

in some cerebrocortical regions in schizophrenia. Concentrations of NT in the CSF are reproducibly decreased in nonmedicated schizophrenics. These levels return to normal with effective treatment, and lower NT concentrations have been correlated with more severe psychopathology, particularly negative symptoms. Similar findings of NT abnormalities have not been found in affective disorders, anorexia, or Alzheimer's disease, suggesting some specificity of the findings in schizophrenia. Post mortem CCK levels have been consistently decreased in cerebrocortical and limbic regions of schizophrenic subjects, but CSF CCK changes have not been as reproducible. See *Schizophrenia, Treatment of*.

3. Summary

Since the 1970s, the biology and behavioral roles of many neuropeptides have been elucidated. They have moved from a position of relative unimportance in behavioral neuroscience to pre-eminence. In their roles as neurotransmitter and neuromodulator, paracrine and endocrine hormone, individual neuropeptides may at times subserve different functions in the CNS and periphery. However, many neuropeptides share a conserved function organizing different neural systems with the periphery in behaviors important for co-ordinated activity of the organism.

Corticotropin-releasing factor is essential in the physiologic mediation of stress, and likely critical in the pathophysiology of depression and anxiety. Oxytocin and AVP subserve many social roles from bonding to parental behavior, and they may underly some pathologic processes involving socialization such as autism. Finally, the peptides NT and CCK have similar roles in feeding, autonomic and analgesic regulation, and DA modulation in the brain. Their dysfunction may contribute to the pathophysiology of schizophrenia.

The knowledge of these neuropeptide systems in psychopathology provides wonderful opportunities for future rational therapeutic approaches. CRF₁ receptor antagonists show great promise in preclinical and early clinical trials for the treatment of depression and anxiety. Oxytocin has been found to improve socialization in some experiments of schizophrenic patients and may provide future hope for autistic disorders. Neurotensin and CCK receptor agonists provide important targets for future system-directed treatment options in schizophrenia. In summary, via their role in the organization of behavioral repertoires, neuropeptide systems may ultimately elucidate mechanisms and provide novel treatment options for many psychiatric diseases.

See also: Endocrinology and Psychiatry; Hypothalamic-Pituitary-Adrenal Axis, Psychobiology of; Neurotransmitters; Women and Psychiatry

Bibliography

- Arborelius L, Owens M J, Plotsky P M, Nemeroff C B 1999 The role of corticotropin-releasing factor in depression and anxiety disorders. *Journal of Endocrinology* **160**: 1–12
- Argiolas A, Gessa G L 1991 Central functions of oxytocin. *Neuroscience Biobehavioral Reviews* **15**: 217–31
- Bissette G, Nemeroff C B 1995 The neurobiology of neurotensin. In: Bloom F E, Kupfer D J (eds.) *Psychopharmacology: The Fourth Generation of Progress*. Raven Press, New York
- Brownstein M G 1993 Neuropeptides. In: Siegal G, Agranoff B, Albers W, Molinoff P (eds.) *Basic Neurochemistry*, 5th edn. Raven Press, New York
- Burbach J P, de Wied D (eds.) 1993 *Brain Functions of Neuropeptides: A Current View*. Parthenon, Carnforth, NY
- Fink H, Rex A, Voits M, Voigt J P 1998 Major biological actions of CCK—a critical evaluation of research findings. *Experimental Brain Research* **123**: 77–83
- Gariano R F, Groves P M 1989 A mechanism for the involvement of colocalized neuropeptides in the actions of antipsychotic drugs. *Biological Psychiatry* **26**: 303–14
- Hokfelt T G, Castel M-N, Morino P, Zhang X, Dagerlind A 1995 General overview of neuropeptides. In: Bloom F E, Kupfer D J (eds.) *Psychopharmacology: The Fourth Generation of Progress*. Raven Press, New York
- Insel T R, O'Brien D J, Leckman J F 1999 Oxytocin, vasopressin, and autism: Is there a connection? *Biological Psychiatry* **45**: 145–57
- Kinkead B, Binder E B, Nemeroff C B 1999 Does neurotensin mediate the effects of antipsychotic drugs? *Biological Psychiatry* **46**: 340–51
- Koob G F 1999 Corticotropin-releasing factor, norepinephrine and stress. *Biological Psychiatry* **46**: 1167–80
- Modahl C, Green L A, Fein D, Morris M, Waterhouse L, Feinstein C, Levin H 1998 Plasma oxytocin levels in autistic children. *Biological Psychiatry* **43**: 270–7
- Nemeroff C B (ed.) 1991 *Neuropeptides and Psychiatric Disorders*. American Psychiatric Press, Washington, DC
- Owens M J, Nemeroff C B 1992 The physiology and pharmacology of corticotropin-releasing factor. *Pharmacology Review* **43**: 425–73
- Plotsky P M, Owens M J, Nemeroff C B 1995 Neuropeptide alterations in mood disorders. In: Bloom F E, Kupfer D J (eds.) *Psychopharmacology: The Fourth Generation of Progress*. Raven Press, New York
- Rostene W H, Alexander M J 1997 Neurotensin and neuroendocrine regulation. *Frontiers in Neuroendocrinology* **18**(2): 115–73
- Smock T, Albeck D, Stark P 1998 A peptidergic basis for sexual behavior in mammals. *Progress in Brain Research* **119**: 467–81
- Wang Z X, Young L J, DeVries G J, Insel T R 1998 Voles and vasopressin: A review of molecular, cellular, and behavioral studies of pair bonding and paternal behaviors. *Progress in Brain Research* **119**: 483–99

K. J. Ressler and C. B. Nemeroff

Perception and Action

Perceiving without acting is hardly possible: scrutinizing an object visually presupposes directing the eyes at it, which sometimes involves moving the head or even

the whole body; a tactile investigation of an interesting object requires moving the fingers across its surface; and localizing a sound source is much easier when moving the ears and head (Dewey 1896). Likewise, acting without perceiving makes no sense; after all, actions, defined as goal-directed behavior, aim at producing some perceivable event—the goal. Performing an appropriate action requires perceptual information about suitable starting and context conditions and, in the case of complex actions, about the current progress in the action sequence. Thus, perception and action are interdependent. However, in the course of evolution humans have developed several ways to relate action to perception, ranging from simple and rigid stimulus–response (S–R) reflexes shared with many species to flexible and adaptive behavioral rules that can be tailored on the spot to the situation at hand.

1. Reflexes

In most species, behavior is triggered by the present situation and, thus, directly reflects the animal's immediate environmental conditions. Such reflexes can also be observed in humans, especially in infants, but here they constitute a negligible part of the behavioral repertoire. Interestingly, however, even reflexes already show the close mutual relationship between perception and action. Perhaps the best demonstration of this relationship is provided by the orientation reflex, which we experience when encountering a novel and unexpected event. On the one hand, this reflex inhibits ongoing actions and tends to freeze the body—a prime example of a stimulus–triggered response. At the same time, however, it draws attention towards the stimulus source by increasing arousal and facilitating stimulus-directed body movements. That is, the novel stimulus triggers actions that lead to a better perception of itself, thus producing a full S–R–S cycle.

Even though reflexes themselves represent a relatively inflexible way to coordinate perception and action, some researchers have suspected them to provide the basis for voluntary action (Easton 1972). For instance, the tonic neck reflex, an asymmetric pose observed in newborns with head and arm extended to one side and arm and leg flexed on the other, might facilitate the development of eye–hand coordination. Likewise, the stepping reflex, in which babies move their feet in succession when coming in contact with a solid surface, might underlie our ability to walk.

2. Associations

Human behavior (and that of other higher species) is surely much more flexible than exclusive control by reflexes would allow. Not only can we learn to react to

particular environmental conditions and situations in a certain way, we also can unlearn what we have acquired and learn new relationships between situations and actions. Our ability to associate actions with stimulus conditions was the major topic of American behaviorism around 1890–1940, when most of the basic principles of S–R learning were empirically established. In particular, stimuli and responses become associated only if they co-occur in time, if there is at least some degree of contingency between them, and if the response is judged to be appropriate (Thorndike 1927). Although the empirical approach and the theoretical language of behaviorism has long been abandoned, its results still have a major impact on modern connectionism, the attempt to model psychological phenomena by means of artificial neural or neurally inspired networks on computers or in robots.

A major objection against the behavioristic approach to S–R learning relates to the assumed role of action outcomes. In behavioristic theories, the outcome of a given action is only judged regarding its hedonic value: a positive evaluation results in strengthening the association between the action and its antecedents whereas a negative evaluation weakens the association. However, whether it feels good or bad, the outcome of an action also informs the actor about its consequences, that is, about what he or she can achieve by performing it (Tolman 1932). And as actions aim at producing intended outcomes, perception–action learning should not be restricted to forming stimulus–response associations but comprise response–effect associations also. Indeed, studies reveal that humans (and also rats and pigeons) do acquire very stable associations between their actions and the consequences that these actions produce. Moreover, there is evidence that these associations play a major role in the control of voluntary action. That is, people control their overt behavior by forming or reactivating perceptual representations of intended goal events, which through learning have become associated with the motor patterns that have been—and must be—carried out to reach them.

3. Rules

The ability to learn new relations between environmental conditions and appropriate behavior provides an enormous gain in flexibility for an individual in allowing it to adapt to environmental change. Yet, learning and relearning take time and require at least some experience with a given new condition—it is thus necessarily reactive and, in a way, conservative in reflecting what one has become used to. Indeed, many forms of human behavior show these characteristics, as witnessed by the difficulties of introducing new behavioral patterns regarding, say, women, ethnic minorities, or the use of environmental resources.

Nevertheless, there are many instances where people can switch between different reactions to the same stimulus conditions on the spot, and hence more or less independently of the amount of experience with the situation. For example, even though one may have used one route to go to work 1,000 times already, it is easy to take an alternative route from one day to another, without having to unlearn the old habit or to learn the new one, and although the fact that in the case of absent-mindedness one might again go by the old route shows that the overlearned associations still exist. Therefore, people must be able to choose deliberately among alternative ways to relate environmental situations to their actions, that is, to select one out of many possible S–R rules, and behave accordingly.

The interplay between overlearned S–R associations and the voluntary implementation of intentionally selected S–R rules ('habit' vs. 'will') was a major issue in the psychological literature between 1870 and 1935, and Narziss Ach (1935) was the first to study this interplay empirically in a systematic way. In his 'combined method' he first had subjects build up new, strong associations between nonsense syllables and one type of action, and then asked them to perform another than the practiced action to the same stimuli. The resulting increase in reaction time and errors as compared with actions with neutral stimuli was taken to represent the individual 'will power' needed to overcome the previously acquired habits. After many years of neglect, the issue of how people implement and switch between alternative S–R rules received renewed interest during the 1980s and 1990s, especially in experimental and neuropsychology (Monsell and Driver 2000). The (still preliminary) results of this research provide new insights into the relationship between, and the control of, perception and action. As one would expect, the implementation of S–R rules takes effort and time. If people are to apply several sets of S–R rules concurrently, or in short succession, their performance is impaired and more error prone. In particular, they will sometimes apply the wrong rule or apply the right rule at the wrong time, especially if effort and attention deteriorate. However, even under ideal conditions, intentional control is not absolute. That is, voluntarily implementing a particular rule does not exclude or prevent contributions from overlearned S–R associations (habits). Therefore, although any S–R rule can be implemented in principle, those rules are easier to implement and to apply if they are in accordance with natural S–R relations, acquired S–R associations, and previously implemented S–R rules than if not. For instance, performance is better if stimuli and responses have features in common than with arbitrary S–R relations, so that pressing a left or right key, or turning to the left or right, is easier if signaled by the location of a stimulus that also appears on the left or right side than by the color, shape, or meaning of a stimulus.

The ability to implement and switch between the most arbitrary S–R rules allows for the highest degrees of behavioral flexibility but it is at the same time costly in terms of attentional resources. Therefore, it makes sense to see intentional rule implementation and the more automatic guidance by overlearned S–R associations as mechanisms that complement each other: implementing and acting out the same rules repeatedly and with sufficient success provides the basis for forming increasingly stronger associations between the corresponding environmental conditions and actions, in this way transforming rules into habits.

4. Plans

In one sense, perception and action are interdependent to a degree that makes it difficult to say where action ends and perception begins—just think of the eye-movement example. In another sense, however, evolution has provided humans with the important ability to temporally decouple our actions from perception. That is, actions can be planned, prepared, and scheduled long before their environmental trigger conditions occur. Although we are only beginning to understand how action planning works, there is evidence that it can be likened to self-automatization.

At least three phases of planning can be distinguished. First, the features of the intended action effect (i.e., the goal) need to be specified, such as the direction or end location of a reach, and the effector to be used. Next, the features belonging to one plan are integrated (i.e., their cognitive representations are temporarily coupled), to avoid confusing features belonging to different, concurrently maintained action plans. This integration process will often involve linking the plan to its anticipated trigger conditions, and hence to representations of the event that is intended to trigger the planned action. That is, planning comprises anticipating both perceptual and action events. Accordingly, planning an action changes our perception. For instance, after having planned a particular action, action-related objects and events are more salient and more easily processed, action-related features of objects are more conspicuous than other features, and objects appearing at action-related locations catch more attention than others.

The final step of planning consists of initiating the planned action. Initiation may be triggered internally, such as when a plan is carried out immediately after construction, or externally, such as when the anticipated trigger event is perceived. Interestingly, this last step does not seem to underlie overly strict cognitive control. For instance, internal initiation is more or less indifferent to the content of the plan or the progress of planning, and externally triggered plans can be seen to be called up even under inappropriate conditions or at the wrong point in time. Thus,

planning is like automatizing oneself by means of delegating control to future, often environmental, events.

See also: Attention and Action; Perceptual Constancy: Direct versus Constructivist Theories; Vision for Action: Neural Mechanisms

Bibliography

- Ach N 1935 *Analyse des Willens*. Urban and Schwarzenberg, Berlin
- Dewey J 1896 The reflex arc concept in psychology. *Psychological Review* 3: 357–70
- Easton T A 1972 On the normal use of reflexes. *American Scientist* 60: 591–9
- Gibson J J 1979 *The Ecological Approach to Visual Perception*. Houghton Mifflin, Boston
- Jordan J S *Systems Theory and A Priori Aspects of Perception*. North-Holland, Amsterdam
- Monsell S, Driver J 2000 *Control of Cognitive Processes*. MIT Press, Cambridge, MA
- Piaget J 1946 *La Formation du Symbole chez l'Enfant*. Delachaux and Niestlé, Paris
- Prinz W 1990 A common coding approach to perception and action. In: Neumann O, Prinz W (eds.) *Relationships Between Perception and Action*. Springer, Berlin, pp. 167–201
- Thorndike E L 1927 The law of effect. *American Journal of Psychology* 39: 212–22
- Tolman E C 1932 *Purposive Behavior in Animals and Man*. Century, New York
- Turvey M T 1977 Preliminaries to a theory of action with reference to vision. In: Shaw R, Bransford J (eds.) *Perceiving, Acting, and Knowing*. Erlbaum, Hillsdale, NJ, pp. 211–65

B. Hommel

Perception and Cognition, Single-/Multi-neuronal Recording Studies of

Recording of isolated single neurons from brain provides a means of estimating the relationship between an animal's behavior and the activity of the brain region from which the neuron was recorded. In this manner, neurophysiologists seek to explain all behaviors in terms of neural activity, and pair all neural activity with some perceptual, behavioral or cognitive event. Thus, the ultimate goal of neural recording and analysis is to determine how activity within a brain area relates to behavioral and/or cognitive events, in essence, seeking to answer the question: 'What do neurons encode?' This question is answered in part by recording and analyzing one neuron at a time, but there are additional character-

istics of encoding which can only be answered by examining the interactions between neurons which likely underlie the overall activity of a brain region. The purpose of both single and multineuron recording, thus, is to obtain a more representative view of the neural activity in a particular brain region (Singer 2000).

Single and multiple neuron recordings are particularly powerful when applied to experiments in which the brain must form some neural 'calculation' in order to make the appropriate response. This can be manifested on many levels, from the purely mechanical, such as integration of multiple inputs in a simple neuronal circuit, to complex behavioral responses dependent on an animal's ability to 'remember' prior stimuli. Inasmuch as the recorded neural activity reveals a pattern that correlates to the cognitive process, the neural activity can therefore be considered to 'encode' information related to the process. This does not necessarily mean that the neural pattern is essential to cognition, but that the neural activity suggests information, which is available to the brain during cognition.

1. Single vs. Multiple Neuron Recording

Single neuron recording has revealed the function of many brain areas in terms of stimulus and response. For example, Hubel and Wiesel (1962) mapped columns of neurons in the occipital cortex that responded to specific visual stimuli. The identification of these 'ocular dominance columns'—in which successive columns responded to incremental rotations of a bar of light, and alternating regions mapped the left vs. right visual fields—were critical to understanding how visual information was encoded by the brain. Similarly, the identification of 'place cells' in hippocampus—neurons that fire only when the subject is in fairly limited regions of its environment (O'Keefe and Dostrovsky 1971), provided a correlation between neural activity and behavior, even if the exact purpose of that activity is still being debated. Single neuron recording has thus been used to identify the type of information processed by different brain areas, not just the five senses, but also control of muscles, attention, and memory. To this end, the brain has been mapped anatomically and, to a certain extent, neurophysiologically.

Broader questions of function and cognitive processing are difficult to answer with only single neuron recordings. In essence, all neurophysiological experiments use multiple neuron recording, since the activity of a single neuron is not necessarily representative of that brain area. Instead, many single neurons are recorded, then analyzed to see if a pattern is detected which is representative of neural activity in that region. As long as single neurons are recorded under con-