differing relative strengths of

activation. These higher centres act in a coordinated manner. This is the first aspect to be paralleled - variable differential control of a basic topography by a cooperative network.

The repertoire of movements is holistically dependent upon stimulus patterns. Ignoring for the moment the influence of other modalities, a particular pattern of activation in the topography of the somatosensory area can be used by the higher areas to induce one of the patterns of muscle activation. For example, a tap on the shoulder might induce an orienting response, while a tap on the forehead might cause drawing back. An interrupting stimulus from somewhere else on the body may alter these responses. More simply, one component of a complex movement leads to the next through sensory feedback, though an interrupting stimulus from elsewhere might alter the sequence.

The whole system accomplishes spatial representation in virtue of the features described above, or at least Dennett ought to accept this conclusion. Essentially, different complexes of stimulus qualities and locations induce varying spatially coordinated muscular responses. Responses occur *as if* each spatial part, each sensory input (whether touch or pain or temperature) is represented in the context of a spatial whole. For Dennett, there is no "*as if*" - adopting the intentional or conscious stance, the organism set up in this manner (e.g. a rat or a human) just does spatially represent.

Now we must see if we can attribute spatial representation to the ANS. As usual, the relevant ANS studies over the last twenty years have been more conclusive on the motor side of things. Prior

to this, researchers were hindered by a belief that the ANS has only very generalized effects. Langley (1921) was perfectly aware of the independent control of autonomic target organs, but later in the century, researchers took Cannon (1939) and Hess's (1948) generalizations more literally than they were intended, and the ANS was regarded as a simple, undifferentiated effector system (see Jänig and McLachlan [1992] for discussion.) In the 1970's, this misimpression was corrected through the efforts of Chandler Brooks and others (see, for example, Uchizono et al. 1975).

In the cardiovascular system, particularly the control of blood pressure, it is clear that there is variable differential control of a basic topography. I will suggest that the rostroventrolateral medulla (RVLM) is an analogue to the primary motor cortex. This type of control on the motor side is in itself suggestive of a matching complexity on the afferent side, but there are also anatomical considerations and experimental results which support such an hypothesis. I will propose the NTS as an analogue to the primary somatosensory cortex. The areas of the CAN intermediate to the NTS and RVLM are analogous to higher cortical areas. So what I will attempt to show in sections 2.5 and 2.6 is that the motor and "sensory"[3] sides of cardiovascular control form a spatially representational system.

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[3] This use of "sensory" is not meant to imply conscious sensation; it is used merely to indicate the receipt of afferent input. I will often use the term "sensory" to apply to events in the ANS, enclosed in scare quotes to indicate its non-conscious nature.

2.5 Spatial representation in the ANS - the motor side

Shepherd and Shepherd (1992) summarize the motor capabilities of the system which controls the vasculature:

> It is not surprising, in view of the complexity of these peripheral sensors and of the brain centres that control the cardiovascular system, that... sympathetic nerve discharge occurs in a highly differentiated pattern. Thus, in response to reflex or central stimuli, the efferent sympathetic activity varies between the different organs and tissues and, in the same organ or tissue, can vary between resistance and capacitance vessels. In some instances, it may increase in some organs and decrease in others.

The basis for this directedness of output is control of a topographic pattern which is found in the rostroventrolateral medulla (RVLM). To demonstrate a parallel to the primary motor cortex, we must examine the three levels discussed in section 2.4 - the topography of the RVLM, the higher level structures which project to the RVLM, and the cooperation amongst these higher level structures.

2.5.1 The RVLM is topographically organized

The RVLM contains presympathetic vasomotor neurons, especially in the subretrofacial nucleus (defined in the cat), which is exclusively cardiovascular. It projects directly to preganglionic neurons, especially in the intermediolateral cell column (IML). Other sympathetic premotor nuclei may play a role in modifying the vasculature regionally, and have descending projections to the IML, but the RVLM seems to be the most important (Dampney 1994). Stimulation of the RVLM causes an increase in blood pressure due to

vasoconstrictor fibres innervating blood vessels throughout the body, and may also raise the heart rate and cause release of adrenomedullary catecholamines (Dampney 1994).

The most convincing studies to show a topographic distribution of RVLM neurons are those which involve local discrete application of excitatory amino acids, resulting in preferential vasoconstriction in one or several vascular beds. An early study by Lovick (1987) incorporated microinjections of the non-specific glutamate agonist DL-homocysteic acid (DLH) onto various subregions of the nucleus paragigantocellularis lateralis (pgl, a lateral region of .the RVLM) in the cat. It was possible to elicit varying combinations of increased and decreased blood flow and conductance in the hindlimb, renal, and mesenteric vascular beds. Sometimes all three would be affected, sometimes any two, or just one. There was also a rostral to caudal topography of renal to mesenteric to hindlimb vasoconstriction sites, which overlapped somewhat. It was hypothesised that other neuronal pools existed which had selective effects upon other vascular beds.

This hypothesis was borne out by later studies. For example, Key and Wigfield (1994) demonstrated a topographic organization in the RVLM for cutaneous regions, where vasomotor tone was measured indirectly through skin temperatures in the tail, front feet, hind feet, hind leg, nose, neck, and back of the rat. As for the Lovick study, injections of DLH into different RVLM cells resulted in variable vasoconstriction in these vascular beds, and the same effect was obtained with electrical stimulation. It was found that

vasoconstrictor cells selective for the tail were located ventrally, and centrally within the rostrocaudal aspect of the RVLM. The front and hind feet were affected by injections in the same region, but more dorsal, with the hind foot sensitive area more caudal than the front foot. Again, some overlap was observed. Areas selective for the back, nose, and neck were smaller and more circumscribed. (Compare this with the motor homunculus on the precentral gyrus, where more finely controlled structures cover a proportionally larger area.) There were also regions which, when stimulated, failed to produce a response in any of the recording areas, thus related to other functions or other vascular beds.

It is also possible to elicit ipsilateral vs. contralateral vs. bilateral vasoconstriction depending upon stimulation site (e.g. for the femoral artery in Wang et al. 1994). Regional hemodynamic effects are also sensitive to rate of electrical stimulation and concentration of chemical stimulation, and several different transmitters or transmitter agonists injected into the RVLM cause differential vasoconstriction (Lovick 1989; Miyawaki et al. 1993; Dampney 1994). Individual differences and experimental limitations, especially upon the number of possible recordings from a single animal due to the sensitivity and importance to survival of the region, have prevented the formulation of a definitive body map on the RVLM, but it is clear that it exhibits a topographic organization. (Sun [1995] reports only one contradictory study - Ermirio et al. 1993 - and I find this group's reasoning to be problematic [see section 2.6.5].) The next step is to show that this basic topography

may be *variably* and *differentially* controlled by higher areas in the autonomic neuraxis.

2.5.2   Variable and differential control of the RVLM

There are many components of the central autonomic network (CAN) which exhibit variable and differential control the RVLM topography; the example I will use is the peri-aqueductal grey matter (PAG, or central grey matter), which is located around the midbrain aqueduct and has been implicated in the defense reaction as well as normal autonomic regulation.   Largely through the combined efforts of Pascal Carrive, Richard Bandler, and Michael Shipley (see Bandler and Shipley 1994), our knowledge of the operation of the PAG has recently been greatly increased.

Opposing patterns of cardiovascular change are elicited through stimulation of the lateral vs. ventrolateral PAG columns; the former leads to increased mean arterial pressure and tachycardia, while the latter causes decreased pressure and bradycardia.   Since pressor effects occur within the lateral PAG, it is a natural place to look for RVLM control.   Here, regional hemodynamic effects were pronounced and functionally relevant.   Blood pressure and heart rate effects were constant, but the regional composition of the pressor response varied between stimulation of the caudal vs. intermediate regions of the lateral PAG column.   Caudal stimulation was associated with an increased blood flow to the limbs and a decreased flow to the viscera and face; it was suggested that this pattern was characteristic of a "flight" response.   On the other hand, a "fight" or confrontational

response was educed by intermediate stimulation, i.e. an increased flow to the face but decreased flow to the viscera and limbs (Carrive and Bandler 1991b). Note that for both areas, flow to the viscera is reduced, and the differential effects are observed with respect to the limbs and face. The brain and heart have consistent increases in both cases (Nakai and Maeda 1994).

That these effects are achieved through differential control of the RVLM is indicated by both anterograde and retrograde tracing studies (Carrive et al. 1988). Such studies have also been performed upon other parts of the PAG which show differential control of the vasculature, and an RVLM mechanism has been similarly implicated (e.g. Carrive and Bandler 1991a; see Bandler and Shipley 1994 for review). Overall, the PAG exerts variable differential control on the topography of the "primary motor" controller of the cardiovascular system, the RVLM.

2.5.3   This control is achieved by a cooperative network

Other higher areas in the autonomic neuraxis show patterns of differential control of the basic RVLM topography resulting in regional hemodynamic variation. These include, among others, the locus coeruleus (Miyawaki et al. 1993), the caudal ventrolateral medulla, which inhibits the RVLM (Willette et al. 1987), the parabrachial nucleus (Dampney 1994), the medial preoptic area of the hypothalamus (Rizvi et al. 1996), and other hypothalamic subnuclei (Ninomiya et al. 1970; Okada and Ninomiya 1983).

Completing the analogy to higher cortical control of the primary motor cortex, the PAG and the areas mentioned above do not act independently on the RVLM, but form part of a cooperative network. The extensive studies of rhythmic sympathetic discharge done in Gebber and Barman's laboratory provide the best evidence for this. There are two principle centrally generated rhythms in sympathetic discharge, one at 2-6 Hz ("the cardiac-related rhythm") and another at 7-13 Hz ("the 10-Hz rhythm"). The generation of these two rhythms involves (at least) the RVLM, CVLM, caudal medullary raphe, medullary reticular formation, medullary lateral tegmental field, NTS, parabrachial nucleus, Kölliker-Fuse nucleus, posterior hypothalamus, and the PAG (Barman et al. 1984; Barman 1990; Zhong et al. 1992; Gebber et al. 1994; Barman et al. 1995).

Cohen and Gootman (1970) were the first to propose that intrinsically generated brainstem rhythms reflected the fundamental organization of circuits controlling sympathetic nerve discharge (SND). Barman and Gebber have shown that neurons throughout the CAN which are correlated with either rhythm and which show selective effects on regional sympathetic outflow are differentially regulated in the context of either or both of the cardiac and 10-Hz "carrier frequencies." In the usual experimental condition, i.e. constant temperature with baroreceptor deafferented and decerebrate or anaesthetized cats, one would expect little regional differentiation in blood flow. And indeed, under these conditions, the rhythms are coherent across all sympathetic nerves. However, with the application of forcing stimuli into parts of the central

network, decoherence between different nerves is observed, which can be manipulated according to the site of central stimulation (Huang et al. 1992). The results are implied in more physiologically natural situations by partial coherence analysis (Gebber et al. 1994) or phase spectral analysis (Gebber et al. 1995).

What appears to be happening is that the complex central circuits which target particular regions of the vasculature, or at least which exert regionally disproportionate vasoconstrictor effects, are related to all other region targeting circuits via a series of interconnected non-linear oscillators. These central oscillators are dynamically coupled, such that the reinforcement or inhibition of SND to a particular region with respect to another region depends upon the frequency and phase relationships between the other relevant central oscillators at that time. Given the large number of regions which can be differentially controlled, very finely tuned directionality of response is possible. Moreover, since each central oscillator is coupled with the others (dynamic differential effects are observed between all nerve pairs tested), the vasoconstriction directed towards one region is achieved only in the context of responses directed towards all of the other regions - in other words, this implies spatial representation. (We will revisit the model of Gebber and Barman in Chapter 5.)

Thus the motor responses involved in the regulation of blood pressure and blood flow can be described as variable differential control of a basic topography (in the RVLM) by a cooperative network. On the motor side, then, we have our requirements for

spatial representation. Now we must show a dependence of these responses upon the spatial properties of stimuli.

2.6   Spatial representation in the ANS - the "sensory" side

2.6.1   Intermodal integration and the cardiovascular system as common motor system

Cardiovascular responses, in particular vasoconstriction and vasodilation, are not determined solely by baroreceptor inputs. Furthermore, blood pressure is not the only variable to be manipulated. Other states which must be controlled in conjunction with pressure are temperature, cardiac output, circulating blood volume, and blood gas tensions (Spyer 1990). These last two link the cardiovascular system with the gastrointestinal and excretory systems, and respiratory system respectively. The complexity of these interactions is remarkable (Spyer 1992) and evident from the fact that even in rigorously controlled experimental situations, baroreceptor inputs do not cause stereotypical cardiovascular reactions (Abboud and Thames 1983). For the moment we are concerned with the inputs which have a spatial component that determines, in a contextual and holistic manner, the directedness of sympathetic vasoconstriction.

The regional differentiation on the motor side is itself indicative that cardiovascular control is carried out by a spatially representative sensorimotor system. For one thing, the nervous system seems to be set up for feedback, such that any central controller monitors the success of its actions. Since central regional

control of the vasculature exists, one would expect regional feedback. And indeed, stimulation of different afferent nerves has regionally differential effects on the RVLM (Ermirio et al. 1993). Based upon these results, it is unfortunately impossible to determine which afferent modalities are responsible for this differential activation of the topographically arranged RVLM. There are probably several modalities which can be used in a spatially representational way, though the paucity of information on the subtleties of visceral afferent function is somewhat restrictive to the theorist on this point.

We are looking for spatial representation of stimulus qualities, so it would be best if we could demonstrate its presence in a particular modality of afferent input. We could then say, for example, that the property of blood pressure is spatially represented. I will consider several different modalities, primarily pressure, temperature, and muscle contraction. Each of these afferent modalities has effects on the vasculature which are achieved via the CAN and eventually the RVLM, and thus are candidates for participation in the particular spatially representational system I am considering. We shall see that the evidence for spatial representation improves in the progression from baroreceptor to thermoreceptor to ergoreceptor inputs, but that it cannot be absolutely proven for any specific modality. Nonetheless, the modality aspecific evidence allows us to draw the conclusion that spatial representation is instantiated in the central control of the vasculature.

The main autonomic "sensory" nucleus related to cardiovascular control, the NTS, is topographically organized, and it is this area that I equate to the primary sensory areas of the cortex.[4] It has both organ specific nuclei which participate in relatively simple reflexes (Loewy 1990b), and a topographic organization in the commissural NTS (Spyer 1992; Sun 1995). It is this latter nucleus which participates in more of the elaborate responses which are most interesting for our purposes. Further, in a manner similar to the RVLM studies mentioned above, varying local application of glutamate to the NTS elicits varying regional variations in arterial pressure (Yin et al. 1994). Since the NTS is a member of the previously discussed oscillatory network which is responsible for cardiovascular control, it is reasonable to hypothesize that it is on the "sensory" side of a spatially representational system. But which afferent modalities are spatially represented, i.e. which feature discriminations would Dennett consider qualitative?

2.6.2 Baroreceptors

In order for the regional differentiation present in sympathetic nerve discharge to have its equal on the "sensory" side, relevant receptors must be distributed throughout the body. The baroreceptors upon which almost all studies focus are those located in the aortic arch and the carotid sinuses. However, there are

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[4] Visceral afferent information can reach the CNS by routes other than the NTS, expecially the reticular formation and the parabrachial nucleus, but the NTS is the most important for non-conscious effects (Cervero and Foreman 1990; Loewy 1990b).

mechanoreceptors located in the arterial supply to the kidney (Spyer 1990), lungs, heart, (Shepherd and Shepherd 1992) and perhaps other organs as well (Spyer 1990). The receptors in the lungs at least have been shown to play a role in regionally variable hemodynamic effects resulting from changes in posture (Shepherd and Shepherd 1992). The vasculature of the GI tract receives a autonomic afferent innervation (Sharkey and Pittman, forthcoming), some of which could terminate in mechanoreceptors. In skin, muscle, and subcutaneous adipose (fat cell) tissue, there are receptors which respond to venous conjestion, which trigger a local axon response causing constriction in arterioles. It may be that they exert an influence centrally as well.

It has been assumed, perhaps, that these "other" baroreceptor afferents do not have central effects because pressure responses are eliminated by aortic and carotid baroreceptor denervation. It may be that the drastic measures taken to accomplish this (e.g. section of the carotid sinus, aortic depressor, and vagus nerves [Barman et al. 1984]), though aimed at the aortic arch and carotid sinus baroreceptors, also succeed in cutting off other baroreceptors from the CAN. Alternatively, with the principle afferent routes completely removed, the influence of the remainder may be nullified, perhaps through a central mechanism.

In any case, there is not enough information available to evaluate the role of these baroreceptor afferents in spatial representation. The baroreceptors which have been carefully studied, i.e. in the carotid sinuses, aortic arch, and cardiopulmonary

region, do not have a spatial distribution which begins to match that of the sympathetic outflow. More work needs to be done to determine if there are more widely distributed baroreceptors which exert a central influence.

The second main group of cardiovascular mechanoreceptors are found in and around the heart. They signal atrial contraction, atrial filling, blood volume, and the like (Shepherd and Shepherd 1992). They do not have the wide spatial distribution we are looking for. Chemoreceptors, which detect levels of oxygen, carbon dioxide, and pH in the blood, are more widely distributed (Sun and Reis 1994). They terminate primarily in the NTS (Finley and Katz 1992), and act ultimately via the RVLM (Koshiya et al. 1993). Thus they seem very similar in their organization to baroreceptor afferents; unfortunately this similarity extends to a paucity of information about peripheral receptors other than those found in the carotid bodies. We had best look at some other modalities for clear evidence of use of regional afferents in a spatially representational network.

2.6.3   Thermoreceptors

The experimental situation is somewhat more helpful in the case of thermal afferents. There are both central (hypothalamic, brainstem, and spinal) and peripheral thermoreceptors, with the former containing a larger number of heat detecting receptors and the latter cold detecting receptors (Jänig 1990). The peripheral afferents are spread throughout the skin, muscles, and viscera (Kupfermann 1991), and so are candidates for input into a spatially

representational system. The main autonomically mediated thermoregulatory effector mechanisms are shivering (controlled by the hypothalamus via somatic motor pathways), thermogenesis in brown adipose tissue, blood flow, sweat secretion, piloerection, and endocrine responses (Collins 1992). We will be primarily concerned with cutaneous, visceral, and muscular blood flow, but also sweat secretion since it is coupled with a poorly understood sympathetic vasodilation (Jänig 1990).

Both evaporative heat loss and convective heat transfer from the core to the body surface by the bloodstream depend upon intact neuronal control with multiple afferent and efferent links (Jänig 1990). Even anaesthesia disrupts these processes (Jänig 1990; Collins 1992), due not to effects on the cortex but on the brainstem. (The myth of anaesthetics as purely "consciousness eliminating" drugs is refuted simply by noting the amount of effort anaesthesiologists must expend upon maintaining a patient's autonomic functions [see eg. Martner and Biber 1982; Kaufman 1985].) Thermoregulatory responses are initiated from the hypothalamus, which determines a variable set point which "depends virtually on more or less all regulations that contribute to maintenance and adaption [sic] of the internal environment of the organism," (Jänig 1990, p. 344.)

Recall that the hypothalamus is a member of the network which has regional control over the vasculature in relation to blood pressure, and highly variable and differentiated regional vasoconstriction can be elicited by circumscribed application of neurotransmitters in the medial preoptic area (Rizvi et al. 1996) and

other subnuclei of the hypothalamus including the posterior region (Ninomiya et al. 1970; Okada and Ninomiya 1983). Both the preoptic/anterior and posterior hypothalamus are important in thermoregulation (Kupfermann 1991), and the entire hypothalamic structure is highly interconnected (Pittman 1991). There are also strong reciprocal connections between the "sensory" NTS and the hypothalamus (Pittman 1991) as well as the hypothalamus and the motor RVLM (Dampney 1994). The preoptic/anterior hypothalamus projects directly to the PAG (Rizvi et al. 1996) and the RVLM (Goodson et al. 1993), and one of the principle output nuclei of the hypothalamus, the paraventricular nucleus, innervates sympathetic preganglionic neurons directly and topographically. This nucleus also projects to the PAG, parabrachial nucleus, RVLM, NTS, dorsal vagal nucleus, and the nucleus ambiguus, the latter two being the principle parasympathetic output nuclei (Dampney 1994). Overall, the hypothalamus has an anatomy perfectly suited to orchestrating regional vascular responses to regional thermal inputs.

These anatomical details are also suggestive of cooperation between blood pressure and thermoregulatory control, and when one considers the fact that under severe heat conditions, the cutaneous circulation can more than double its role in blood flow to comprise over 60% of the total vascular conductance (Johnson 1986), such interaction appears mandatory. There are several possible scenarios. First, vasomotor commands may be regionally directed via the RVLM by the hypothalamus and CAN based in part upon regional thermal information (and, one would expect, regional pressure information.)

If this is the case, and in light of our earlier discussion of CAN cooperativity, the project of demonstrating a fully spatially representational system in the ANS will be complete.

Before we can come to this conclusion, however, the other scenarios must be ruled out. These are scenarios which are consistent with non-representational thermally driven regional variation in hemodynamics. First, there might be no central interaction between temperature and pressure control. In this case, regional hemodynamic variation might be entirely due to "central commands" (Jansen et al. 1995) related to blood pressure control in the defense reaction for instance, or any such thermally related variation could be due to purely local or spinal mechanisms. The interactions between temperature and pressure would occur only at the effector, i.e. the blood vessels. Second, the central interaction between the two systems might be relevant only to global output, again with central pressure commands or local/spinal mechanisms explaining regional variation. The regional variation might even be regulated by a separate, non-representational, non-integrative higher central network which interacts with the pressure control system only in a global fashion - this would be functionally equivalent to point-to-point spinal reflex regional control.

Unfortunately, the physiologists have not caught up with the anatomists here. Results of investigations into regional vascular control as a result of thermal inputs have been equivocal about the role of central structures. Some of the effects are certainly due to local release of vasodilatory chemicals in direct response to heat

(Jänig 1990). But simply because, for example, some locally mediated thermal stimulus linked regional hemodynamics have been demonstrated does not mean that central mechanisms of accomplishing the same task do not exist. The nervous system commonly possesses distinct mechanisms and structures for doing the same job, either in parallel or as "backup." Let us look at what evidence there for the involvement of central structures.

Is there central integration between temperature and blood pressure control? The functional independence of the thermoregulatory system from the pressure control system is felt to be indicated by the different discharge patterns of the relevant sympathetic postganglionic neurons. Vasoconstrictor neurons which project to skeletal muscle exhibit the cardiac-related rhythm thought to be characteristic of pressure related control, whereas cutaneous vasoconstrictor neurons lack this rhythm (Jänig and McLachlan 1992). So, it is suggested, the cutaneous vasoconstriction might be a product of generalized action of functionally autonomous preganglionic neurons in the paraventricular hypothalamus, which bypass the topographically organized RVLM. Since stimulation of the RVLM evokes regional cutaneous vasoconstriction, presumably relevant to blood pressure (Key and Wigfield 1994; see section 2.5.1), cutaneous pressure and thermoregulatory responses would be additive on this model.

They are not additive, however. Blood pressure affects both the threshold and slope of cutaneous thermoregulation (Johnson 1986), and if the effects were purely additive, only the slope would

vary. So there is at least some integration of pressure and temperature regulation before the postganglionic neuron or effector is reached. (Johnson [1986] suggests that the cardiac rhythm is difficult to detect in cutaneous nerves because of the low ambient temperature used in the typical experiment, and cites a study [Bini et al. 1980] where higher temperatures were used and pulse-synchronous activity was observed in sympathetic cutaneous nerves.)

The threshold for cutaneous thermoregulatory response also depends upon core temperature (Johnson et al. 1984), providing further evidence that cutaneous vasomotor responses due to thermal stimuli are not purely local effects or peripheral reflexes. An alteration in set-point probably occurs at the level of the hypothalamus, since that is where the set-point is determined.

So we know that thermally related vasomotor responses are centrally controlled, and that there is central cooperation between this system and the pressure control system. This, however, still leaves open the possibility that thermal stimulus related *regional variation* in hemodynamics are determined purely peripherally, by spinal reflexes, axon reflexes, and local release of diffusable factors (Jänig 1990). Is this all there is to it? The regional control of the vasculature by amino acid injections into the hypothalamus suggests not, but absolute proof is lacking. Let us look at one more modality.

2.6.4 Ergoreceptors

So-called "ergoreceptors" are a heterogeneous group found within skeletal muscle, hypothesized to play a major role in cardiovascular responses to exercise, movement (Shepherd and Shepherd 1992), and posture changes (Wieling and Shepherd 1992). These responses are called the somatosympathetic and somatoparasympathetic reflexes; I will focus on the former.

Ergoreceptors give rise to group II, III (Aδ) and IV (C, unmyelinated) afferents, all of which have access to the ANS (Person 1989), though approximately 50% of the total give rise to conscious effects as well, mostly pain due to group IV fibres. The foremost autonomic afferents, group III and IV, outnumber group I and II afferents arising from mammalian skeletal muscle (Kniffki et al. 1981); group I afferents have virtually no access to the ANS (Sato and Schmidt 1973) and project via the dorsal column-medial lemniscal path to the thalamocortical system (Martin and Jessell 1991). So the projections we are concerned with are groups II, III and IV fibres which synapse solely or via collaterals (especially for group IV) in the CAN. All of the studies cited here make use of anaesthetized or decerebrate animals, so participation of conscious systems may be ruled out. The anaesthetized animal may give somewhat abnormal responses, but the main thing is that the thalamocortical system is not involved. Apparently, anaesthesia does not eliminate early cortical responses generally (Llinás and Paré 1991), but there appears to be no such cortical participation in the somatosympathetic reflex (McKitrick and Calaresu 1993).

Ergoreceptors may respond to specific chemical stimuli such as the products of muscle metabolism (nociceptors only), movement, or temperature. (It has been suggested that some may have a broad response profile, preferring one but reacting to many different types of stimuli. However, histological studies and other considerations tell against this proposal [Kniffki et al. 1981].) Their vast numbers and widespread distribution suggest participation in spatially representational cardiovascular responses. Their effects are achieved via input to the NTS (Person 1989) and output from the RVLM (Zanziger et al. 1994), which are the structures at either end of the system I contend accomplishes spatial representation. In between, a Fos study[5] has implied involvement of many other CAN structures, including the locus coeruleus, lateral parabrachial nucleus, the Edinger-Westphal nucleus, the peripeduncular nucleus, the central nucleus of the amygdala, the para- and periventricular hypothalamus, supraoptic nucleus, subfornical organ, and bed nucleus of the stria terminalis. It has long been known that somatosympathetic responses are strongly influenced by the internally generated cardiac rhythm recently described by Gebber and Barman (Sato and Schmidt 1973), which further suggests participation of the central cardiovascular network

The spatial selectivity of somatosympathetic reflexes is indicated by a number of lines of evidence. First, they are

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[5] Fos or C-Fos is a transcription factor, the protein product of a proto-oncogene (c-*fos*) that is expressed in synaptically active neurons. It is detected by antibodies with attached dyes, and is helpful in elucidating pathways activated by particular stimuli.

hypothesized to be responsible for the spatially selective effects of acupuncture (Sato and Schmidt 1987). Second, there are somatic stimulus-dependent spatially selective effects on sympathetic nerve discharge and vasoconstriction (Sato and Schmidt 1973; Jänig 1975; Sato and Schmidt 1987). Typically, it is assumed that this directedness is accomplished by the non-representational early spinal reflex component (Sato and Schmidt 1987; Person 1989), and the regional differentiation of the late, supraspinal component is dismissed as an epiphenomenon (Person 1989). However, there is at least a functionally relevant lateral selectivity of the supraspinal component, due in part to selective activation of the RVLM topography (Zanziger et al. 1994). Further, there is a similar stimulus dependent selectivity for cutaneous vs. subcutaneous vasoconstriction. Given the topography of the RVLM, and the conclusion of several researchers that in the intact animal, the somatosympathetic reflex is predominantly supraspinal (Sato and Schmidt 1987; Zanziger et al. 1994) it would seem that a more careful examination of centrally caused regional variation in SND as a result of stimulation of somatic afferents is in order. This modality or group of modalities seems to hold the most potential for a clear demonstration of spatial representation of qualities/feature discriminations on the "sensory" side of the ANS.

2.6.5 Final analysis

The modality-specific experimental results, especially for ergoreceptors, are suggestive of spatial representation on the

"sensory" side of a cardiovascular control system having the NTS as a primary sensory area analogue, and the RVLM as a primary motor area analogue. However, the results for each separate modality are not conclusive, so we cannot say which stimulus qualities are spatially represented. Nevertheless, I think we can be fairly confident that the ANS spatially represents. This conclusion is warranted by the cumulative evidence of the individual modalities supplemented with the result of Ermirio et al. (1993) mentioned above in section 2.6.1.

Ermirio et al.'s result was that the topographically organized RVLM responds differentially to regional afferent stimulation. That this regional activation difference in the RVLM is functionally relevant is supported by studies in which varying regional vasoconstriction was observed with varying (modality indeterminate) afferent stimulation (Aars and Akre 1970; Calaresu et al. 1984; Ammons, 1988; Nosaka et al. 1991). These afferents were stimulated at an anatomical level where local effects and axon reflexes may be ruled out. So the RVLM, and thus regional vasoconstriction, are differentially controlled by the CAN based upon the spatial location of the relevant stimuli. It simply remains to be seen which stimulus modalities are responsible for this effect.

Oddly enough, Ermirio and her coworkers believe their results support the opposite conclusion. After alluding to the studies where regional vasoconstriction was obtained by amino acid injection into the RVLM, they go on to say:

However, the existence of efferent topographical organization within the RVLM does not necessarily imply that afferent inputs should be organized in a [sic] same manner. On the contrary, the demonstration of multiple inputs on single RVLM units suggests that such neurons should be involved in generating global autonomic responses to different peripheral inputs.

Even though the RVLM responses they observed were differential with respect to regional afferent stimulation, they are worried by the fact that RVLM neurons can respond to more than one regional afferent. Such a worry does not warrant the conclusion they draw, that different afferents have only a global effect on sympathetic outflow. Multiple afferent responses for a single RVLM neuron is certainly inconsistent with a non-representational, simple point-to-point reflex control of regional blood pressure, but it is precisely what is to be expected from spatially representational control by a cooperative network, where inputs from different areas are related to one another in the context of the whole.

2.7 Conclusion

If one takes the line whose inevitability I am suggesting, and accepts that the CAN spatially represents, then the complex "sensory" and motor aspects of the cardiorespiratory system should easily meet Dennett's requirements for adopting the "conscious stance" and considering the ANS to be phenomenally conscious. The CAN performs feature discriminations, perhaps of blood pressure, temperature, and/or muscular contraction, and regionally directed autonomic responses are determined by the locations of these stimuli

in the context of the whole body. This meets all of Dennett's requirements for the basic attribution of experience. However, we simply do not feel our blood pressure (see Chapter 1), so Dennett's theory cannot be correct.

Dennett, in fact, would be happy to attribute consciousness to the ANS, since he views conscious beings as a continuum extending from the simplest organisms and complex artifacts (e.g. computers) all the way to human beings. The complexity of experience simply depends upon the experiential content one is prepared to grant a system through adoption of the conscious stance. In conversation, after I pointed out some of the complexities of ANS operation, he suggested to me that the ANS would have approximately the same degree of consciousness as someone blind and deaf since birth. (He seemed to be assuming that the ANS "consciousness" would somehow be separate from consciousness associated with the somatomotor system, a questionable assumption in itself given the extensive connections between the two [Cechetto and Saper 1990]). I suggest that those of us who take this to be a *reductio* of his view turn to another account of representation.

CHAPTER 3
Misrepresentation and Temporal Representation

3.1   Dretske, sensory representation, and natural functions

Now that Dennett's instrumental theory of representation has been shown to apply to the ANS, it is time to consider Dretske's thoughts on representation.   There are three aspects of Dretske's theory which need to be considered.   The first two, which I will address in this chapter, are his "natural functions" approach to phenomenal consciousness, and the importance he attaches to misrepresentation.   In Chapter 4, we will examine Dretske's analyses of belief and desire.   An understanding of all three of these components is needed in order to grasp Dretske's view of consciousness, but the ANS comparison strategy may be applied to each component separately.

Remember that there is little difference between Dennett's heterophenomenology/conscious stance and his intentional stance. There are just differences in the degree of complexity of the judgements one is prepared to grant a system or subsystem the ability to make.   Dennett says that qualitative states simply have a richer content (commentary section in Block 1995).

Though Dretske's theory (1995) is representational, he draws a stronger distinction than Dennett between propositional attitude type states and perceptual/imagistic type states.   The former, he says, involve conceptual representation, while the latter involve non-

conceptual representation. This is the difference between visually sensing the blueness of a shirt and seeing *that* the shirt is blue. To visually sense blue, one need not possess the concept of blueness, whereas to see a shirt *as* blue, one must possess the concept because one is performing a categorization. The shirt is blue *rather* than red, or green...

We are concerned with phenomenal consciousness, which is Dretske's non-conceptual representation. He also calls this *sensory* representation, the content of which is fixed by the biologically determined *function* of a sensory system. These functions are natural functions, as opposed to conventional functions. A spring scale has a conventional function, assigned by us, of determining an object's weight. We could just as easily have assigned it the function of determining height above sea level (with a constant mass attached), since the acceleration due to gravity decreases as the distance from the centre of the earth increases.

On the other hand, a heart has a very different way of acquiring its function. The designer of a heart is evolution, so it has a natural function of pumping blood. Crucially, the heart exists *because* it performs the function of pumping blood, or more accurately, because past hearts of which the present one is a replica performed the function of pumping blood. Hearts have offered their owners an advantage in the face of natural selection in virtue of their pumping of blood, at least at some point in phylogenetic history. Thus a heart does not have the function of making thumping noises, because these have conferred no evolutionary advantage. (Other

niceties must be added to avoid counting a screwdriver as having a natural function because it was created by someone who saw another screwdriver operating, became enthusiastic, and made one of her own. See Millikan 1989a for a fuller story.)

Dretske proposes that a sensory representation has the natural function of providing information about the properties of objects or states of affairs. The phenomenal nature of a sensory representation is determined by the discriminatory powers a sensory system has as part of its natural function. Our taste system has evolved such that it gives us the capacity to distinguish between Châteauneuf-du-Pape and Rumpole of the Bailey's "Château Thames Embankment" (a.k.a. "Pomeroy's Plonk"), and our qualia are correspondingly detailed. Dretske emphasizes that this phenomenal detail does not depend on my actually being able to distinguish between the two. This further step depends upon my ability to discriminate and conceptualize the difference, something that must be learned (see chapter 4). I must, in this case, realize the capacity I have thanks to the information my sensory states have the naturally acquired function of providing. In other words, I must learn to *use* this information.

It is hard to doubt that the ANS possesses sensory representations according to Dretske's theory. The ANS is certainly the product of evolution and development, and considerable evidence was adduced in Chapter 2 suggesting that it represents qualities, like temperature, at certain locations in the body. But there is another level to Dretske's theory. He requires that sensory representations, in order to be truly "experiential" and mental, must

service a system which can learn, so that they can be used to meet needs and desires. The information that sensory representations have the natural function of providing must be poised for use, though as pointed out above in the wine example, this capacity need not be realized. Both learning and desire will be examined in the next chapter. For the moment, we will examine an issue which is one of the main forces which shaped Dretske's theory - the need for an account of misrepresentation.

3.2   Misrepresentation

One of Dretke's main reasons for developing his theory of sensory representation along the lines that he does, i.e. using evolutionarily determined natural functions, is his belief that a theory of representation must explain the capacity for misrepresentation. In *The Power to Misrepresent* (1957), Roderick Chisholm calls this capacity the first mark of intentionality. Misrepresentation is ubiquitous, possibly more common even than correct representation. Consider for example how often we unknowingly misrepresent how far away an object is (those mountains in the distance), the fine details of an object in plain view, peripheral stimuli, or the dark side of the moon. Since we do misrepresent, a theory of representation must explain how this is possible. Unfortunately, both causal/informational theories of representation and causal role theories of representation face formidable difficulties in providing such an explanation. I will attempt to describe how a combination of these two theories is able

to give a naturalistic account of representational error, where the need to cite external properties, like evolutionary histories (Millikan 1989a, 1989b; Dretske 1995) is avoided.

3.2.1   Causal theories

Most of the literature about misrepresentation (e.g. Dretske 1986, 1995; Millikan 1989a, 1989b; Papineau 1987; Fodor 1990) has been concerned with the case of perceptual misrepresentation, presumably on the assumption that once you have that, an account of representation more removed from one's immediate surroundings will come with relative ease.   This assumption certainly applies to the account that I will eventually give, so I too will start with the case of perception.

On the simplest causal theory, an object or state of affairs S causes in some representational system a state R, which represents precisely the object or state of affairs which caused it.   But there can be no case of misrepresentation on this account since R can only be a representation of whatever caused it.   In order for there to be an error, R, *per impossibile*, would have to be caused by something it was not caused by.   R could be taken to represent the disjunction of all the states of affairs which can cause it, not a contradictory result, but certainly an unsatisfactory one as it does not allow for misrepresentation.

Another problem with this simplistic view is that there is no principled way of deciding which of its causes R represents - S could

be taken as a proximal cause (e.g. light waves) or a distal cause (the object reflecting light.)

There are a number of strategies one might follow in an attempt to rescue this view. Perhaps R, in actual fact, must "reliably indicate" S. That is, actual past or past-and-future R-tokens (given that they may be subsumed unproblematically under a type) must predominantly co-occur with S-tokens. This would disallow cases of perceptual representations which predominantly occur in the absence of their representeds. Are there such cases? Most certainly - Dostoyevsky's Raskolnikov who sees in every passer-by the man who has come to arrest him, for instance. Or the monkey who screeches to indicate danger to the rest of his troupe, though actual danger may only rarely be present (Millikan 1989b). These cases also present problems for similar rescue attempts phrased in dispositional language, such as "R is more strongly disposed to co-occur with S than any other object or state of affairs." A particular non-threatening state of affairs may have just as strong or an even stronger tendency to cause the monkey to screech as a threatening state of affairs. Compare the shaking of tree branches by a harmless giraffe or anthropologist to the silent approach of a poisonous snake. Even the majority of states of affairs which are threatening to monkeys could have weaker tendencies to cause R than the anthropologist.

Another possibility to rescue the simple causal theory would be to define correct perceptual representation as that which occurs under "ideal conditions." But what are these? They would depend

upon the stimulus. Its predominant modality (e.g. visual vs. olfactory) would determine ideal conditions, and so would particular aspects of the stimulus within a modality. Some objects are seen most easily with infra-red light, others under fluorescent white light for example. Different aspects of a stimulus may thus have different ideal conditions. Could one define a correct representation under a disjunction of ideal conditions? No, for in each condition, one could attend to an aspect of the object for which the conditions were not ideal, allowing for misrepresentation under any of the disjuncts. And to specify to which aspect of the stimulus attention is directed under each condition would be to smuggle in correct representation. What mental state counts as attending to the motion rather than the colour of a merry-go-round?

"Normal conditions" would be equally unhelpful, since misrepresentation may occur more frequently than correct representation, as in the case of the monkey sensing danger. And any appeal to "conditions under which correct representation in fact occurs" is of course question-begging.

It is not my intention to enumerate all of the problems with causal theories of representation, nor to trace the course of recent debate. I simply wish to make vivid some of the most important problems a theory of representation must overcome in order to account for error.

Millikan's and Dretske's appeals to evolutionary history are meant to solve the problem of misrepresentation in the following manner. Phylogeny defines what a representation indicates as its

natural function. This gives us a definition of correct representation which does not depend upon what is *actually* causing instantiation of the representation *now*. Thus, when the tokening of a representation is *now* caused by something other than what it is the natural function of the representation to indicate, we can say that misrepresentation has occurred.

The causal history account of natural functions and representations falls victim to the "swamp grandmother" objection (Davidson 1987). Suppose, against astronomical odds, an exact replica of your grandmother congealed out of a swamp in the Florida Everglades. According to Dretske, Millikan et al., even though this replica is physically indistinguishable from your grandmother, the replica's heart does not have the function of pumping blood, and neither do her mental states represent anything. This is because the replica does not have the right evolutionary history. Millikan, for one, is prepared to bite this bullet (1989a), but for those who find that impossible, it would be nice to have an alternative account which can explain misrepresentation.

3.2.2 Causal role theories

In causal role theories, representations get their meaning from their location in a causal nexus consisting of inputs, other representations, and outputs. For example, certain retinal stimulations may cause the tokening of R, "cat", which in turn causes "fun to pet," "makes me sneeze," etc. and in conjunction with the appropriate desire, the act of taking an anti-histamine. Different

theories specify the constituents of the causal nexus in different ways; conceptual role theories, for instance, require that inference relations apply between constituents. But no matter how they are specified, causal role theories maintain that the meaning of a representation comes down to place in such a system, or, perhaps more accurately, a certain subset of a representation's dispositions.

Here is the problem with regard to misrepresentation: if meaning comes down to a representation's *actual* dispositions, how are mistakes possible? If R ("cat") can be caused by a particular retinal disturbance (caused, in fact, by a dog), and has the same dispositions as "cat" caused by retinal disturbances caused by a cat, then there are two possibilities. First, the dog-caused retinal stimulations can be included in the causal role analysis defining the representation "cat." Alternatively, the dog-caused retinal stimulations can be included in the causal role analysis defining a different representation. In neither case is there anything like misrepresentation, since their is nothing about the dispositions of "cat" itself which ties it uniquely to cats, but which allows it to be caused *via* some faulty machinery by dogs as well.

One can imagine similar rescue strategies to save causal role theories as for causal/informational theories. They fail for similar reasons. For example, one might attempt to define the "ideal" or "normal" causal role of a representation by appealing to external or internal (brain) conditions, but ideal conditions may vary and correct representation may be quite abnormal.

There is another type of rescue available to the causal role theorist. (The causal/informational theorist might tack it on as well, but this would change the nature of the theory, bringing it closer to a causal role analysis.) It involves an appeal to benefits for the organism. Correct representation, on this account, is more likely than misrepresentation to lead to the satisfaction of the organism's desires, needs, or other good things. The problem with this is that there are many misrepresentations which are beneficial to an organism. The placebo effect, operative not only for placebos but active drugs as well (Wall 1993), is an obvious case. Misrepresentation of the placebo as a drug results in the misrepresenter's health improving.

3.3   Misrepresentation continued: The combined theory

3.3.1   Imagery and perceptual expectations

The theory of misrepresentation I am proposing is based upon C. B. Martin's theory of metaphysics, mind, and brain. One of the keystones to Martin's theory of mind is the proposal that thought is always imagistic. (This has also been suggested by Jackendoff (1987), among others.) That is, conscious thought involves (but does not consist in) the manipulation of images. Percepts may also be involved. The value of these imagistic manipulations in all modalities - sight, olfaction, propriokinesthesis etc. - is that one can "try out" various perceptual/behavioural possibilities on an "internal stage", thus preparing oneself for the actual situations. (The internal stage is not of course located in a Cartesian Theatre!) The

preponderance of neuroscientific evidence suggests that imagery and perception occur in the same brain regions (visual - Farah 1995; Kosslyn and Shin 1994; auditory - Intons-Peterson 1992), so plastic effects of internal staging affect subsequent perception and action. That is to say, modification of neuronal properties due to imagistic processes can have useful long term effects.

Neuroscience and neuropsychology are beginning to show that the importance of imagery to perception has been greatly underestimated. Top-down influences in perception have long been recognized (see e.g. Gregory 1970, Ramachandran and Anstis 1983), but only recently have theorists begun insisting upon the pervasiveness in perception of "predictive representations" (Churchland et al. 1994).

> [T]he increased 'intelligence' commonly associated with increased size of the cortical mantle may be a function chiefly of greater predictive-goal-relevant representational power, not to greater representational power per se (Churchland et al. 1994, p. 58).

If Martin is right, and mental representations are founded in imagery, perception emerges as continual, active, and predictive imagistic modeling of the external world based on sensory cues, rather than mere passive absorption of the stimuli the world throws at us. At any time, an experience would consist largely of entirely internally generated representations, or those which have been "helped along" by external stimuli sometime in their immediate past or are being so helped presently.

Such a model is supported by comparing the extremely small window from which detailed visual information may be gathered, with the knowledge and apparent awareness one typically has of one's surround, extending even out to the periphery and beyond (Rayner et al. 1980). Computational models have shown that shape recognition is more efficient when stored "models" are activated to complement input (Lowe 1987), and neuropsychological evidence supports this role of imagery in recognition, especially when a stimulus is partially obscured or otherwise rendered more difficult to perceive (Cave and Kosslyn 1989).

Brain imaging studies also support the model of imagery participating in perception in a predictive manner. Based upon a magnetoencephalographic comparison between wakefulness and dreaming, Llinás and Paré (1991) have suggested that wakefulness is an internally generated, dreamlike state "modulated" by sensory input. Kosslyn and his colleagues have shown that imagery primes perception (Kosslyn and Sussman 1995), and Freyd (1987) has described a phenomenon called "representational momentum" which strongly suggests the presence of imagistic perceptual expectations. When an observer sees a sequence of images following a trajectory, he or she tends to recall the end of the sequence as if the object had gone further than it actually did. Finke and Shyi (1988) found that these memories of extended trajectories were highly correlated with the actual rate of the implied motion of the object, suggesting an imagistic extrapolation.

3.3.2 The theory

In order to get started on a theory of misrepresentation, one needs to accept the implications of the above, though the extent of the phenomenon of imagistic perceptual expectations is uncertain. Taking that step into theory, though, consider a brain state R, purported to be a representation of object X.   R is possessed of indefinitely many dispositions; according to Martin, these dispositions determine R's content.[1]   We are assuming that some of the dispositions of R must include imagistic perceptual expectations (by which I refer to the dispositions rather than the imagery manifestations).[2]   These dispositions are only a subset of those which determine R's content, but their manifestations are very special ones in that they are phenomenal and sensation-like.   If the perceptual

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[1] Thus far, Martin's theory sounds as though it has much in common with causal role theories, which it possibly does. But the set of dispositions of R which Martin counts as relevant to content are delimited very differently from any causal role theory in print today. The dispositions which count are "use" dispositions, in particular *representational* use dispositions. Martin gives a naturalistic account of representational use in *The Powers of Mind and Their Role in Nature* (ms), and I have tried to explain a part of it in the lengthy discussion of spatial representation above, and more on temporal representation below. In this section, I am giving an account of the minimal requirements for misrepresentation; the full story requires the other half, namely some fundamental requirements for what makes something even a candidate for representational status. If it is felt that the potential for misrepresentation is also necessary for representation, it comes on top of these other, basic requirements.

[2] A brief outline of Martin's metaphysical framework for causation is in order here. Martin claims that all properties are dispositional (though not purely so), and that all properties which are operative for a particular result in a causal situation are "reciprocal partners" for their "manifestation" (the result). So the expression "mutual manifestation of reciprocal disposition partners" is meant to replace the expression "cause and effect." Dispositions exist whether or not their reciprocal partners do, and the basic notion is not disposition-for-manifestation, but dispositions-with-reciprocal-partners-for-mutual-manifestation. Qualitatively identical manifestations may be the product of very different reciprocal partners. (In the main text, qualitatively identical manifestations are called the same manifestation.)

expectations of R are *correct*, their manifestations will be very similar to the sensations that would occur if further observation, exploration, and manipulation of the object being represented were to happen. If they are incorrect, these manifestations will differ. In the former case, R is a correct representation, and in the latter case, it is a misrepresentation.

The important similarity or difference is between the manifestations in imagery and perception. Here is a schematic of the two situations:

1) Reciprocal partners - a) activity in a brain region corresponding to the internal representation

   b) brain region corresponding to the sensory field

Manifestation - an image

2) Reciprocal partners - a) external object or state of affairs

   b) brain region corresponding to the sensory field

Manifestation - a percept

Note that there is a common reciprocal partner between the two, i.e. the sensory field, and it is there that the similarity or difference is determined. The model is anatomically plausible since there are massive feedback connections from "higher" to "lower" visual areas (the modality for which there are the most detailed anatomical maps) which even exceed projections in the opposite direction (Llinás and Ribary 1994).

To illustrate - let us say there is a dog curled up on a chair, and I look at it and misrepresent it as a cat. I am suggesting that my representation of "cat" possesses dispositions for imagery of the cat

as I observe it further, perhaps from different angles or if I manipulate it, if I listen to it, etc. The representation of "cat" might have dispositions for imagery of the shape of its ear when it moves its paw away in a cattish manner, for the look of its face which is presently hidden, for auditory imagery of a "meow." Correct representation occurs when these perceptual expectations are met, or would be met if the further observation and exploration were to take place. Misrepresentation occurs when there isn't enough similarity between the perceptual expectations and the actual counterfactual perceptual situation. If I were to continue to observe the dog, or examine it more closely, or if it were to move, the perceptual results would not match the imagistic perceptual expectations of the "cat" representation.

3.3.3 An alternative to match/mismatch - reinforcement

Since single neurons may participate in many different networks, when misrepresenting it is even possible for the perceptual expectations to be physically inconsistent with the actual perceptual situation. If the further perception were to occur, there are two possible results, depending upon whether there is correct or misrepresentation:

> If the generated image strengthens the input to visual memory, then it matched the input image. In this case, the generated image would simply add onto the image from the eyes, producing a greater signal to areas farther downstream. When the generated image does not match the image in the visual buffer, the input to visual

memory would become noisier, not stronger (Kosslyn and Sussman 1995).

(The "visual buffer" is the brain area [whatever it happens to be] corresponding to the visual field.) Kosslyn and Sussman assume that the perceptual expectation image is actually generated prior to the perception; this need not be the case, since the manifestation in the sensory buffer may have as its sources the dispositions of the buffer itself, the external object, *and* the internal representation, with the latter two in varying combinations. This gives us another way to determine correct or misrepresentation, if one is suspicious of the similarity and difference alluded to earlier. One could simply refer to the strengthening or weakening of the further sensory input, were it to occur.

3.3.4   The specificity of representation

There will be different degrees of misrepresentation - if there is no similarity between the manifestations of a representation's perceptual expectations and the actual perceptual results of further exploration and observation, then the representation is probably more appropriately described as an hallucination, rather than a misrepresentation. Absolute similarity would be rare; if there is a high degree of similarity, then one might want to call R a correct representation. I think this fuzziness of the natural line matches the fuzziness of our conceptual line between correct and mis-representation.

If a representation is rather vague, which is often the case, then the perceptual situation corresponding to/reinforced by the representation's perceptual expectations will be more general, perhaps disjunctive, determining a set of possible brain results in the sensory buffer. A correct representation will be one in which the sensations of the actual perceptual situation fall within the range determined by the perceptual expectations. This makes sense, since the possibilities for misrepresentation should match the complexity of the representation. Representing the dog as an animal of a certain size implies perceptual expectations consistent with the represented being either a cat or a dog, or any other beast of that size. When I see a person in the distance, my perceptual representation may possess dispositions for further non-specific perceptual expectation imagery, blurry and faceless, or a range of imagery of my friends Tom, Dick, Harry, and everyone else I know.[3] It may also, for instance, lack any perceptual expectations of odour. The specificity of a representation depends in part upon both the richness in detail and narrowness in range of its perceptual expectations, the expectations which will reinforce the sensory buffer in the actual perceptual situation.

Analogously, a simple thermostat will give the same response in a wide variety of situations, but a complex thermostat which measures rate of temperature change and the distribution of heat in

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[3] Here I am ignoring worries about externalism and rigid designation. It is the *internal* part of intentionality that is getting attention. Surely there is always some internal part - as C. B. Martin says, the external world does not just magically zap us with content (Armstrong et al. 1996).

a room will have more specific directedness. The thermoregulatory system of the ANS will exhibit more specific directedness still. Whether any of these systems *misrepresent* depends upon whether they have something equivalent to perceptual expectations (see section 3.4).

3.3.5 Replies to objections

At no point am I illicitly smuggling representation in. All that is required is that a particular perceptual situation have a determinate neurophysiological result in the sensory fields or buffers of the brain. This result can either match/reinforce or fail to match/reinforce perceptual expectations, which are determinate dispositions possessed by a representation. The match or non-match is determined simply by a comparison of particular sets of neurons firing, or by reinforcing feedback.

There are three questions that could be asked in challenge. First, is a sensory state really determinate? For example, couldn't malfunction result in an object causing very strange sensations, nothing like the normal ones? Then a match of perceptual expectations might be obtained when there ought to be a case of misrepresentation. Second, how is the representation identified with a particular brain state? And third, how is the "actual perceptual situation" specified non-question-beggingly?

The first two questions may be answered together. Given an external state of affairs, a sensory state is determinate, or determinate enough, because there are a finite number of brain

states that can be truly caused by a particular object or state of affairs. Any brain state might co-occur with any external object in an organism's perceptual field, but assuming some robust, realist, non-regularist theory of causation, only a certain number of brain states can actually be caused by the external object. This will be another fuzzy line, but one can imagine a causal chain leading to the misrepresentation of a tomato as an orange, but not the misrepresentation of a tomato as an elephant.[4] The latter case will be an hallucination, not a misrepresentation.

On Martin's view of causality, there will always be a fact of the matter of which dispositions are manifested in a particular causal situation. You can be sure that when a person represents "elephant" when looking at a tomato, the vast majority of dispositions manifested will not be the tomato's for the visual buffer and vice versa. Or at least not the visual buffer's for the representation and vice versa. Each of these links is required for both representation and misrepresentation, and this is where the causal theory contributes an important element to the combined theory.

Similarly, in a visual scene, an object will be causally related to its representation in the brain, while the background will not be. Thus the causal connection in perception helps determine what is being represented and what in the brain is actually doing the representation. There will also be specific tracking mechanisms disposed to keep the object or state of affairs in the perceptual field

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[4] C. B. Martin has made this point in lectures for years, with respect to the issue of infallibility/incorrigibility with respect to one's own mental states.

in order to maintain the representation. The tracking might malfunction, of course, but sensory feedback will correct it - the disposition is for maintaining the object in the perceptual field (for which there are perfectly determinate physical conditions), not for some specific tracking mechanism.

So given a perceptual situation physically specified, a sensory state is determinate because there is a fact of the matter about what items are causally related. And because a physically specified object, sensory buffer, and representation can be determined as causally related or not, one can specify what physical state of the brain is actually a representation without first appealing to the notion of representation. That leaves the third question, of how a perceptual situation can be specified by perceptual expectations without appealing to representation.

This third question needs some clarification by illustration. A particular representation will have dispositions for imagery which are not predictions of the results of further observation and exploration of the object or state of affairs represented. For example, the representation of a sheep might have associations with representations of a sheep shearing instrument, and thus possess dispositions to produce imagery of a sheep shearing instrument. So there will exist some dispositions for imagery which matches perception of a sheep shearing instrument, even though that is not what one is representing. But if one looks at a sheep shearer and represents it as a sheep, why is this not correct representation since the sheep representation has dispositions for sheep shearer imagery,

which match and/or will be reinforced by the actual perceptual situation? (Representing a sheep shearer as a sheep would probably be more properly called an hallucination, but one can imagine a case where the objects are similar enough to be classified as misrepresentation. I use the sheep and sheep-shearing instrument to make the example more vivid.)

In order to avoid this problem, there must be a principled way of distinguishing between perceptual expectations and other dispositions for imagery. The first thing to say is that upon closer examination of the sheep shearer, not only will one. of the sheep representation's dispositions be manifested, but the whole representational structure will shift to one of "sheep shearer." This will be marked in two ways. First, the neural assembly which is the representation (as determined by the causal links) will change. Second, the new assembly will have very different dispositions from the old one - in a true case of correct representation, the original representation is/would be *reinforced* by the actual perceptual situation.

Second, there is a built-in difference between dispositions for expected perceptions and dispositions for other imagery. The former are accompanied by motor and attentional dispositions, while the latter are not or are much more weakly so accompanied. In mental rotation experiments, where a stimulus is imagistically rotated, it has been hypothesized that one is anticipating what one would see if one performed a specific action (Kosslyn and Sussman 1995). The action

is straightforwardly implied by the dispositions to activate motor systems in a particular way, without a mediating representation.

I have come to the end my responses to potential objections to the combined causal/causal role theory of misrepresentation. It is really quite a simple theory, depending only upon the existence of perceptual expectations, which are dispositions a representation possesses. When one misrepresents, these perceptual expectations are for imagery which would fail to match some counterfactual perceptual situations. Or, if one prefers, these perceptual expectations would not be manifested in the counterfactual perceptual situations, and the neural assembly which is the representation would fail to be reinforced.

3.4 Misrepresentation in the ANS

3.4.1 Thermoregulation

We have already seen that the requirements for the capacity to misrepresent imposed by Dretske's natural function theory are easily satisfied by the ANS. All that was needed was for the CAN to possess internal states which were evolutionarily "designed" to indicate states of the body, such as spatially located blood pressures or temperatures (see section 3.1).[5] However, Dretske's theory was deemed inadequate because of its susceptibility to the "swamp grandmother" objection. This is why I felt it necessary to develop a

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5 Strictly speaking, applying Dretske's theory to the ANS does not require demonstrating the spatial representation of stimulus qualities, though in his (1995), especially in Chapter 3, Dretske often speaks of sensory representations as having spatial location content.

different account of misrepresentation, the "perceptual expectations" theory, based upon Martin's framework. Now we need to see if the ANS meets the requirements imposed by this new theory.

So in order to show the possibility of misrepresentation in the ANS, one needs to demonstrate the presence of perceptual expectations, which is one half of temporal representation (the anticipation half, as opposed to the "working memory" half - see section 3.4.3.) This is difficult enough to do for conscious systems, but the sort of evidence that would count is also found in the ANS. The most common example given of anticipation in the ANS, controlled by the CAN, is in thermoregulatory control:

> It is the ability to respond to rapid changes in the ambient temperature that provides the vertebrate thermostat with its predictive capability: the animal is able to anticipate a change in body heat content and take corrective action before that change actually occurs (Heller et al. 1978).

Changes in ambient temperature are detected by cutaneous thermoreceptors, which feed into the hypothalamus and CAN. Some evidence was proffered in Chapter 2 suggesting that these afferents are used by a spatially representational central system - there is certainly extensive integration of the peripheral and central temperature signals. Can the system be truly described as *anticipating* central signals? These might be signals from receptor neurons within the hypothalamus itself, or the spinal cord (Heller et al. 1978).

This is what would have to occur. Based upon temperature signals from the periphery, the CAN would internally generate the central representations of decreased temperature which were expected to result from future stimulation of central receptors. These central inputs would be expected because the cold environment would eventually cool down the body core (though of course the CAN would not "reason" this way; the expectations would simply be present.) The internally generated replicas of expected inputs would bring about an anticipatory heat generating response.

If this is indeed what happens, then the presence of perceptual expectations generate the possibility for misrepresentation. In this case, the misrepresentation would be of a state of affairs (a temperature distribution) rather than an object. The CAN represents a certain temperature distribution (e.g. cold at the periphery); this representation possesses dispositions which may be described as perceptual expectations - expectations for inputs resulting from stimulation of central cold receptors, and decreased firing of central warm receptors. If the periphery is not in fact cold, then these perceptual expectations will not be met. There will be a mismatch of the expected inputs from central receptors - "the core is cold" - and the inputs that would actually occur - "the core is just right." Alternatively, there will be a lack of reinforcement of the current representation of the temperature distribution. The overall result is that the current representation - "the periphery is cold" - is in fact a misrepresentation.

This is certainly a plausible mechanism, but very difficult to prove. One would first have to identify exactly what the input signals from cold stimulated central receptors were, to see if they are replicated in the anticipatory situation.

The nature of the shifting hypothalamic "set-point" or "gain" determinant remains enigmatic, but one proposed explanation sits well with the above hypothesis. It is that tonic input to the hypothalamic set point determining cells increases or decreases, i.e. in *imitation* of afferent input, thus altering the effectiveness of actual afferent input (Collins 1992). (The "content" of thermoregulatory representation, then, would not be a specific temperature, but rather like the Three Bears' porridge: "too hot," "too cold," or "just right.") If this model is correct, anticipation of temperature change in the core would presumably be accomplished in the same manner, i.e. with imitation of anticipated input - perceptual expectations. What evidence is there which is consistent with this model, in thermoregulation or any other autonomic modality?

3.4.2 Feedforward

The simple fact that the anticipatory response described above is to a rapid *change* in ambient temperature indicates that temporal representation may be occurring. Any sensitivity to rate of change of input potentially involves a comparison of input at one moment with that from some previous moment, in order to predict and counteract input from some future moment. A population of receptor cells with different rates of adaptation is capable of

generating rate of change dependent signals (see J. H. Martin 1991), but central responses to rate of change may involve genuine feedforward control.

The term "feedforward" is often used merely to refer to connections which are not feedback, i.e. which go in the general direction of sensory afferents to higher control. However, feedforward in its original sense is a functional notion (Arbib 1987). Its primary advantage is speed of response - based on current environmental disturbances, i.e. current input, future input is predicted (perceptual expectations) and appropriate efferent signals are sent in the absence of feedback. "The cost [of feedforward] is paid in controller complexity: for the controller must have an accurate model of the effect of all such disturbances upon the system..." (Arbib 1987).

The first requirement for our perceptual expectation, feedforward model, is that there must be CAN neurons which are responsive to rate of change. These are ubiquitous to the CAN, not only in thermoregulation. For example, there are second order neurons (i.e. which do not directly receive "sensory" afferent projections) in the NTS whose firing rate depends upon both the absolute blood pressure and its rate of change (Rogers et al. 1995). Let us then turn to the control of blood pressure.

3.4.3 Anticipatory blood pressure control based upon somatic afferent information

In Chapter 2 we saw that somatic afferent inputs were relevant to blood pressure control. There are a number of empirical considerations which suggest a model wherein the CAN uses somatic afferent inputs to predict future blood pressure inputs. This would be an example of perceptual expectation, and thus would endow the CAN with the capacity to misrepresent.

Toney and Mifflin (1994) have shown a selective time-dependent inhibition in single units of the NTS which receive both aortic baroreceptor and hindlimb somatic inputs. When aortic baroreceptor inputs were activated first, after a delay subsequent NTS cell responses to somatic nerve inputs were significantly attenuated. On the other hand, if the somatic afferents were stimulated first, no inhibitory effect was observed for later baroreceptor stimulation. This is not dependent on the baroreceptor afferents, since the asymmetric effect is absent when the comparison is between baroreceptor afferents and other autonomic afferents (Mifflin and Felder 1990.) That is, delayed inhibition is observed in both directions. These data are consistent with a model in which future baroreceptor input is predicted on the basis of somatic afferent input, which typically signals the initiation of exercise or a change in posture.

Individual response patterns of NTS neurons in a somatosympathetic reflex paradigm reflect not only autonomically

relevant somatic afferent input but also higher centre input. Thus R. J. Person (1989) suggests:

> A second reasonable conclusion is that the NTS passes on to both sympathetic and parasympathetic effector areas of the medulla information concerning the level of immediate and planned activity in somatic and visceral structures. Autonomic end-organ activity is then modulated on a second by second basis according to the present and anticipated metabolic needs of both somatic and visceral organs by these sympathetic and parasympathetic effector areas.

This "planned activity" is not consciously planned activity - Person's experiments were carried out on anaesthetized cats. It is the planned activity of higher autonomic centres based upon somatic afferent input. The necessity for such prediction in the exercise reflex and postural change is obvious when one considers the speed with which the cardiovascular system responds to the change in cardiovascular variables when posture is altered. The variables begin to change almost immediately, and the sympathetic system simultaneously begins to counteract them (Wieling and Shepherd 1992). Typically, due to a certain inertia, the sympathetic system has a five to ten second response delay to experimentally induced cardiovascular alterations (Sato and Schmidt 1973), so the postural effect must be due to prediction on the part of the CAN.

Mathematical modeling of cardiovascular control shows that extensive temporal integration must occur. The "memory" side of temporal integration is like working memory. A representation is kept active in order to interact with later inputs. For accurate, individual specific prediction of cardiovascular responses in a simple

mathematical model system with only two vascular beds and the heart, information about pressure and instantaneous heart rate from several previous heartbeats must be used in order to accurately predict the current state of the system (Toska et al. 1996). (Dependence on actual prediction cannot be proven with mathematical modeling since the model only predicts behaviour, not the internal processes of the system. The system might use information in an anticipatory way to generate the behaviour, but this is invisible to the model which simply predicts the behaviour.) The time interval over which information is relevant to sympathetic operation seems to be about ten seconds.

What is being suggested here is that the CAN is temporally representational such that there is variable and differential control of the timing of outputs based on the timing of inputs. It is also very likely that the CAN achieves this temporal control by possessing perceptual expectations, in the above example as a result of previous somatic input from the muscles. For convenience, call the CAN's representation of the variables associated with standing a representation of "standing." This representation also possesses dispositions which are perceptual expectations for cardiovascular inputs. The expectations may not be met, or the original representation may not be reinforced, and thus the representation of standing will in fact be a misrepresentation. The actual representations in the CAN must be identified before there can be absolute proof that this model is instantiated, requiring very substantial advances in neuroscience. However, in the meantime, we

can still be reasonably certain that the ANS is capable of temporal representation, perceptual expectation, and misrepresentation.

3.5 The match/mismatch neuropsychological theory of consciousness

If, as I suggest, misrepresentation is possible in the ANS then we have gone one step further towards discrediting Dretske's theory of consciousness. But this potential for misrepresentation also shows that a particular type of neuropsychological theory of consciousness also cannot be correct. This is the "match/mismatch" theory, advocated by Jeffrey Gray (1993, 1995) and in part by Bernard J. Baars (1988). Both Gray and Baars have worked out (different) anatomies for the system that subserves the functional characteristic they describe, but I need only show that the ANS indeed possesses the function.

Baars uses the functional feature of match or mismatch detection to define representation, which he regards as necessary for consciousness. Gray, on the other hand, suggests that the contents of consciousness are generated by a comparison of the current state of an organism's perceptual world with a predicted state. This should sound awfully familiar, as this is precisely what is accomplished when perceptual expectations match or fail to match the actual perceptual situation. When they match, reinforcement of the input occurs. When they do not match, a noisy interference is generated.

Gray adds the further twist that when a mismatch is detected, new motor programs are induced. Consider the model of the thermoregulatory system wherein detection of a sharp rise in

ambient temperature by peripheral receptors causes a replica of expected response in the central thermostat. If the core temperature were to suddenly cool - failing to match prediction - one can be sure that a new thermoregulatory motor program would ensue. So the match/mismatch theory does not present any new obstacles to overcome in our project to parallel the features of conscious systems in the ANS.

3.6   Conclusion

Dretske's sensory representations have their equivalents in the ANS, since the ANS is the product of evolution and thus has natural functions of providing information about bodily states. Also, Dretske requires that for there to be true representation, a system must have the capacity to misrepresent. Dretske's own theory of misrepresentation is unsatisfactory because it falls victim to the "swamp grandmother" objection. However, the combined causal/causal role theory presented above was also shown to apply to the ANS. This is because the ANS possesses perceptual expectations. We are left with one final aspect of Dretske's theory which we have failed to address. He requires that "phenomenal information" be able to influence learning, and to take part in a belief-desire psychology. The naturalization of these concepts and their application to the ANS is what I shall address in the next chapter.

CHAPTER 4
Learning, Belief, and Desire

4.1   Introduction

I noted in the previous chapter that Dretske requires that sensory representations be used in learning for a system to be considered conscious.   In particular, the learning must occur in the context of a system describable as having beliefs and desires.   In this chapter, I will alter my usual order of exposition.   First I will show what sorts of learning of which the ANS is capable.   Then I will describe Dretske's theoretical account of learning, beliefs, and desires, and show how the ANS fits his model, using the evidence from earlier in the chapter.

If the basis of learning is the modification of cellular properties, such as the changes which occur in the phenomenon of long term potentiation (LTP), then it would be truly surprising if the ANS did not show some form of learning.[1]   LTP has been demonstrated in invertebrates like *Aplysia*; surely a system like the ANS, which is far more complex than these invertebrate nervous systems, would show activity dependent cellular modification as

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[1] The application of the term "learning" is a highly contentious issue, which is confused by the fact that it is often used in very diverse contexts. Psychologists of different stripes require either very strict behavioural or cognitive criteria to be met, whereas some neuroscientists call LTP learning.   I will use the term very broadly, covering LTP, certain aspects of development, as well as conditioning.   Nothing hangs on my use of the term - the important facts lie in the nature of the phenomena described.

well. It turns out that this intuition is true (Adamec 1993; Bennett 1994; Brooks and Glaum 1995). But we can show much more.

4.2   ANS development

Development of the nervous system is often activity dependent, for example in the formation of ocular dominance columns in the primary visual cortex (Kandel and Jessell 1991b). Development is thus a time highly concentrated in adaptive processes, and the ANS cannot be excluded from this generalization. It is not "hard-wired" system, with its structure determined solely by genetic instructions.

Autonomic systems, just like conscious ones, have a steep adaptation (learning) curve in the first few years of life. In the enteric nervous system (ENS), which is largely independent of the CNS, complex integratory functions are performed by the submucosal plexus and the myenteric plexus, both located in the wall of the gastrointestinal tract (see Chapter 1). The adaptivity of the ENS is demonstrated by the fact that

> the differentiation of neuroblasts into enteric ganglion cells and mature plexuses is quite delayed; in fact, at birth only approximately one-third of the neuroblasts are differentiated and development continues throughout the first 5 years of life. (Hamill and LaGamma 1992.)

Even a system as vital as thermoregulatory control displays incomplete responses until two to three months of age (Hamill and LaGamma 1992.) In fact, all divisions of the ANS are subject to environmental influences in development:

> Environmental signals are known to influence autonomic neuron maturation from the earliest stages of neural crest migration to the development and maintenance of the neuron's adult character. Mature neurons apparently are not immutable since alteration of the environmental milieu during adulthood will alter neuronal characteristics (Hammill and LaGamma 1992).

There is strong evidence to suggest that the tragic sudden infant death syndrome (SIDS) is due to improper ANS development in the brainstem (Schäfer and Schläfke 1995).

Hamill and LaGamma suggest that ANS adaptivity also occurs in the adult. The ENS provides another example here. The influence of the CNS on the ENS is minimal but present, such that cutting off CNS input results in reduced tone and degree of peristalsis (pushing food along by rhythmic contraction, as in swallowing.) However the ENS eventually compensates for disconnection from central systems by increasing the intrinsic excitability of controlling neurons in its plexi (Aber-Bishop and Polak 1992). I shall consider further examples of adult adaptivity in the cardiovascular system in section 4.5.

4.3 Individual specificity in ANS responses

A necessary consequence of the extended, environmentally dependent development of the ANS would be individual specific adaptivities. This prediction is borne out by autonomic responses in children and adults. An extended four year study of responses to the cold pressor test in children ranging from age six to seventeen (at the beginning of the four year period) indicates that early development

is individual specific (Lacey and Lacey 1962). In any individual, cardiovascular responses to immersion of the foot in cold water changed over the four year period. However, upon comparison of individuals of the same age, sex, and weight, individual specific characteristics or trends in response patterns were observed, and these were consistent over the four year period. Presumably these individual characteristics were determined earlier in development.

In another study of ten adults (mean age 23, standard deviation ±2), individual differences in autonomic function attributed to central control were discovered (Toska et al. 1996). Averages for each individual were taken over several runs of a procedure involving very rapid bilateral thigh cuff inflation. Individual differences in cardiovascular responses could be almost entirely accounted for by different values of a subset of eleven constants, which formed a part of a mathematical model developed from earlier empirical studies. The fact that an individually tailored mathematical model can predict an individual's cardiovascular response indicates that the variation is not due to random fluctuation.

This variation was not trivial. For instance, there was a seven-fold difference in gain (ratio of output to input) for sympathetic control of vascular conductance between two subjects, and a difference in the delay of this response as well. These subjects were less than a year apart in age; one was overweight. A significant portion of the difference in the extent of sympathetic vasoconstriction must be due to central control factors, since this

accounts for the vast majority of the response (see Chapter 2). There was also a twofold difference in sensitivity of the heart rate to parasympathetic control. This large variation is consistent with individual specific environmentally dependent adaptivity.

4.4   Problems with the notion of a "hardwired" system

C. B. Martin (ms) has shown that there is a fundamental difficulty in describing any complex, developing system as "hardwired." The nature of the genetic material is such that it provides a dispositional framework which, given the right disposition partners, will result in the acquisition of further dispositions, which given the right partners will result in the acquisition further dispositions... etc. The need for such an arrangement is apparent from the fact that there are only 50,000 genes expressed solely in the human nervous system (at a high estimate) but the brain alone contains 10^{13} synapses (at a low estimate.) Specific genetic determination of each synapse is an obvious absurdity - there is only one gene for every 200 million synapses! The dispositional framework responsible for development involves glial cell guidance, neurotrophic factors such as nerve growth factor (NGF), intrinsic and environmentally imposed neuronal activity, and many other processes which depend upon both intrinsic and external properties for their operation.[2] In the nervous system, conscious-related or

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[2] Glial cells are "supportive" cells in the nervous system, and they outnumber neurons ten to one. (They may in fact be involved in signalling, so the "supportive" description should be taken with a grain of salt - in general, glial cell function is not very well understood.) One of their functions is to guide developing neurons down the right path. Trophic factors and the like are

autonomic, to assign particular stages solely to the intrinsic or solely to the external contradicts the facts of development, and the use of the term "hardwired" cannot be taken literally.

4.5 Cardiovascular adaptivity

One of the best examples of ANS learning in the adult is the cardiovascular adaptations which occur during extended exposure to microgravity ("weightlessness" in space) or long periods of bedrest. Misconceived as a form of "deconditioning", the changes in the cardiovascular system which occur in astronauts during space flight are truly adaptive (Convertino and Robertson 1995). There is an initial period of adjustment lasting several days, after which astronauts are able to undertake physically strenuous activities, and there is a further period of re-adaptation required upon returning to terrestrial gravity in order to overcome orthostatic intolerance. Before the use of positive pressure anti-gravity suits, upon return to earth astronauts were often carried away from their spacecraft on stretchers and could give no stand-up press conferences for days (Convertino and Robertson 1995). The time scale involved here strongly suggests that it is an adaptive process which takes place, rather than pre-programmed response switching. The ANS would certainly not be "hardwired" for microgravity environments.

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substances which encourage or discourage a neuron to grow in a particular direction. For instance, a neuron could secrete a substance to attract another particular type of neuron towards it, thus increasing the chances to create a connection.

The alterations in the distribution of blood due to microgravity and the drastically reduced requirements for counteracting gravitational effects results in reduced stroke volume, reduced blood volume, the attenuation of neurocardiovascular reflexes, and other adaptivities (Wieling and Shepherd 1992). For example, in normal conditions the ANS counteracts the effects of gravity to ensure adequate perfusion of the brain in the standing position. This involves cardiovascular, skeletal muscle, and vestibular inputs, the latter two apparently used in a predictive manner (Wieling and Shepherd 1992; Yates et al. 1995a; see also Chapter 3). In space, initially there is an overperfusion of the upper extremities, but the ANS learns to redistribute the blood flow after a few days. Some of the changes most likely due to altered central circuits are a reduced efficiency of the baroreflex and the somatosympathetic reflex, which occur in both microgravity environments and with prolonged bedrest (Wieling and Shepherd 1992; Convertino and Robertson 1995). The exact nature of this central circuit adaptivity is uncertain.

4.6   Conditioning

Coming from the other direction, the behavioural studies of psychologists, the most basic types of learning are classical and operant conditioning. In classical conditioning, two stimuli are "associated." That is, the animal learns to associate a "conditional stimulus" (CS, the bell) with another, "unconditional stimulus" (US, food) which normally evokes an automatic or previously learned response, the "unconditional response" (UR, salivation. This example

of course comes from Pavlov's famous experiments with dogs.) Thus the CS comes to evoke the UR, which, after learning, is called the "conditional response" (CR).

In instrumental or operant conditioning, the animal learns to associate a behaviour with a future stimulus, called the "reinforcer." Thus a rat in a Skinner box learns to associate pressing a bar with getting food. In this type of conditioning, an animal "operates" on its environment.

4.6.1 Classical conditioning of the ANS

Autonomic responses can be classically conditioned, but most studies have been equivocal as to the locus for synaptic modification. Autonomic conditioning studies are performed on conscious animals, using stimuli such as tones and flashes of light as CS (Cohen and Randall 1984; Engel 1986, 1993). There are direct inputs into the ANS from modalities which are associated with conscious responses (visual [Martin 1989, Ch. 14], vestibular [Yates et al. 1995b], somatosensory [see chapter 2], gustatory [Loewy 1990b], olfactory [Loewy 1990a]), but the structures actually involved in the learning cannot be determined from behavioural studies alone. All the learning could be occurring in the cortex. Neither can the learning relevant structures be determined from behavioural lesion studies (see Kapp et al. 1981; Eldridge et al. 1981). The ablated region might be the locus of synaptic modification, but it also might be a conduit for the transmissible results of modification in some other area, or merely responsible for some aspect of performance of the learned

response, entirely unconnected with the learning itself (Vanderwolf and Cain 1994).

However, since spinal and decerebrate animals can be classically conditioned for a variety of somatic responses (Beggs et al. 1983), one would expect that decerebrate animals could have autonomic responses classically conditioned as well.[3] There are a number of lines of evidence from autonomic conditioning studies which support this contention, though no attempt has been made to autonomically condition a decerebrate animal using stimuli, such as blood pressure, having no conscious implications.

The short latencies of both sympathetic and parasympathetic responses to the CS are suggestive that the newly formed circuitry is subcortical. The late, consciousness-associated event related potentials fall 10 ms or more after the learned autonomic responses are initiated (Cohen and Randall 1984; Llinás and Paré 1991). But this does not eliminate the possibility that the cortex (or hippocampus) is necessary for the induction of the new sub-cortical pathway.

A dissociation between the time of emergence of somatomotor and autonomic conditioned responses in neonates of various species has been observed (Sebastiani et al. 1994). In rabbits, with a tone as

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[3] There is less of a difference between the capacities of the human and animal brainstem with respect to autonomic responses than other types of responses. For example, the decerebrate rat is capable of performing a wide range of well coordinated behavioural patterns (Lovick 1972), but a human who loses his cortex is reduced to a persistent vegetative state (Ingvar et al. 1978). One of the few major differences between the capabilities of humans and other animals in autonomic control is the well developed central control of vasodilation in humans (Kenney and Johnson 1992).

CS and a shock as US (which provokes tachycardia in both adults and neonates), a conditioned bradycardia is obtained in adult animals, as well as escape behaviour. However, in neonates older than ten days but younger than 18 days, the somatomotor but not the autonomic response is learned. Since it is neither an inability to learn nor an inability to demonstrate the normal cardiovascular response to a shock which explains the disparity, the two must be mediated by different mechanisms.

The dissociation between autonomic and somatomotor classical conditioning is supported by studies in humans as well. According to the cognitivist interpretation of human Pavlovian conditioning, including autonomic conditioning, cognitive awareness of the CS-US contingency is fully responsible for the conditioning phenomenon. This is false, since in a large number of studies, there is no correlation between cognitive awareness of the contingency and autonomic learning either within or between subjects (Furedy 1991). If the cognitive interpretation is correct about somatomotor responses, this suggests that autonomic conditioning is mediated by a non-conscious mechanism, quite likely located subcortically.

None of this is conclusive, unfortunately. The main difficulty in proving the existence of autonomic conditioning using the studies mentioned above is that the stimuli used are ones with conscious upshots. It would be easier to show true autonomic conditioning by using a US and CS which have solely autonomic consequences, such as pressure inputs. The problem here, as one might guess having seen much evidence of intermodal integration in this and previous

chapters, is that there are very few autonomic stimuli which are neutral for some other part of the system. (Indeed, there are very few stimuli in consciousness associated modalities which are neutral to the ANS [Furedy 1991].) In the usual classical conditioning paradigm, the CS is neutral. A related problem is that it is difficult to design an experimental setup where, for instance, respiratory inputs (the CS) are paired not with their usual consequences, but rather some other cardiovascular result (the US).

It seems that the astronaut examples provided above are perhaps one of the few situations past early development which could be interpreted as the pairing of CS and US to obtain a novel autonomic response. The cardiovascular system, in development, comes to "expect" certain cardiovascular responses given other cardiovascular inputs, respiratory inputs, vestibular inputs, inputs from the muscles, and perhaps others as well. When the system's "expectations" are contradicted in the microgravitational environments, new pairings are learned, resulting in the modified responses described in section 4.5. (It also seems plausible to intepret the initial development of intermodal ANS responses as classical conditioning. Indeed, stereotypical pure cardiovascular responses [i.e. based solely upon cardiovascular inputs] develop earlier than cardiorespiratory interactions [Lawrenson and Elliott 1981]. I rely more heavily upon the microgravity example because changes in the adult are less likely to be dismissed as "hardwired," though cf. Martin's concerns about this concept above.)

4.6.2 Operant conditioning in the ANS

It is difficult to apply the concept of operant conditioning to the ANS without cashing in the mentalistic notion of desire for some naturalistic replacement. The Skinnerian concept of an operant, as an activity of unknown internal origin (thus "emitted") whose later performance is influenced by its current consequences (Brener's commentary in Engel 1986) is unsatisfactory. This seems to rule out the presence of operant conditioning in the ANS, since autonomic behaviour is always in part a response to a stimulus. However, the origin of somatomotor operant response is not entirely internal or unknown. Presumably the rat's pressing the bar is in part explained by its seeing the bar, just as the autonomic behaviour caused by the CAN is in part explained by, say, a vestibular input. This stimulus dependence blurs the distinction between operant and classical conditioning. Blurring the distinction even further, components of an operant response are partially determined by "automatic" responses to stimulus conditions (Vanderwolf and Cain 1994).

On a more cognitive model, operant conditioning depends upon the organism having some desire, such as a desire for food, or a desire to avoid pain. This creates a more satisfactory distinction between classical and operant conditioning. In the classical case, the association is made between two stimuli (CS and US), whereas the association in the operant case is made between an action and an object of desire (the reinforcer). If the ANS can be considered to have a desire to maintain homeostasis, or more specifically to maintain blood pressure, for instance, then it might very well be

capable of operant conditioning. Here is where we again turn to Dretske's attempt at naturalizing the mind.

4.7 Dretske on beliefs and desires

For his explicit views on belief and desire, we need to consult Dretske's book prior to *Naturalizing the Mind*, called *Explaining Behavior* (1988). In it, he offers a naturalistic framework to explain volition. He allows that naturally evolved systems which lack the ability to learn may possess representations, but only through learning can an organism possess beliefs and desires, and thus be capable of true (i.e. voluntary) action. Further, only with learning can an organism be conscious (according to *Naturalizing the Mind*). Thus Dretske takes it as necessary for consciousness that sensory representations have the potential to be used in a belief-desire framework. In essence, he requires, in addition to representation, the potential for voluntary action. This was one of the alternatives to the common-sense explanation of consciousness presented in Chapter 1.

Instinctive behaviour, Dretske says, involves representations which have the natural function of indicating some object or state of affairs in virtue of their evolutionary history. *Beliefs*, on the other hand, are representations which acquire their natural functions of indicating through learning. The result of this is that a belief is not only an internal representation which leads to output, but it is an internal representation which leads to a particular output *because* it indicates what it does.

> The places to look for these cases are places where individual learning is occurring, places where internal states *acquire* control duties or *change* their effect on motor output as a result of their relation to the circumstances on which the success of this output depends (1988, p. 95).

This mention of "success" is already suggestive of operant conditioning, where success is determined by a reinforcer.

The first requirement in this process is that there be a natural indicator of the stimulus or condition to which the learned response will occur. A rat can see and phenomenally represent a bar or a red light, and the ANS can detect and represent a blood pressure or a temperature. Once this requirement is satisfied, all that remains is to harness this indicator to an effector such that appropriate movements are produced when and only when the indicator registers the presence of the stimulus or condition. This is accomplished in artifacts by human design, in instinctive systems by evolution, and in conscious systems by the kind of consequences the produced movements have. "By the timely reinforcement of certain output - by rewarding this output *when*, and generally *only when*, it occurs in certain conditions - internal indicators of these conditions are recruited as causes of this output" (p. 98).

If successfully re-establishing homeostasis can be considered a reward, then the ANS likely fits this model. Consider the mechanisms that ensure adequate perfusion to the upper extremities and brain during standing in terrestrial gravity. In space, these

mechanisms result in overperfusion in these regions (Convertino and Robertson 1995), and the ANS must learn to associate new combinations of cardiovascular inputs, vestibular inputs, somatosensory signals, and whatever other inputs are relevant, with new cardiovascular responses. Successful homeostasis - the reward - reinforces the new configuration. How does Dretske naturalize reward?

Dretske tells us that the timely administration of rewards only increases the probability of an indicator-linked movement's occurence if the organism is in a certain internal state of *receptivity* for the reward. This state of receptivity is a desire (D), and is correlative with the notion of reward (R). D is an internal state upon which the reinforcing character of R depends. Without D, R does not reinforce the behaviour that brought R about. So D is causally relevant to an indicator-linked movement *because* the movement results in R. So far, we have nothing to disqualify autonomic homeostatic drives as D-states. Let me demonstrate through example.

Dretske does not care how desires are individuated. He says that one might have a desire for a cookie, a desire for food, or a desire for satiation. Of course, whether these desires are present or not depends upon previous stimuli, but that does not matter. Let us consider the thermoregulatory system when the core temperature is rising. One might attribute to it a D-state directed towards cooling the body. In the absence of this D-state, for instance during exercise when metabolic demands take precedence (Kenney and Johnson

1992), regulatory behaviour does not ensue, though higher core temperatures may still be detected.

Dretske even mentions the autonomic nervous system (1988, p. 122), but believes that he can rule it out as a case of belief-desire behaviour because he mistakenly thinks that the apparently goal-directed behaviour of the ANS can be explained as a stereotypical motor program which is solely a product of evolution. He goes on to use the example of fixed action patterns, like the squirrel who continues his attemps to bury nuts in a hardwood floor despite his lack of success. This is a programmed behaviour which is not modified by success or lack of it under certain conditions. But we have already seen that the ANS is not engaged in such fixed motor patterns. When exposed to a microgravity environment, the cardiovascular system does not continue in its maladaptive behaviour of overperfusing the brain, but modifies its internal structure to achieve its homeostatic goal.

Further evidence demonstrating that ANS responses are not fixed action patterns is found in cardiovascular responses to glutamate stimulation of the lateral hypothalamic area (LHA) (Spencer et al. 1989). In a particular area of the LHA, glutamate microinjections cause a fall in blood pressure. In the intact animal, this is achieved by reducing cardiac output. However, if the heart rate was held constant by pharmacological blockade (not a physiological circumstance of course, and thus not evolutionarily adapted to), the hypotension was achieved by decreasing total peripheral resistance. Thus the hypothalamic stimulation induces a

D-state directed towards hypotension, the achievement of which *by any mechanism* satiates the D-state.

4.8 Conclusion

It would be useful to set out the complete example which parallels Dretske's account. Let us consider the CAN of the astronaut who returns to earth. When he moves to a standing position, certain vestibular and somatic inputs enter into the NTS and perhaps affect other CAN structures, causing instantiations of representations of these inputs. According to Dretske, these representations have their information providing function in virtue of their evolutionary history. They have natural functions of providing information about muscle contraction and head acceleration, for instance.

Due to gravitational effects, these inputs occur at the same time as a loss of blood to the head. The CAN also detects this change, and it has a "desire" or "D-state" to restore proper perfusion. Gradually, and with increasing efficiency each time the "standing" complex of vestibular and somatic inputs is received, an association is made between these inputs and the cardiac and vascular changes which restore proper perfusion to the head. The restoration of proper perfusion and the presence of the D-state for that goal ensure that the connection between the representation of the vestibular and somatic inputs and the autonomic behaviour is reinforced.

The success of this entire operation depends upon the circumstances - standing - which the vestibular and somatic inputs indicate. Without these inputs, i.e. in the absence of a move to the

standing position, increasing perfusion to the head is not beneficial. This is the set of facts upon which the learning and reinforcement depend. So the representations of the somatic and vestibular inputs lead to the cardiac and vascular behaviour *because* they indicate what they do. If they indicated some state of affairs other than standing, no reinforcement would occur. That is why, according to Dretske, the representations of somatic and vestibular inputs count as beliefs. The CAN "believes" that the body is in an upright position[4], "desires" to maintain proper perfusion to the head, and "acts" to do so.

So it seems that Dretske's beliefs and desires are easily paralleled in the ANS. The ANS exhibits goal-directed behaviour which is not a fixed action pattern, but rather can be explained by autonomic "desires" or D-states. Adaptivities in central autonomic function, for instance when entering or returning from a microgravitational environment, can thus be interpreted as learning in a framework of beliefs and desires, at least according to Dretske's naturalization.

Thus we come to the end of representational and related theories of consciousness. Both Daniel Dennett's and Fred Dretske's theories of phenomenal consciousness as representation have been adequately paralleled, as have some other alternatives to the common sense explanation, such as match/mismatch and dispositions

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[4] The exact content of this belief is arguable, but unimportant for our purposes.

for voluntary action.   In Chapter 5, I go on to consider binding, attention, and internal signals.

CHAPTER 5
Binding, Attention, and Internal Signals

5.1 Introduction

This chapter serves to tie up some loose ends and address three theories of consciousness which have not been dealt with in previous chapters. The results of the comparisons in this chapter are perhaps less conclusive than in the previous chapters, especially with regard to C. B. Martin's theory of internal signals. However, some new directions for research are indicated.

5.2 Oscillations and synchrony

5.2.1 Oscillations and synchrony in conscious systems

Neuronal oscillations have come to the forefront of theoretical neuroscience in many areas, including research into two phylogenetically distant systems - central pattern generators in invertebrates and sensory systems in the mammalian thalamocortical loop. The demonstration of an evolutionary relationship between such vastly different systems would be a coup for neuroscience, and contribute greatly to our knowledge of the general principles of nervous system operation. The central controllers of the ANS are a phylogenetically intermediate system, and so might shed light on the role of rhythmicity as well as providing a foil for theories of consciousness based on oscillations. The thalamocortical loop has been proposed to be intimately related to consciousness (Llinás & Paré 1991; implied in Stériade et al.

1993b; Crick & Koch 1990 [they have now rejected this theory, see Crick 1994]) or less ambitiously, to perceptual feature binding (first suggested by Milner 1974, and in detail by von der Malsburg 1981; Gray et al. 1989; see also Eckhorn et al. 1988). The latter may be an alternative to the common sense explanation of consciousness, as discussed in section 1.3.4.

Oscillations in the gamma range (35-75 Hz) appear during global electroencephalographic (EEG) states termed "desynchronized", namely wakefulness and REM sleep, and also at regular intervals during deep sleep and certain types of anaesthesia (Stériade et al. 1996a, b). These latter states are known as "EEG synchronized" because they are characterized by global EEG oscillations at delta (1 to 4 Hz) and slow (< 1 Hz) rhythms. Lower range gamma oscillations occur in the depolarizing phase of the latter (Stériade et al. 1996a.) The presence of gamma oscillations in both dreaming/wakefulness and deep sleep demonstrates that they cannot be characteristic of consciousness (though note that a limited amount of dreaming seems to occur in delta sleep). The presence of massive amounts of synchrony during deep sleep demonstrates that synchrony *simpliciter* is also not characteristic of conscious states. Thus the above proposals for the importance of synchrony and oscillations to consciousness must be to the effect that there is something special about synchrony and oscillations at gamma frequencies at times other than the depolarizing phase of the slow oscillation.

Perhaps the special feature we are looking for can be discovered in the generational mechanism of the oscillations. There

are several variables which must be solved. First, are the oscillations generated in the thalamus, the cortex, or both? Is there an oscillatory drive in the form of intrinsically active pacemaker cells, or are only network effects operative? Or are the oscillations stimulus dependent, driven (for the visual system) by rhythmic input from the retina?

This last possibility has been advocated by Ghose and Freeman (1992) in a widely cited and nearly equally widely opposed article. They deny that oscillations in the visual system have any interesting functional role, since they found that the behaviour of the oscillations did not depend consistently upon any of the following stimulus parameters: binocularity vs. monocularity, relative coherence, and contrast. *Contra* Gray and Singer (1989), not only did Ghose and Freeman find gamma range oscillations in the lateral geniculate nucleus (LGN) of the thalamus, which projects to primary visual cortex, but they were actually more pronounced than the cortical oscillations. Since the frequency of thalamic oscillation (50 Hz) matched values for spontaneous oscillations in retinal ganglion cells, Ghose and Freeman suggested that the propagation of this spontaneous activity throughout the visual system was responsible for the oscillations at higher levels. This suggestion was supported by their observation of essentially no variation of the LGN oscillations, no matter what variation in stimulus parameter.

Ghose and Freeman are certainly correct about the presence of thalamic gamma activity (Stériade et al. 1991, 1993a,1996b) but their gross measurements of stimulus dependence have been

overturned by the finely tuned studies of Gray and Singer. In the first place, consistency in oscillatory frequency, denied by Ghose and Freeman, has not been claimed as functionally important (Gray 1994):

> However, it is highly unlikely that the oscillations per se play any direct role in the actual coding of information, such as a temporal code. They are simply too variable and unspecific. It is more likely that the oscillations provide a local mechanism to enable the establishment of synchrony among a much larger population of synaptically coupled cells. In this context oscillations of firing probability convey no information but provide a carrier wave for the coupling of large distributed populations of cells into functionally coherent patterns.

Ghose and Freeman were therefore attacking something of a straw man. König et al. (1995) have shown that synchronization of cortical firing which occurs over long distances (>2mm) is almost always associated with some oscillation. This occurs with little or no phase lag, even between the two hemispheres. Modelling studies (e.g. König and Schillen 1991) have shown that oscillations may overcome the transmission delays associated with such long distances, allowing for this remarkable synchronization. All of this suggests that Gray is correct, in that oscillations are a mechanism for achieving synchrony, and it may be that the exact frequency of oscillation is relatively inconsequential.

As for stimulus dependence, the Singer group's most recent study (Kreiter and Singer 1996) goes beyond single cortical column and multiple unit measurements to single unit measurements of stimulus dependent synchronization. Another advantage of this

recent study is that it was performed on awake monkeys, rather than the anaesthetized animals used in most previous preparations. They found that in area MT (V5), two cells with different orientation selectivities were synchronously activated by a single bar moving in an intermediate orientation, while their activation was much less synchronous when two separate bars were presented, each of which could activate either or both cells when presented individually. Controls excluded response amplitude, the mere presence of two stimuli, or the specific orientation of the bars as being responsible for the synchrony. The strength of correlation depended only upon whether there was a common stimulus or two different stimuli (with different directions of motion) activating each cell. The correlation observed was not as strong as for their previous population studies, but this is to be expected in a process which is hypothesized to make use of a population code.

So it seems that there is stimulus dependent synchronization occurring in the visual system, which makes use of some oscillatory mechanism. The thalamus can oscillate at similar frequencies; is it involved in the same network? Sillito and his colleagues' work (1994) suggests that it is. They demonstrated similar stimulus dependent synchronization in the LGN, but the synchrony disappeared when the visual cortex was removed. This suggests that the thalamus can generate oscillations, but that the cortex is responsible for stimulus-related synchrony; in the normal conscious or dreaming animal (one is tempted to say), the thalamocortical

system operates in concert, just as Llinás and Ribary (1993) have proposed based on magneto-encephalographic (MEG) data.

It seems synchrony is a cortical effect, but the source of oscillation is less clear. It is likely a product of several different network effects combined with conditional burster/pacemaker cells. Many cells in both the thalamus and cortex have been shown to have intrinsic oscillatory capabilities in the gamma range. In the cortex, these include cortical interneurons (stellate cells) (Llinás et al. 1991), and several types of cortical pyramidal cells from different areas (e.g. Nuñez et al. 1992; Connors et al. 1982; Franceschetti et al. 1995). Non-stimulus dependent synchronous oscillation has been demonstrated in interneuronal networks (Whittington et al. 1995), including such networks found in the hippocampus (Buzsáki and Chrobak 1995). In the thalamus, a subset of intralaminar thalamocortical cells (Stériade et al. 1993a) and reticular cells (Pinault and Deschênes 1992) are capable of intrinsically generated gamma oscillations as well. (The latter case is controversial - see Stériade et al. 1996b). If synchronized, cortical interneurons and reticular cells/local thalamic interneurons could generate rhythmic firing in pyramidal cells and principle thalamic cells (respectively) through rebound effects from GABAergic IPSPs.[1]

Therefore if any of the oscillatory effects are due to pacemaker cells, it is difficult to determine which type(s). When one factors in

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[1] That is, interneurons which release the inhibitory transmitter gamma-aminobutyric acid (GABA) upon many cells simultaneously could cause their targets to fire, also simultaneously, due to an effect called "post-inhibitory rebound." An IPSP is an inhibitory post-synaptic potential.

the apparent network effects between and within the thalamus and cortex, one must conclude that the full story involves a complex interplay of intrinsic and synaptic activities, probably involving many if not all of the elements above.

5.2.2   Oscillations and synchrony in the ANS

As in the case of invertebrate central pattern generators, the role of oscillations in the ANS has been primarily focused on the motor side of things, though some work has been done on the nucleus tractus solitarius (NTS), the thoroughfare for most autonomic afferent information.   This   stands   in   stark   contrast   to   the thalamocortical work, which has mostly involved studies of the early sensory cortices.   An appropriate research strategy to suggest then is for ANS researchers to examine the effects of different types of stimuli on oscillations and synchrony, and for the thalamocortical workers to examine the oscillatory relations between sensory and motor cortical areas.   Most of the conclusions I draw are tentative, testable by further research in this vein.

One would naturally expect rhythmic activity to be present in the ANS, given that much of its operation, e.g. the cardiac and respiratory cycles, is rhythmic in nature.   Two related questions arise as   a   result: 1)   Is   the   rhythmicity   generated   only spinally/peripherally, or is there a higher central component to the oscillations?   2) If there are oscillations on the "viscerosensory"[2] side

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2 Again, this use of "sensory" is not meant to have any conscious implications (see Chapter 2, footnote 3).

of things, are these intrinsic to the central network, or merely stimulus-locked effects? If both motor and "sensory" aspects of the oscillations can be shown to have central components, the hypothesis of a relatively autonomous "intrinsic functional realm" (Llinás and Paré, 1991, discussing the thalamocortical loop and consciousness) in the central autonomic network becomes plausible.

Let us consider the motor side. Adrian et al. (1932) were the first to demonstrate the cardiac related rhythm in sympathetic nerve discharge (SND).[3] For a considerable length of time, it was thought that this rhythm was due to the pulse synchronous activity of baroreceptor afferents, i.e. a mere stimulus effect. However, in a series of studies Gebber and Barman showed that the oscillation is centrally generated, and *entrained* by baroreceptor input (Gebber 1980; see also Chapter 2). Several experimental results strongly support this conclusion. First, surgical denervation of the baroreceptor input leaves a rhythm in SND which, at 2-6 Hz, is similar to the cardiac cycle. Further, the phase relations between the heart rate and this "cardiac-related rhythm" in SND are entirely disrupted after baroreceptor denervation, suggesting central generation of the rhythm rather than time locking to non-baroreceptor cardiac related inputs. It persists after decerebration and thus is not due to thalamocortical influences, but disappears after section of the spinal cord at the cervical level. This points to the brainstem/midbrain as the oscillatory source.

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[3] The respiratory related rhythm, which I will not consider, was discovered by the same group at the same time.

There is another SND rhythm, at 7-13 Hz but normally called "the 10 Hz rhythm", present in all sympathetic nerves before and after baroreceptor denervation and revealed by power spectrum analysis. In baroreceptor denervated cats, the 10 Hz rhythm can on occasion account for almost all of the power in SND (Gebber et al. 1994). Whereas the cardiac-related rhythm was eliminated by ablation of the rostro-ventrolateral medulla (RVLM) only, the 10 Hz rhythm was dependent upon the RVLM, medullary raphe complex, parabrachial nucleus, and Kölliker-Fuse nucleus. (The cardiac related rhythm seems to involve the medullary reticular formation and medullary raphe complex, and the 10 Hz rhythm also definitely implicates the periaqueductal grey matter, though neither is actually eliminated by ablations in these areas) (Zhong et al. 1992). Other structures have subsequently been shown to participate in this network, including the CVLM, lateral tegmental field, NTS, and posterior hypothalamus (Paton et al. 1991; Gebber et al. 1994; Barman et al. 1995).

I will focus on the central network responsible for the 10-Hz rhythm, as it is the more complex and therefore more likely to parallel the thalamocortical system. It should not be forgotten, however, that the two rhythms interact dynamically - they have common parts to their central generating networks, and both components can be simultaneously present in sympathetic nerve discharge (Ando et al. 1994). In fact, there is a third order rhythm which also seems to be centrally generated, which may even subdivide into two separate oscillations of ~0.12 and ~0.34 Hz. When

one adds to this is the respiratory related rhythm (0.2- to 0.3-Hz) which is intimately connected with the cardiovascular system (Felman and Smith 1995), the complexity of the oscillations in cardiovascular control certainly rivals that of the thalamocortical loop. But to simplify matters to a manageable level, let us examine the 10-Hz network.

The 10-Hz rhythm in SND is not correlated to either inferior olivary activity or cortical spindles, which feature oscillations at a similar frequency (Barman et al. 1995). In addition, the 10-Hz rhythm in medullary populations persists after high cervical spinal cord transection, though the 10-Hz component in SND does not (Gebber et al. 1994). These facts support the hypothesis first put forward by Cohen and Gootman (1970) that the 10-Hz rhythm in SND reflects the organization of a central sympathetic discharge determining system in the brainstem. Correlations observed are between cells in the central network, between these cells and the discharge of the efferent nerves, and between the efferent discharges themselves.

When experimental animals were decerebrated, baroreceptor deafferented, and vagotomized (to eliminate the effects of feedback projections), the 10-Hz components of discharge in the various sympathetic nerves (e.g. cardiac, renal, and splenic) were highly correlated (coherence values approaching one, Kocsis et al. 1990). This suggests a common source, but as mentioned in Chapter 2, when forcing stimuli were applied to cardiovascular related sites in the medulla, the discharges of different nerve pairs could be dissociated.

For example, if a 3.3 Hz forcing stimulus were applied to the medullary raphe complex, the vertebral sympathetic nerve and renal sympathetic nerve lost their correlation, while retaining their correlation with some other nerves (Huang et al. 1992). The differential correlations between the various nerve pairings could be manipulated in any fashion, depending upon the site of forced stimulation, though none of the nerve-specific effects were limited to a specific nucleus. Similar conclusions were drawn from more physiological circumstances, where partial coherence analysis, able to winnow out subtle coherence effects, replaced forced stimulation (Gebber et al. 1994).

This variable coherence in the efferent nerve discharges was also found between medullary neurons and efferent discharge and between medullary neurons themselves (Zhong et al. 1992, Barman et al. 1995). What is observed here, then, is variable *target* dependent synchronization rather than *stimulus* dependent synchronization, as observed in the Singer cortical studies. This is what earned us spatial representation on the motor side in chapter 2. If it could be shown that oscillations in the "sensory" component of the cardiovascular circuitry synchronized with each other and with those on the motor side, then a functional role for stimulus dependent synchrony would be plausible.

This has not been demonstrated conclusively, but there are a number of considerations which support a functional role for stimulus dependent synchrony in the ANS. First, it makes evolutionary sense. The simplest oscillatory systems are found in

invertebrate central pattern generators. These are usually entirely motor systems, where "sensory" input has a modulatory effect, with phasic inputs causing pattern switching or circuit reorganization. However, it has recently been found that there are systems in which tonic "sensory" input has "essentially the same properties as any other component of the pattern-generating circuit" (Katz 1996, referring to work by Keir Pearson). As the role of "sensory" input becomes more important, areas which do not have direct motor effects would be expected to participate in the oscillating circuit, since fine-tuning responses would seem to require such participation. Indeed, looked at in this way, parts of the central cardiovascular network which do not have direct projections to the intermediolateral cell column in the spinal cord (the pathway for sympathetic outflow) could almost be considered "sensory" areas. These would then include the caudal ventrolateral medulla, area postrema, parabrachial nucleus, some hypothalamic nuclei, and the PAG, among others.

An attempt has been made to detect synchronization between SND and the parabrachial complex, but unfortunately only at a rather gross population level. Limited synchrony (coherence value of 0.21) was found (Zhong et al. 1992). However, sodium dependent oscillations at 10-Hz have been found in individual parabrachial neurons (Leonard and Llinás 1990), and the parabrachial complex is next up in the autonomic "sensory" hierarchy from the NTS. Given the presence of feedback projections between almost all levels of the central autonomic network (Loewy 1990b), it would not be

surprising to find cooperative oscillatory effects between, for example, the NTS, parabrachial nucleus, and the RVLM.

The NTS itself contains cardiovascular related rhythmically active neurons (1-15 Hz), some of which are intrinsically oscillatory and others of which depend upon synaptic input for their rhythmic discharge (Paton et al. 1991). Extensive correlation studies between these neurons and others in the cardiovascular network have yet to take place, though there are already some promising results. There is some indication that there is a correlation between some NTS neurons and the cardiac-related rhythm, which is not a stimulus-locked effect (Langhorst et al. 1992). There has also been one study in which 40% of the barosensitive neurons examined in the NTS showed a correlation with renal sympathetic nerve discharge, and approximately two thirds of these had correlations with the ECG (Hayward and Felder 1995.) One half of the barosensitive NTS neurons showed rhythmicity (by autocorrelation) which was unrelated to the cardiac cycle. The NTS neurons in this study fired at a rate between 7.4 and 12.3 Hz, i.e. in the range of the (7-13 Hz) "10-Hz rhythm." These preliminary results show the need for correlation studies within the central cardiovascular network, which may feature a primitive sort of binding via synchrony.

The mixture of intrinsic oscillators and cells dependent upon synaptic input for rhythm generation which are found in the NTS, are also characteristic of the nuclei listed above as participating in the network responsible for the 10-Hz rhythm in SND. These include the RVLM, medullary raphe complex, parabrachial nucleus, and Kölliker-

Fuse nucleus (Dampney 1994). The details of generation of the oscillations are more obscure than in the thalamocortical system, but again, a mixture of network and pacemaker operations is indicated.

The comparison between the thalamocortical system and the ANS with regard to oscillations and synchrony looks promising, and further studies, particularly on the ANS side, are urgently needed. If it turns out that there is "feature binding" via synchrony using oscillations in the non-conscious ANS, it must be shown why *prolonged* oscillations (longer than the depolarizing phase of the delta oscillation) in *gamma* frequencies should make the difference in conscious systems.

R. R. Llinás and his colleagues (Llinás and Paré 1991; Llinás and Ribary 1993, 1994) have proposed a higher level model for a type of binding which seems to be of the experience unifying sort - what they call "temporal binding". Their theory describes a complex interaction between a specific and a non-specific thalamocortical loop. The specific loop involves oscillations between the specific thalamic nuclei, reticular nucleus, and cortex. The non-specific loop also involves the reticular nucleus and cortex, but includes the intralaminar nucleus as well. A rostrocaudal phase shift (over both the thalamus and cortex) of the oscillation driven by the non-specific loop and its conjunction with the various specific loops is proposed to generate temporal binding. This pattern has been measured using MEG, and the 12.5 ms length of the rostrocaudal scan correlates well with the resolution of auditory clicks. Until the details of network operations in the ANS (and the thalamocortical system!) have been

worked out, one cannot hope to show a parallel to the Llinás model. Thus if this speculative model is correct, it may describe a feature unique to conscious systems.

5.3   Attention

Some "theories" of consciousness are based upon the simple idea that a critical mass of concentrated neuronal activity is required for consciousness to "emerge" (e.g. Kinsbourne 1993; Greenfield 1994).   This is certainly inadequate - the area of the ventral surface of the brainstem which is actively involved in the response to some set of cardiovascular variables (Harper et al. 1996) is larger than the area of primary visual cortex that is activated upon perception of a point of light (Mason and Kandel 1991, Posner and Raichle 1994). But Kinsbourne's term "dominant focus" suggests a more interpreted version of this naïve view, that the area of concentrated neural activity is the result of an attentional process.

What is attention, in neurophysiological terms?   In most perceptual situations, there are several co-occurrent stimuli which may be selected for further processing.   In the presently favoured model of attention, selection of particular neuronal assemblies over others is viewed as the product of biased competition (Desimone and Duncan 1995).   Previous stimuli result in the activation of top-down influences which potentiate particular assemblies.   Thus when further stimuli impinge upon the system, the various assemblies

which are possibly resultant are selected from based on their current activation and tendency to engage further processing.

If attention is defined purely perceptually, as a selection from amongst a group of possible perceptual representations given a set of inputs, it will be difficult to demonstrate a parallel in the ANS since the assemblies which actually constitute the representations are unknown. (Note that this would also apply to the cortex if one were examining it with purely physiological techniques and ignoring introspective reports.) However, consider a definition of an attentional process as an event where some representation successfully competes against others for access to a common motor system. This definition makes introspective sense, since it is what we attend to that affects our behaviour most profoundly. When something in our peripheral vision "grabs our attention," we become better able to react to it.

The ANS is rife with examples of this version of attention. To take one example, when exercising there is a drive for redistribution of blood flow away from metabolically inactive tissues, including the skin, to active muscles. However, since the active muscles also create heat, there is a simultaneous drive to increase skin blood flow thus dissipating that heat (Kenney and Johnson 1992). The thermoregulatory inputs from skeletal muscle, core, and skin are present simultaneously with the ergoreceptor input from skeletal muscle. Baroreceptor inputs can also be involved (Johnson 1986). Throughout the course of exercise, these inputs are in constant competition for access to their common effector, the cardiovascular

system. Depending upon other circumstances, sometimes thermoregulation is sacrificed for metabolic demands, and sometimes vice versa (Kenny and Johnson 1992). This is a very clear example of autonomic attention.

A more complex definition of attention may prove more difficult to parallel in the ANS. However, there are no adequate neurophysiological theories at the moment which suggest something more complicated than competing access to a common motor system. So I draw the tentative conclusion that attention is not unique to conscious systems.

5.4   Internal signals

C. B. Martin (ms) has proposed that conscious systems are characterized by internal signals, qualitatively similar to external signals, which are for primarily internal use. In Chapter 3, I mentioned the importance of imagery to Martin's theory. Imagery, dreaming, and hallucination are all examples of internal signals - they are internally generated, for the reciprocal disposition partners for the mental event manifestation are located within the brain. External signals are perceptual, where the perception-manifestation has one of its reciprocal disposition partners in the environment.

The value of imagery, Martin suggests, lies in its use for planning. Manipulation of images on an internal "stage" results in the long term modification of neuronal properties, modifications which may later play a role in behaviour. Since the internal and external signals are qualitatively similar, and they involve activation

of largely the same sets of neurons (see section 3.3.1), imagistic manipulations (and possibly dreams) can have effects in the brain which are highly relevant to possible perceptual situations.

However, much or most of the inner life of the mind has no behavioural upshot, so the use of imagery is actually primarily internal. The same things applies to dreaming, which may reinforce memories (Winson 1993). Martin claims that "the cortex is *built* for possible waste rather than pared-down tidiness." So imagery and dreaming, according to Martin, are examples of internal signals, qualitatively similar to external signals, which are used primarily internally. This, he suggests, is what is unique to consciousness.

Examples of internally generated signals are plentiful in the ANS. The perceptual expectations discussed in Chapter 3 are internal signals when manifested, and they are probably even qualitatively similar to external signals - recall the example of somatic inputs at the initiation of exercise resulting in higher centres creating an anticipatory response in the NTS. It makes sense that this NTS response would be similar to the inputs that would result from the cardiovascular situation the CAN is anticipating, allowing adjustment even before the actual inputs are received. However, these internal signals are not for primarily internal use. They have an immediate behavioural upshot.

Other examples of internal signals are "hot flashes" in menopause (Woodward and Freedman 1994) and the generation of low frequency blood pressure variability (Just et al. 1995), but again, these are not for primarily internal use. The best candidate for

internal signals primarily for internal use is a potential equivalent to dreaming, found in the CAN during rapid eye movement (REM) sleep.

During REM sleep, when most dreaming occurs and the cortex is in a wakefulness-like EEG state, the cortex is somehow cut off from the motor system resulting in complete muscular atonia (Llinás and Paré 1991). A much ignored fact is that a similar situation occurs in the CAN, where higher centres such as the hypothalamus relinquish control over lower brainstem regions like the RVLM (Parmeggiani and Morrison 1990). One consequence of this is that during REM sleep, the body becomes particularly susceptible to rapid changes in autonomically controlled variables such as temperature and blood pressure. Homeostasis is severely affected in all autonomic modalities. Thermoregulation becomes nearly an open-loop (i.e. entirely non-homeostatic) system, and the decrease in blood pressure would be disastrous without peripheral refexes (Parmeggiani and Morrison 1990). This stands in contrast to the well controlled temperature, blood pressure, and breathing rates during non-REM sleep (McGinty et al. 1974).

The hypothalamus appears to continue to be active while cut off from the rest of the system during REM sleep (Heller and Glotzbach 1985; Parmeggiani et al. 1987). First, one must ask whether these signals are internally generated. It is possible that cortical inputs cause this activity, and thus the hypothalamus would respond entirely according to dream content. To discover if the signals are generated internally to the CAN, one could examine hypothalamic activity in decerebrate cats, who enter into a REM state

with simple stimuli such as pinching (Parmeggiani and Morrison 1990).

Next, one must ask whether these signals are actually used, and if they are qualitatively similar to external signals. These are both very difficult questions to answer, and would require a neurophysiological identification of hypothalamic representations of temperature and blood pressure, for instance. Such identifications are of course not forthcoming, but it seems there is at least a possibility that the ANS possesses internally generated and used signals which are similar to external signals.

<u>Conclusion</u>

In my evaluation of theories of consciousness using the autonomic nervous system for comparison, I cannot pretend to have exhausted the current repertoire of explanations for phenomenal consciousness. However, some major contenders have been found wanting since the features they postulate as unique to consciousness are found in the non-conscious ANS.

In a way, the entire thesis is relevant to Daniel Dennett's theory of consciousness, because he believes conscious experience becomes more robust with increasing complexity. The presence of spatially represented qualities in the central autonomic network, strongly suggested by the evidence discussed in Chapter 2, parallels the essential aspect of Dennett's theory of phenomenal consciousness. Based upon this evidence, one can adopt the "conscious stance" towards the ANS. However, the presence of misrepresentation, learning, and perhaps binding and attention in the ANS moves it even further up on Dennett's continuum.

Fred Dretske offers a realist theory of representation which he claims can account for consciousness. We saw, on the contrary, that the ANS possesses "sensory" representations, it can misrepresent, and Dretske's versions of belief and desire apply to a truly adaptive central autonomic network which learns from its environment, the body. So Dretske's theory cannot be correct, since the ANS is decidedly non-conscious. At the same. time, it was seen that theories

based upon match and mismatch cannot successfully explain consciousness, and neither can dispositions for voluntary action.

Neural synchrony and oscillations have been proposed by neuroscientists as the basis for consciousness, and also as a solution to the multi-dimensional "binding problem." However, the central autonomic network operates in the context of intrinsic oscillations, and likely exhibits stimulus dependent synchrony as well. In order for synchrony and oscillations to be plausible explanation for consciousness, it must be explained why the faster, gamma range (35-75 Hz) thalamocortical oscillations generate conscious experience, while the slower oscillations (less than 15 Hz) in the ANS do not. The rate by itself cannot account for such a vast difference in kind.

Neurophysiological models of attention also seem to have straightforward parallels in the central control of the ANS. Any theory which gives an attentional account of consciousness must provide an alternative, plausible characterization of attention which does not match some ANS function. C. B. Martin's theory of internal signals seems to offer the most promising candidate for a function unique to conscious systems, but the neurophysiological evidence from autonomic studies is consistent even with it.

If it is true that these functional features of conscious systems are also found in the ANS, we are left with two alternatives. First, we can attempt to find the right functional characteristic or group of characterstics which are unique to all and only conscious systems. Perhaps it is easy to come up with features that are unique to conscious systems - doing philosophy might be an example - but

finding a particular group which *typifies* consciousness will be far more difficult. It may be that there is *no* group of functional features which all conscious systems possess uniquely.

If such is the case, we must adopt the second alternative. This is to reject functionalism, and other theories of mentality and consciousness which deny the importance of the intrinsic properties of neurons, or other constituents of thinking objects. In other words, rather than adopting some alternative to the common sense explanation of consciousness, we would accept the importance to consciousness of the intrinsic qualities of subpersonal states. The most promising proposal of a feature unique to consciousness, Martin's theory of internal signals for primarily internal use, makes explicit mention of the qualitative similarity of internal and external signals. In fact, it is an instance of the common sense explanation, rather than an alternative to it (though it has a functional aspect to it as well.[1])

Obviously further studies are needed in order to determine which alternative - the acceptance or rejection of functionalism - is the correct one. I myself have suggested some experiments which may contribute to this project. In the meantime, theorists who examine consciousness would do well to keep the capabilities of the autonomic nervous system in the backs of their minds, lest they

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[1] Consciousness must have *some* functional importance, or there would be no evolutionary explanation for it. However, a conscious state may have non-functional aspects to it as well, which are relevant to its identity and mentality.

unintentionally attribute consciousness to the structures responsible for central autonomic control.

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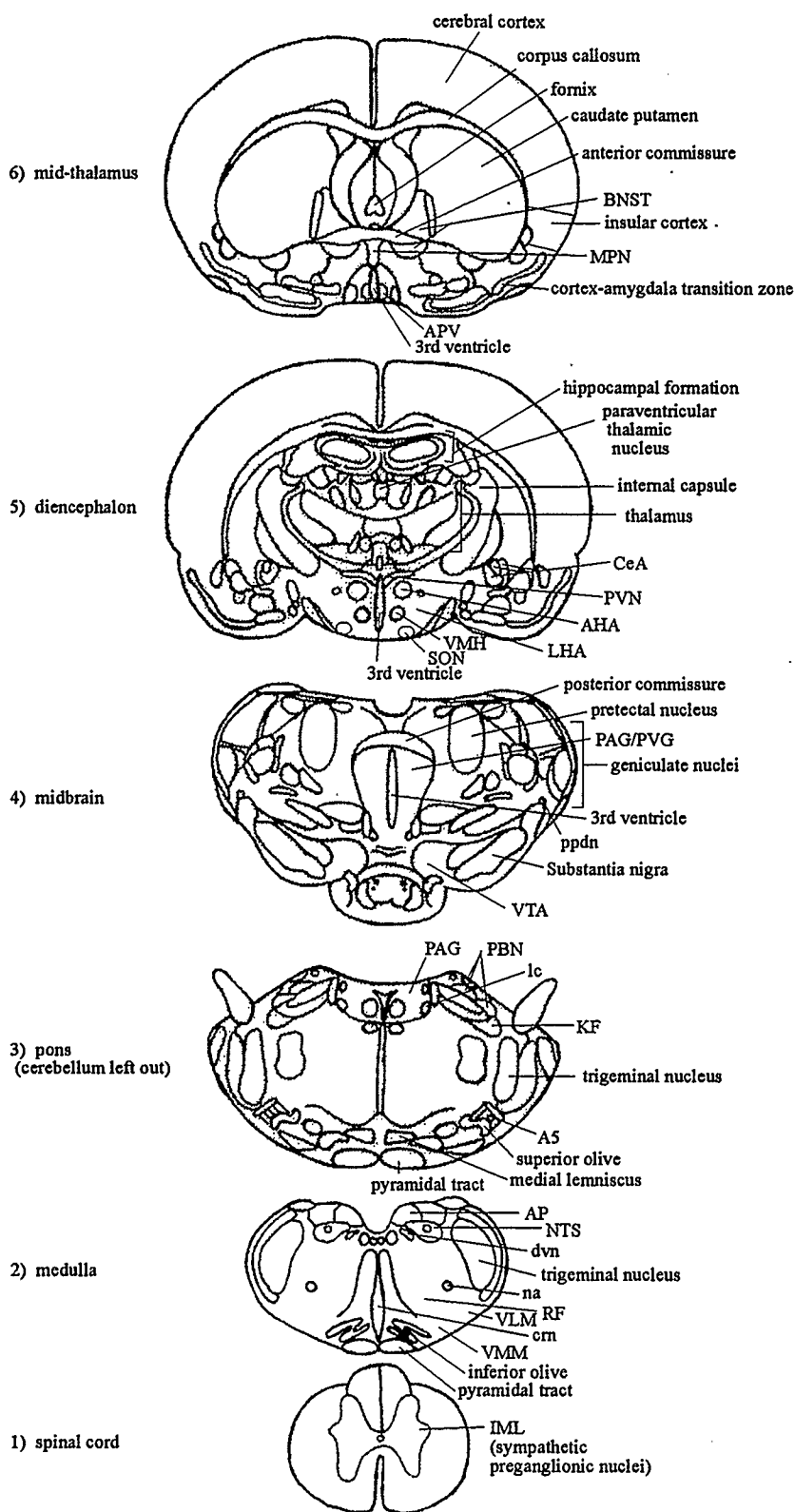
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Appendix A- Anatomy of the Central Autonomic Network

Abbreviations:

A5 - A5 noradrenergic cell group
AHA - anterior hypothalamic area
AP - area postrema
APV - anterior periventricular region
BNST - bed nucleus of the stria terminalis
CeA - central nucleus of the amygdala
crn - caudal raphe nuclei
dvn - dorsal vagal nucleus
IML - intermediolateral cell column
KF - Kölliker-Fuse nucleus
lc - locus coeruleus
LHA - lateral hypothalamic area
MPN - median preoptic nucleus
na - nucleus ambiguus
NTS - nucleus tractus solitarius
PAG - periaqueductal grey matter
PBN - parabrachial nucleus
POA - preoptic area
ppdn - peripeduncular nucleus
PVG - periventricular grey matter
PVN - paraventricular hypothalamic nucleus
RF - reticular formation
SON - supraoptic nucleus
VLM - ventrolateral medulla
VMH - ventromedial hypothalamic nucleus
VMM - ventromedial medulla
VTA - ventral tegmental area

cerebral cortex
corpus callosum
fornix
caudate putamen
anterior commissure

6) mid-thalamus

BNST
insular cortex
MPN
cortex-amygdala transition zone
APV
3rd ventricle

hippocampal formation
paraventricular
thalamic
nucleus

5) diencephalon

internal capsule
thalamus

CeA
PVN
AHA
VMH
SON LHA
3rd ventricle

posterior commissure
pretectal nucleus
PAG/PVG
geniculate nuclei

4) midbrain

3rd ventricle
ppdn
Substantia nigra
VTA

PAG PBN
lc

3) pons
(cerebellum left out)

KF
trigeminal nucleus

A5
superior olive
pyramidal tract medial lemniscus

AP
NTS
dvn
trigeminal nucleus
na
VLM RF
crn
VMM
inferior olive
pyramidal tract

2) medulla

1) spinal cord

IML
(sympathetic
preganglionic nuclei)

Figure 1 - Anatomy of the Central Autonomic Network
(See legend on previous page, and see Figure 2 for rostrocaudal slice locations. See Table 1 for connections.)

Sources: Benarroch 1992, Chokroverty 1992, Dampney 1994, Johnson and Loewy 1990, Loewy 1990b, Loewy and Spyer 1990b, Martin 1989, Paxinos and Watson 1986, and Spyer 1992.
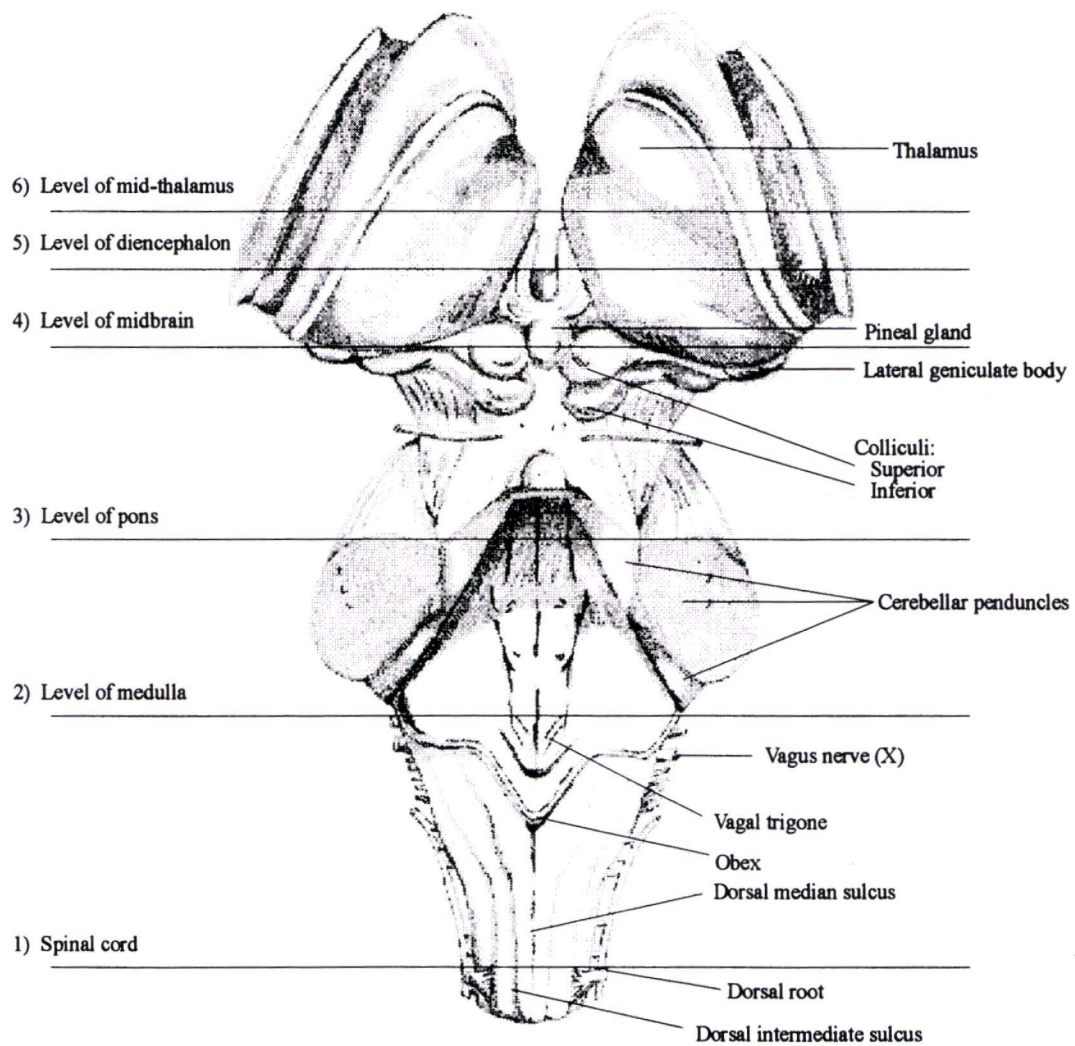
Figure 2 - Dorsal Surface of the Brainstem
(with rostrocaudal levels of slices from Figure 1)

Sources: Chokroverty 1992, Dampney 1994, Martin 1989, Paxinos and Watson 1986, and Spyer 1992.

	A5	AHA	AP	APV	BNST	CeA	crn	dvn	IML	KF	Ic	LHA	na	NTS	PAG	PBN	POA	PVN	RF	SON	VLM	VMH	VMM	VTA
A5	XXXX								•	•				•				•						
AHA		XXXX					•					•					•	•		•		•		
AP			XXXX											•				•			•			
APV		•		XXXX								•			•		•	•						
BNST					XXXX	•						•		•				•						
CeA	•				•	XXXX		•			•	•		•	•	•			•			•		•
crn						•	XXXX	•						•					•			•		
dvn								XXXX										•						
IML									XXXX					•										
KF	•				•					XXXX				•			•	•				•		
Ic		•	•	•	•	•	•			•	XXXX	•		•	•	•	•	•	•	•	•	•	•	•
LHA		•				•			•			XXXX		•	•		•	•	•	•	•	•		
na													XXXX	•				•						
NTS	•		•		•					•	•	•		XXXX	•	•	•	•	•	•	•	•	•	
PAG						•	•							•	XXXX	•	•	•			•			
PBN	•					•	•							•		XXXX		•	•	•	•			
POA		•					•					•			•		XXXX	•				•		
PVN	•	•				•	•	•	•		•	•		•	•	•	•	XXXX		•		•		
RF						•	•			•		•		•			•		XXXX			•		
SON		•										•					•	•		XXXX		•		
VLM		•				•	•	•	•		•	•			•			•		•	XXXX			
VMH		•										•					•	•		•		XXXX		
VMM							•		•												•		XXXX	
VTA							•																	XXXX

Table 1 Proven connections between major central autonomic structures (emphasis on cardiovascular control)
y-axis = source   x-axis = target   (See Fig. 1 for anatomical locations and p. 159 for abbreviations)

Appendix B - Glossary

adrenal medulla - The central, endocrine region of the kidney, which releases hormones, especially catecholamines.

afferent - Conducting toward the central nervous system or toward a particular central nervous system structure. Compare efferent.

agonist - A chemical, other than the usual physiological one, which specifically activates a receptor.

anterograde - From cell body to axon terminal (usually in reference to axon transport, e.g. in the case of dye labelling studies). Compare retrograde.

atria - The superior (rostral) chambers of the heart.

baroreceptor - A receptor which responds to absolute or changing blood pressure.

behaviourism - Psychological behaviourism is a research methodology and theoretical framework wherein external stimuli and measurable behavioural responses are the only items admissible as data or elements of psychological law statements. Philosophical behaviourism is the thesis that mental items *consist* in dispositions to behave, given certain external stimuli.

bradycardia - A slowing of the heart rate. Compare tachycardia.

brainstem - Region of the brain composed of the midbrain, pons, and medulla.

Cartesian theatre - A theory of consciousness is said to posit a Cartesian theatre if it proposes some central "observer" which

perceives the goings on in the mind. This generates an infinite regress.

catecholamines - A class of neurotransmitters that includes adrenaline (epinephrine), noradrenaline, and dopamine.

caudal - In an animal such as the rat, the caudal direction is towards the tail. In the human, the neuraxis bends at the midbrain, such that the caudal end of the vertically oriented brainstem is towards the bottom, but the caudal end of the horizontally oriented cortex is towards the back. Compare rostral.

central nervous system (CNS) - The CNS includes the brain and spinal cord. The classification of a neuron is determined by the position of its cell body. Compare peripheral nervous system.

central sulcus - Horizontal fissure which divides the frontal from the parietal lobes of the cerebral cortex.

cervical - The vertebral segments at the rostral end of the spinal cord.

cholinergic - A neuron or synapse is cholinergic if its neurotransmitter (or one of its neurotransmitters) is acetylcholine, or ACH.

conductance - In hydrodynamics, fluid flow per unit pressure. (Used here for blood flow, where pressure is mean arterial pressure.)

contralateral - Opposite side (usually when comparing the location of some central structure with a peripheral one to which it is directly or indirectly connected.) Compare ipsilateral.

cutaneous - At the level of the skin.

defense reaction - Commonly known as the "fight or flight" response, the defense reaction is typified by a range of autonomic responses, including a redistribution of blood from the viscera to other vascular beds and release of adrenal catecholamines. (See Chapter 2 on the periaqueductal grey matter for a description of variation within the defense reaction.)

depolarized - When a neuron's electrical potential is more positive than its resting potential, it is depolarized. Compare hyperpolarized.

diencephalon - The region of the brain composed in the main of the thalamus and hypothalamus.

disposition - A causal power. A glass has a disposition to shatter if struck with a hammer, and water has a disposition to extinguish a fire. Some philosophers take dispositions to be fully-fledged properties of objects (e.g. fragility), while others take them to be properties partially considered (C. B. Martin). Martin also believes that dispositions are intrinsic and irreducible; others (e.g. D. M. Armstrong) say that they are reducible to non-dispositional properties and laws. For example, Armstrong would explain the fragility of a glass by appealing to the electrostatic properties of the constituent particles, and laws relating these properties.

efferent - Conducting away from the central nervous system or away from a particular central nervous system structure. Compare afferent.

electroencephalography (EEG) - A technique of varying spatial resolution whereby population neuronal activity is measured. It is thought that the EEG reflects primarily synaptic potentials.

enteric nervous system - An integrative neural system found within the wall of the gastrointestinal tract, which it controls. It is largely independent of the central nervous system.

externalism - Very generally, an externalist about a particular domain of properties maintains that correct attribution of those properties to an object X depends upon items external to X. Thus a physicalist-externalist about meaning would say that the meanings of our thoughts depend on our environment as well as our brains.

gain - The ratio of output to input.

gestalt - A configurational quality to a percept, in addition to its constituent sensations.

glutamate - An amino acid, and the most common excitatory neurotransmitter in the central nervous system.

homeostasis - A term coined by Walter Cannon, homeostasis refers to the tendency of a system to maintain some parameter at a constant level.

homunculus - "Little man." This term is used by Dennett to refer to feature discriminating modules in the brain. It is also used to refer to the topographic pattern of receptive fields in primary somatosensory cortex, and the similar pattern in the primary motor cortex.

hypertension - High blood pressure. Compare hypotension.

hypotension - Low blood pressure. Compare hypertension.

hyperpolarized - When a neuron's electrical potential is more negative than its resting potential, it is hyperpolarized. Compare depolarized.

implicit memory - Explicit memory is when a previous experience is consciously recalled. By contrast, implicit memory is revealed when a previous experience affects performance on a task and explicit recall of the experience does not occur.

instrumentalism - An instrumentalist about a particular domain of inquiry construes theories about that domain as lacking in ontological import. She maintains that theories are mere instruments for predicting future observations from a set of given observations.

intentionality - A philosophical term roughly meaning "aboutness," not to be confused with the common meaning, characterizing an act done on purpose. Beliefs and many other mental states are intentional, but non-mental items may be derivatively so. A belief might be about Antarctica, for instance, and so might a map. Since the nineteenth century philosopher Franz Brentano claimed that intentionality was the mark of the mental, it has been on the forefront of the philosophy of mind.

intermediolateral cell column - A region in the spinal cord gray matter containing sympathetic preganglionic neurons.

interneuron - With respect to the entire nervous system, any neuron which is wholly contained in the central nervous system. With respect to a particular area of the brain (e.g. the hippocampus),

any neuron which is wholly contained within that area. Interneurons are often inhibitory (especially in the cortex, for example.)

intrinsic property - Any property that an object has independently of any other object. Intuitively, mass is an intrinsic property (though Einstein's theory of general relativity suggests that it involves relations between points in spacetime.) Compare relational property.

ipsilateral - Same side (usually when comparing the location of some central structure with a peripheral one to which it is directly or indirectly connected.) Compare contralateral.

latency - The time between presentation of a stimulus and the response of a neuron affected by the stimulus, or between the firing of two neurons in the same pathway.

long term potentiation (LTP) - An increase in synaptic efficiency following a particular pattern of excitatory stimulation.

lumbar - The vertebral segments in between the thoracic and sacral regions of the spinal cord, i.e. in the caudal midsection.

materialism - The thesis that all existent things are composed of matter (as opposed to some "mental substance.")

medulla - The most caudal region of the brainstem, continuous with the spinal cord.

membrane potential - The electrical potential difference, measured in Volts, across a cell's outer (cytoplasmic) membrane. The fluid surrounding the cell is arbitrarily assigned an absolute potential of zero.

midbrain - The region of the brainstem just rostral to the pons. It is composed in the main of the tectum, tegmentum, and cerebral aqueduct.

myelin - The fatty sheath which surrounds certain axons in both the peripheral and central nervous system. Its primary function is to increase the speed of action potential conduction.

naturalism - In the ontological sense, the thesis that everything is composed of natural entities, whose properties determine *all* properties.

neuroblast - An immature cell which is programmed to eventually develop into a neuron.

noradrenergic - A neuron or synapse is noradrenergic if its neurotransmitter (or one of its neurotransmitters) is noradrenaline, or NA.

nucleus - A large clump of neuronal cell bodies and interneurons found within the central nervous system, and a concentrated location for synapses. The other type of organization of cell bodies found in the brain is a laminar one, characterizing the cortex, hippocampus, and cerebellum. See also plexus.

ocular dominance columns - Small, alternating regions in the primary visual cortex which respond primarily to input from either the left or right eye.

ontology - The study of what exists. The items which must exist in order for a theory to be true are its "ontological commitments."

oscillations (neuronal) - Regular, periodic fluctuations in a neuron's membrane potential.

parasympathetic division - A division of the autonomic nervous system traditionally associated with resting, continuous regulatory responses like slowing down the heart, increasing gastric motility and acid secretion, and pupillary contraction (among many others). The sympathetic division was associated with the opposite responses, and with states of excitement. However, modern research has shown that the parasympathetic division is also active during excited states (e.g. sexual excitement), and synergistically as well as antagonistically with the parasympathetic division.

peripheral nervous system (PNS) - The peripheral nervous system includes everything which is not part of the central nervous sysem (CNS), which is made up of the brain and spinal cord. The classification of a particular neuron is determined by the location of its cell body.

plexus - A cluster of cell bodies and/or neuron fibres. (In the enteric nervous system, these clusters are arranged in enveloping sheets called the mesenteric plexus and the myenteric plexus.)

pons - The region of the brainstem just rostral to the medulla.

pre-conscious process - A feature discrimination which occurs early in the processing stream such that the result is available to consciousness, but the discrimination itself cannot be voluntarily performed. An example is the unification of lines into geometrical patterns. (See Churchland et al. 1994 for a critique of this notion.)

priming - Increasing the likelihood of a response or the accessibility of a memory by the prior presentation of relevant cues.

propositional attitude - Beliefs, desires, fears, hopes etc. are traditionally called propositional attitudes. The term comes from an abstract representation of them as relations between subjects and propositions (the content corresponding to sentences). If Don believes that Clinton is president, on this model, he is in a "belief-relation" or attitude towards the proposition *Clinton is president*. He might enter into a different relation or attitude toward that proposition, and *fear* that Clinton is president. All propositional attitudes are characterized by that- clauses.

realist - To be a realist about a particular domain, object, or property, is to assert its existence independently of anyone's conception of it.

reductio - Short for "*reductio ad absurdum*," where a contradiction is derived in logical argument, and it is concluded that one or several of the argument's premisses must be false.

regularist (theory of causation) - A regularist about causation asserts that there is nothing more to causality than regularity. For something to be a cause is for it to be followed by an effect with cosmic regularity (either always or, problematically, with some determinate probability.) The main weakness of a regularist theory of causation is that it cannot differentiate between the intuitive distinction between truly causal regularities and merely accidental regularities. David Hume is the *locus classicus* of regularity theory.

relational property - "Being five miles south of Calgary" is a relational property, since attributing it to an object involves relating it to another object (Calgary.) Compare intrinsic property.

retrograde - From axon terminal to cell body (usually in reference to axon transport, e.g. in the case of dye labelling studies). Compare anterograde.

rostral - In an animal such as the rat, the rostral direction is towards the nose. In the human, the neuraxis bends at the midbrain, such that the rostral end of the vertically oriented brainstem is towards the top, but the rostral end of the horizontally oriented cortex is towards the front. Compare caudal.

rostroventrolateral medulla (RVLM) - A nucleus in the brainstem which contains a large concentration of presympathetic vasomotor neurons, projecting primarily to the intermediolateral cell column of the spinal cord.

sacral - The vertebral segments at the caudal end of the spinal cord.

somatic nervous system - The part of the nervous system concerned with sensation and control of the parts of the body (other than the special sense receptors, i.e. auditory, visual, olfactory, and gustatory) which give rise to conscious sensation and which are not visceral. Compare visceral afferents.

somatotopic - Topographic organization in the somatic nervous system.

sudomotor neurons - Sympathetic fibres which innervate and activate the sweat glands.

sympathetic division - A division of the autonomic nervous system traditionally associated with emergency responses like increasing blood pressure, speeding up the heart, sweating, and pupillary dilation (among many others). The parasympathetic division was associated with the opposite responses, and with resting regulation. However, modern research has shown that the sympathetic division is active continuously, and synergistically as well as antagonistically with the parasympathetic division.

synapse - A connection between nerve cells by which one cell influences the activity of the other. Synapses may be chemical, where the signal is passed by a neurotransmitter, or electrical, where there is a junction between neurons.

tachycardia - A speeding of the heart rate. Compare bradycardia.

thalamus - All extrinsic connections targeting the cerebral cortex synapse in the thalamus. There is a large feedback from the cortex to the thalamus (about ten times that going in the other direction), and the thalamus also has extensive intrinsic connections. It is therefore not a mere relay station, and performs its own integrative processing.

thoracic - The vertebral segments in between the cervical and lumbar regions of the spinal cord, i.e. in the rostral midsection.

topographic organization - The reflection of the spatial organization of receptors in the spatial organization of some area to which those receptors eventually project.

ventricles - The inferior (caudal) chambers of the heart.

vestibular system - A series of canals and chambers in the inner ear which provide information about head position and acceleration. Vestibular inputs are relevant to both conscious and autonomic systems.

visceral afferents - Afferents which arise from the body's internal organs. They may or may not give rise to conscious sensation.