

Neural Mechanisms of Reafference and Their Role in Priming, Conditioned Perceiving, and Remembering

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When *Learning and Complex Behavior (LCB)* was written in 1994, considerable behavioral evidence implicated reafference. By *reafference* is meant that behavior produces covert activity that, ultimately, affects subsequent overt behavior. We are all familiar with something akin to reafference. Consider an example in which an automobile driver looks toward a traffic light, sees that it is red, and steps on the brake. Looking is a behavior that produces a stimulus (seeing the red light) that, in turn, controls braking. The driver's subsequent behavior (braking) was guided by a stimulus (the red light) that was produced by a previous behavior (looking toward the traffic light). Here, the activity that produced the stimulus and the stimulus itself are both detectable at the behavioral level of observation. When the activity that produces the stimulus can be detected by others, it is called an *observing response*. The acquisition and maintenance of observing responses can be understood in terms of basic learning principles (see *LCB*, p. 156 ff). However, in the case of reafference the activity that produces the stimulus and the stimulus itself are not observable at the behavior level. Only the behavioral effects of reafference are observable. Behavior analysis makes no distinction in kind between events that are observable at the behavioral level and at the neural level. Both are the stuff of the physical world, both are understandable through the methods of science, and both are describable in terms of mutually consistent principles. (See the section headed The Status of Covert Responses, pp. 275 ff.) From a behavioral perspective, reafference involves a covert observing response that produces a covert stimulus.

Reafference is not a concept unique to psychology or behavior analysis. In physiology, the distinction between behavioral events and their underlying neural events is also recognized without regarding them as different in kind. Consider the following diagram. The details of a spinal reflex are not of

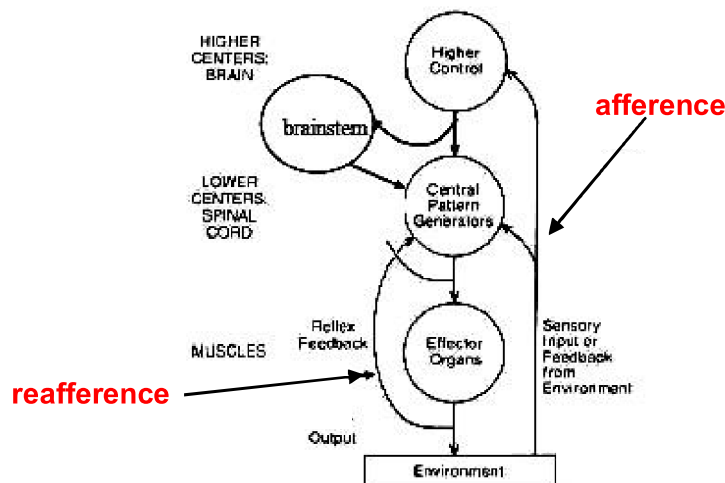


Figure 1. Main elements of a spinal reflex. (from Chez & Gordon, 1995)

interest here. Instead, our emphasis is upon the two types of feedback that affect reflexive behavior. The first, *afference*, reflects feedback that arises from the environment as a result of responding, for example, the sight of one's hand as it grasps an object. The second source of feedback, *reafference*, comes from neural pathways arising from and terminating *within* the organism. These reflect sensations such as those from the muscles when the object is grasped. Note that in reafference neither the source of the

stimulus (receptors in the muscles) nor the feedback to the central nervous system is visible to an outside observer.

We have encountered appeals to refference previously in *LCB*. For example, in priming experiments we found that presentation of one stimulus facilitated the response to a second stimulus when it was presented a very short time later. The time delay required to obtain the facilitating effect varied with the nature of the relation between the two stimuli. If the relation was on the basis of “meaning” (e.g., *sofa-loveseat*), a slightly longer time between words was required for facilitation to occur than if the relation was on the basis of sensory similarity (the naming task in which the two stimuli are identical) or direct conditioning (e.g., *butter-bread*). We interpreted such results as indicating that a longer time was required because the first stimulus had to activate motor-association areas of the brain (the covert behavior, or “meaning,” evoked by the first word) before this activity could feed back to sensory-association areas and facilitate the response to the second stimulus. (See Ch. 9—Functioning of the Experienced Learner, pp. 249 ff). Appeals to refference were also made in interpretations of problem solving (Ch. 10, especially covert behavior, pp. 275 ff) and remembering (Ch. 12, especially imagery, pp. 338 ff).

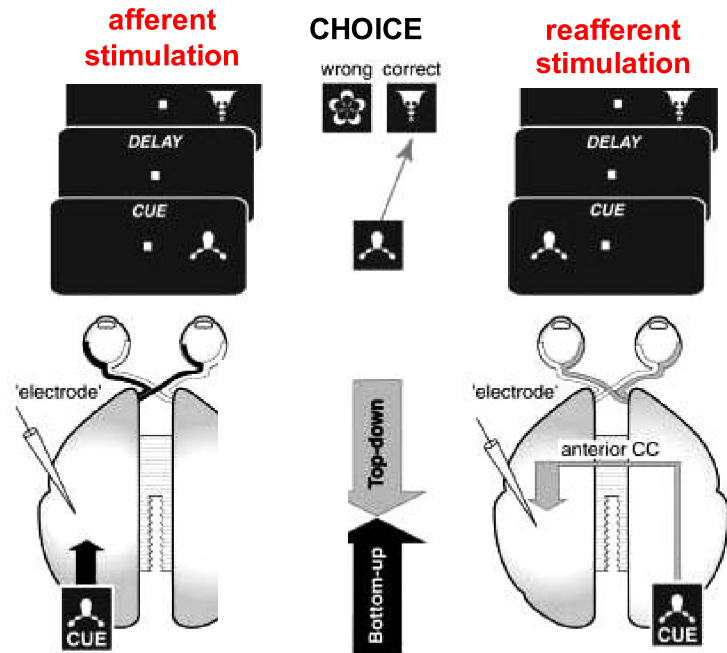
Experimental analysis of refference. When these interpretations were first offered in *LCB*, direct experimental support was largely restricted to neuroanatomical evidence. Experimental analyses at the neural level had documented the existence of extensive pathways (cortico-cortical tracts) from sensory-association to motor-association areas (feed-forward connections) and from motor-association areas back to sensory-association areas (feed-back connections) (Fuster, 1989, 2003). The existence of these pathways allowed for the possibility that such feed-back could have the effects called for by the interpretations. Since that time, however, neuroscientific research has directly demonstrated the functional significance of these feed-back, or recurrent, connections. One such experiment is described below.

As a part of an elegant and extensive research program, Myashita (2004) described the following experiment. (For a downloadable copy of the entire review paper, see <http://www.kjm.keio.ac.jp/past/53/2/59.pdf>) Rhesus monkeys, which are known to have extensive cortico-cortical tracts, were trained on a modified delayed matching-to-sample task. A sample stimulus was presented and, after a delay, one of several possible comparison stimuli was presented. The single comparison stimulus was presented either to the left or the right of the animal’s fixation point. If the comparison stimulus was the “correct” one for that sample stimulus, then the response produced a reinforcer. (See Figure 2.) After the animals were performing at high levels of proficiency, the corpus callosum (*LCB*, p. 257) was sectioned in the posterior portion that contained cortico-cortical tracts that interconnected the sensory-association areas of the left and right hemispheres.

Because of the nature of the neural pathways between the retinas and the visual cortices (see *LCB*, Figure 7.2, p. 181), the left halves of each retina send direct projections to only the left visual hemisphere and the right halves of each retina send direct projections to only the right visual hemisphere. When the corpus callosum is intact, each sensory-association area also receives inputs from the corresponding sensory-association area of the other hemisphere. Thus each hemisphere receives a direct input from one half-retina and a second input from the other half-retina via the corpus callosum. When the posterior corpus callosum is sectioned the connection between sensory-association areas is eliminated. There is, however, another way in which the sensory-association cortex of one hemisphere may be affected by activity in the sensory-association cortex of the other hemisphere. Tracts in the sensory-association cortex project to the motor-association cortex of the same hemisphere and cells in that motor-association cortex are then connected via tracts running through the *anterior* corpus callosum to the sensory-association cortex of the other hemisphere. Thus sectioning only the posterior corpus

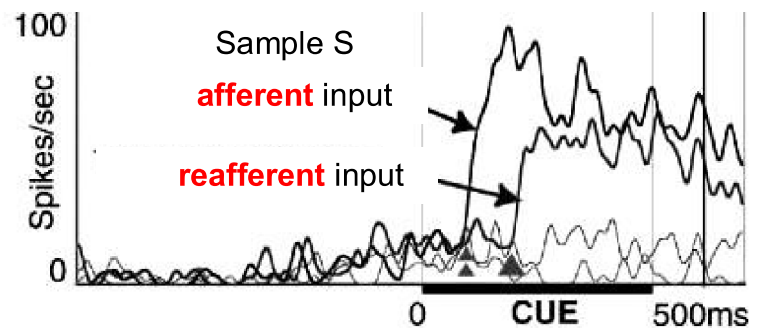
callosum prevents direct communication between the two sensory-association areas but still permits an indirect connection from the motor-association cortex of one hemisphere to the sensory-association cortex of the other hemisphere via the anterior corpus callosum. If the covert behavior initiated in the motor-association cortex of one hemisphere is fed back to the sensory-association area of the other hemisphere, then that feedback may facilitate the guidance of overt behavior.

Figure 2. A modified matching-to-sample procedure in which a sample stimulus (CUE) was presented to a rhesus monkey followed by a brief delay after which one of several comparison stimuli (CHOICE) was presented. If the comparison stimulus was the “correct” one for that sample stimulus, then the response was reinforced. The procedure was implemented with the sample and comparison stimulus presented to the same or different sides of the fixation point. See text for further information. (Modified from Miyashita, 2004)



To test whether neural activity generated in the motor-association cortex of one hemisphere was sufficient to initiate similar activity in the sensory-association cortex of the other hemisphere, an electrode recorded the activity of single cells in the sensory-association cortex. The activity when the cell was directly stimulated by inputs from the retina (afferent activity) was compared with activity when the same cell was indirectly stimulated by inputs from the motor-association area of the other hemisphere (reafferent activity). By locating the briefly presented stimuli on the same or different sides of the fixation point, the experimenter could specify whether stimuli were directly activating a cell in the visual association cortex of the same hemisphere or different hemispheres. (See Figure 2.)

Figure 3. Average frequencies of firing of single neurons in sensory-association cortex when they received direct input from the retina (afferent input) and when they received indirect input (reafferent input) from the opposite hemisphere via the motor-association cortex in that hemisphere and the anterior corpus callosum. (modified from Tomita et al, 1999)



As shown in Figure 3, reafferent input from the motor-association cortex did initiate activity in the same cells in the opposite sensory-association cortex. The rate of firing of a sensory-association cell increased in much the same manner when activated by afferent and reafferent stimulation from the retina. Two characteristics of reafferented activity are especially noteworthy: (1) Reafferent activity

began slightly later than afferent activity. This occurred because refferent activity was initiated via a less direct route—retina to opposite sensory-association cortex to opposite motor-association cortex and finally to the cell in the sensory-association cortex via the anterior corpus callosum. Second, the *same* neuron that was activated more directly by retinal stimulation was activated by the indirect route and, moreover, the changes in the rate of firing over time were similar in the two cases. The behavior was consistent with the neural findings: Matching-to-sample performance continued at high levels when the sample and comparison stimuli were presented on different sides of the fixation point if only the anterior corpus callosum was intact. When the corpus callosum was later completely sectioned, performance declined to chance levels

In nontechnical terms, “thinking” about a stimulus (activity in the motor-association cortex) may induce activity in neurons in the sensory-association cortex that is similar to the activity produced by seeing a stimulus (activity in sensory-association cortex initiated directly by retinal stimulation). Through these neural mechanisms, conditioned perceiving—or imagining—occurs. Activity in the motor-association cortex when feedback to the sensory-association cortex allows the organism to “see” again, if somewhat more dimly, a stimulus that is not now present. Skinner referred to this process as “seeing in the absence of the thing seen.”

The relevance of these findings to the interpretation of the covert responses involved in behavior such as priming and remembering is obvious. Priming based on meaningful relations between stimuli, which require mediation by activity in motor-association cortex (reafference), is slower than priming based upon sensory similarity, which requires interactions only among neurons in the sensory-association cortex of the same hemisphere. As for remembering, remembering involves what might be called self-priming. Repeated cycles of covert behavior initiate, via reafference, conditioned perceptions that may ultimately lead to the overt behavior that is scheduled for reinforcement. Behavioral and neuroscientific interpretations of these complex instances of behavior complement one another.

References

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