

Sensorimotor mechanisms in weight discrimination

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The role of efferent and afferent signals in weight discrimination was investigated by using the tonic vibratory reflex contraction of the biceps muscle. Differential thresholds were obtained for two lifting conditions (normal and reflex) and two static conditions (with and without muscular tonus). Normal lifting gave finer discrimination than reflex lifting (Experiment 1). Normal lifting was also superior to the two static conditions (Experiment 2). Within the static conditions, the addition of muscular tonus gave finer discrimination. The reflex lifting condition gave thresholds similar to those for static holding with muscular tonus, lying between those for normal active lifting and those for static pressure. The reflex lifting and pressure-sensing thresholds were very much finer than the previous literature suggests. The relative contributions of efference and afference to weight discrimination are discussed.

The sensory mechanisms underlying weight perception have been debated for a century and a half. Weber (1834/1978) put it thus:

The weight of an object is perceived in two ways: first by the touch-sense in the skin, and then by the special sense of the voluntary muscles. The latter sense tells us the degree of tension of the muscle when lifting weights and other objects.

Weber went on to measure weight discrimination by the two methods, and concluded that purely tactile discrimination became more than twice as precise with the addition of muscular kinaesthesia. (In fact, he found average Weber fractions of about 1/3 for touch alone, and 1/14 for touch plus kinaesthesia.)

In the latter half of the 19th century, extensive debate occurred over whether "sensations of innervation" or sensations from muscles formed the basis of the kinaesthetic sense. The issue was whether centrally generated (efferent) signals could be sensed in the same way as peripherally generated (afferent) signals, and it led to a great deal of fruitless controversy based on introspection and semantic hair-splitting. With the growth of experimentation and the understanding of sensory physiology, introspection as a method of scientific enquiry went out of use (Boring, 1942). However, a related debate continues in the area of motor skills. Instead of arguing about the nature of volition, modern psychologists and physiologists debate the difference between "closed-loop" and "open-loop"

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models of motor control (e.g., Stelmach, 1979), or "feed-back" and "feed-forward" models (e.g., Roland, 1978). The interest is now in whether efferent information is used at all, either separately or in conjunction with afferent information, for movement and its control. Although physiologists still argue over the relative importance of efference and afference (Roland, 1978), most would concede that both contribute to the position and movement sense of the limbs.

The relative importance of efference and afference in weight discrimination is less clear than it is for the position and movement sense. There can be no simple correspondence between physical and apparent weight, between untransformed sensory input (afference) and apparent weight, or between motor commands (efference) and apparent weight. This is shown by the weight illusions (Ross, 1969) and by weight constancy (Ross, 1981). Some authors have attempted to equate weight perception, the sense of effort, and command signals (e.g., McCloskey, Ebeling, & Goodwin, 1974; Gandevia, 1982). However, those authors were considering only estimates of absolute weight and not weight discrimination.

A few authors have considered the role of efference in weight discrimination. Wundt (1874) took a mixed view on sensations of innervation, and became more cautious about them in his later years (Ross & Bischof, 1981). In 1892, he maintained that the Weber fraction for purely tactile weight discrimination was 1/3, but that with lifting it was 1/17: The finer discrimination in the latter case was due both to the sensations arising from the muscles and to the sensations arising from the motor impulse to the muscles. Waller (1891) stressed the importance of voluntary, as opposed to reflex, muscle contractions. Using himself as subject, he found a Weber fraction of about 1/7 for weight discrimination by voluntary lifting of the fingers, but about 1/1 for reflex contraction due to cathodic excitation of the median nerve, and immeasurably

poor discrimination for reflex contraction due to faradization of the median nerve. It is surprising that Waller found such poor discrimination with reflex lifting. Starling (cited in Lovatt Evans & Hartridge, 1936) found that subjects could still rank order weights when the weights were attached to the wrist and lifted reflexly through electrical stimulation of the biceps muscle. However, no precise details of the experimental method or results were given.

We decided to make use of the tonic vibratory reflex (TVR) contraction (see DeGail, Lance, & Neilson, 1966; Hagbarth & Eklund, 1966) to reopen the investigation into reflex lifting and its effect upon weight discrimination. That is, when a vibratory stimulus is applied to the tendon of the biceps muscle of a relaxed subject, an involuntary, tonic contraction of the muscle is produced and the forearm and hand rise (Marsden, Meadows, & Hodgson, 1969). The subject is not aware of "lifting" the arm, and normal "command signals" are not involved. Thus there can be no involvement of "sensations of innervation" (Wundt, 1874) or "sense of effort" (McCloskey et al., 1974).

There are some difficulties in interpreting the effects of the TVR. When a vibratory stimulus is applied to a muscle, abnormal afferent volleys are produced by the Group 1A receptors associated with that muscle. These can affect position sense (Craske, 1977) and the absolute weight of objects (McCloskey et al., 1974), but no information is available about their effect on weight discrimination. Furthermore, it is possible that vibration of the biceps affects normal afferent transmission from receptors in the wrist and hand. For example, Ferrington, Wail, and Rowe (1977) found that vibration of the palm decreased the tactile sensitivity of some receptors in the fingers. We therefore included an experiment to investigate whether vibration of the biceps affected tactile sensitivity in the hand. If there is a loss of tactile sensitivity, there might be some impairment of weight discrimination. For example, Weber (1834) concluded that static weight discrimination (through pressure alone) was best in those parts of the body that possessed fine tactile discrimination. If this is correct, loss of tactile sensitivity will cause some impairment in weight discrimination.

The aim of the current experiments is to use modern techniques to reinvestigate the earlier findings of poor discrimination through passive touch and very poor discrimination through reflex lifting. Some light might, as a result, be cast upon the relative contributions of afferent and efferent signals in weight discrimination.

METHOD

Experiment 1

Subjects. The subjects were 12 male and 6 female first-year psychology students, naive as to the purpose of the experiment.

Apparatus. There were two identical sets of seven comparison weights, ranging in weight from 52 to 64 g in 2-g intervals, and one set of seven standard weights, each weighing 50 g. All weights were aluminum cylinders, 45 mm in length \times 25 mm in diameter,

with the center removed to distribute the material evenly about the longer axis. Vibratory stimulation was provided by a Pifco Massager (No. 1556) vibrating at 100 Hz with an amplitude of between 0.5 and 1.0 mm.

Procedure. The subject was seated in front of a bench, on which the forearm and hand of his/her preferred arm rested, palm facing upwards. The height of the seat was adjusted so that the angle subtended at the elbow joint was 135°. A practice session of three active and three reflex lifts of weights placed upon the palm was performed to ensure that the optimum point of stimulation for the subject was found and that the subject had the chance to appreciate the rate of lifting produced by the vibrator. The hand was unsupported, and rose with the forearm in the same manner in both active and reflex lifting. The subject was asked not to assist or resist the slow reflex movement of the arm generated by vibratory stimulation. He/she was then asked to match this rate of lifting in the active condition, in which the arm was raised on the command "lift," whereas, in the reflex condition, lifting commenced upon application of the vibrator to the tendon and lower part of the biceps muscle. The subject was required to say which of two weights presented consecutively felt heavier. The experimenter placed the weights gently upon the subject's palm while the arm was rising. The stimulus presentation time was 3 sec, and the interstimulus interval was kept constant at 5 sec. Immediately after the practice session, the subject was blindfolded and the experimental trials began. Half were given the active condition first and half the reflex condition. The total length of the practice and test sessions was about 1 h.

An up-down transformed response rule (UDTR), tracking the 71% correct point, was employed to calculate the differential thresholds in both experiments. The UDTR is a variation of the "staircase" sequential tracking procedure. In order to prevent the subject's learning the tracking procedure, two UDTRs were randomly interspersed (Cornsweet, 1962). The recording of responses commenced after the first incorrect response upon that particular UDTR; to avoid wasted observations at the beginning of testing, an optimum threshold point was used (Wetherill & Levitt, 1965). The differential thresholds were calculated from 16 reversals.

Experiment 2

Subjects. The subjects were 18 students, from the same source as Experiment 1, 8 males and 10 females ranging in age from 18 to 35 years.

Apparatus. The apparatus was the same as for Experiment 1 except that the vibrator was not required.

Procedure. The procedure was essentially the same as that of Experiment 1, in that the weights were placed upon the subject's palm for 3 sec with a 5 sec interstimulus interval. Three conditions were used, the orders being counterbalanced across subjects: (1) *active*, identical to the active condition in Experiment 1 except that the experimenter told the subject at what rate to lift his/her arm, (2) *static raised*, in which the subject kept the hand raised 23 cm above the bench surface with the elbow joint resting upon the bench, and (3) *static horizontal*, in which the subject kept the forearm resting horizontally upon the bench surface. Thresholds were determined by the same procedure as in Experiment 1. The total length of the test session was about 1 h.

Experiment 3

Subjects. There were 8 students from the same source as Experiment 1, 4 males and 4 females ranging in age from 17 to 24 years.

Apparatus. The Pifco vibrator was used, as in Experiment 1, and a graduated V-test tool manufactured out of two rulers joined together at one end and held apart at the other, by bolts, to form a V. This was a version of the Mackworth "V-Test" apparatus, as used by Synodinos and Ross (1979).

Procedure. The subject was seated at a bench in the same manner as in Experiment 1. The vibrator was placed in position and a standard set of instructions was read out. Tactile sensitivity was measured in two conditions, vibration and no vibration. The experimenter ran the V along the subject's middle finger in an ascending manner and in a descending manner. The subject had to inform the experimenter when the one edge of the V parted into two or when the two edges merged into one. The design was counter-balanced for the vibration/no-vibration conditions and for the order of presentation of one edge or two edges. The 50% correct point was tracked using a von Békésy (1947) tracking procedure. The mean distance along the ruler for the ascending and descending thresholds was calculated.

RESULTS

The mean differential thresholds for the various experimental conditions of Experiments 1 and 2 are listed in Table 1. They were calculated at the 71% correct level from the UDTR procedure described earlier.

Thresholds are listed for the two stimulus presentation orders. When the standard, lighter, weight was presented second, the threshold was higher in all of the conditions. The difference was significant on analyses of variance both for Experiment 1 [$F(1,17)=9.54$, $p<.01$] and Experiment 2 [$F(1,17)=47.45$, $p<.001$]. This result is consistent with the literature on the "time error," the bias towards judging the second of two weights as heavier (Ross, 1964).

The mean thresholds from the two presentation orders were calculated. The Weber fractions based on these means are also shown, calculated from the formula $2\Delta W/(W_1+W_2)$ (where ΔW is the differential threshold, W_1 is the standard weight, and $W_2 = W_1 + \Delta W$).

The mean thresholds for the different lifting conditions were compared using analyses of variance. Active lifting gave the significantly lower threshold when compared with TVR in Experiment 1 [$F(1,17)=12.03$, $p<.005$]. In Experiment 2, an analysis of variance showed a significant effect due to lifting conditions [$F(1,17)=14.13$, $p<.001$]. The active threshold was shown, by t tests, to be significantly lower than either the static raised [$t(17)=-3.30$, $p<.005$, two-tailed] or the static horizontal [$t(17)=-4.77$, $p<.001$, two-tailed], and the static raised was also significantly lower than the static horizontal [$t(17)=-2.33$, $p=.05$, two-tailed]. It can thus be concluded that active lifting gives a finer threshold than any of the other conditions.

It is difficult to rank the thresholds across experiments, because different subjects and different numbers of trials were used in Experiments 1 and 2. It was unfortunately necessary to run two different experiments because of the length of the TVR condition and the muscular fatigue induced by it. The active threshold was lower for Experiment 2 than for Experiment 1, perhaps due to the larger number of trials, which afforded additional practice. The difference was not significant [$t(34)=-1.30$, $p>.05$, two-tailed], but it nevertheless hinders a direct comparison of thresholds across experiments.

In Experiment 3, tactile sensitivity of the hand during vibratory stimulation of the biceps muscle was compared with tactile sensitivity of the hand without vibration. Sensitivity was expressed as the number of centimeters along the ruler to discriminate the V. The mean score without vibration was 8.79 cm (SD 1.11 cm); with vibration, it was 8.27 cm (SD 1.04 cm). There was no significant difference between the vibration and nonvibration conditions [$t(7)=2.18$, $p>.05$, two-tailed].

DISCUSSION

Before discussing the main results, it is interesting to compare the Weber fractions we obtained with those obtained by other researchers. Textbooks often quote a Weber fraction of 0.02 for lifted weights, probably following Boring, Langfeld, and Weld (1939), who cited Holway and Pratt (1936). However, this appears to be a "best value" for one subject in one condition. The Weber fraction is known to increase at low stimulus values, so our results should be compared only with those in the 50-g range. Oberlin (1936) obtained a Weber fraction of about 0.07 at 50 g. Holway and Hurvich (1937), using an adjustment method, found a value of about 0.5 at 50 g. More recently, Ross and Reschke (1982) obtained fractions of between 0.09 and 0.12 with active lifting at a stimulus intensity of 54 g. The fractions we obtained (between 0.09 and 0.13) are thus within the middle range of those quoted in the literature for lower stimulus values.

Our results from Experiment 1 demonstrate that reflex lifting impairs discrimination to only a small extent in comparison with active lifting. The DL (differential threshold) rose from 5.42 g with normal active lifting to 6.73 g with TVR lifting—an increase by a factor of only 1.24. This is a much smaller change than the factor of

Table 1
Differential Thresholds (Grams) for 18 Subjects in Experiment 1 and 18 Subjects in Experiment 2

Stimulus Order	Experiment 1				Experiment 2					
	Active		TVR		Active		Static (Raised)		Static (Horizontal)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Standard 1st	4.86	1.76	5.02	2.66	4.12	1.20	4.85	1.64	4.99	1.81
Standard 2nd	5.98	2.17	8.44	2.52	5.74	1.85	7.63	2.64	9.37	2.17
Mean	5.42	1.02	6.73	1.46	4.93	1.25	6.24	1.44	7.18	1.33
Weber Fraction	0.103		0.127		0.094		0.117		0.134	

7 or more reported by Waller (1891) for reflex contraction. We cannot comment fully on Waller's results without repeating his experimental method, but would suggest that the electrical techniques for producing the reflex contraction need adequate control experiments (similar to our Experiment 3) to gauge their effect upon sensory nerve fibre transmission.

The results from Experiments 1 and 2 can demonstrate only that normal efferent signals are not a necessary condition for the comparison of lifted weights. There are various ways of interpreting the fact that the TVR condition falls in between the active lifting and passive pressure conditions: (1) Afferent signals from active lifting could account for all of the improvement between passive pressure and active lifting conditions, and it is abnormal afferents from vibratory stimulation that interfere to make discrimination poorer in the TVR condition. (2) Afferent signals from active lifting could account for some of the improvement, but abnormal afferents interfere with their contribution. Efferent signals also contribute independently to the improvement in discrimination. (3) Normal efferent signals could account for all of the improvement between passive pressure and active lifting conditions. Thus, the interference from abnormal afferents is minimal. (4) An interaction between efferent and afferent signals could be important in weight discrimination in active lifting; it is either the absence of the efferent signals or the presence of the abnormal afferent volleys that interferes with normal interaction.

Vibration may interfere with our perception of weight through abnormal muscle afference or through the occlusion of afferent nerve-fibre transmissions. Experiment 3 provides evidence that the latter suggestion is not valid. If the cutaneous receptors in the hand and tension receptors in the wrist subserve the sense of weight, then it could be argued that we have only demonstrated a masking or interference effect of vibration on these receptors. However, we found that vibrating the biceps muscle does not impair tactile sensitivity of the hand. If anything, there was a trend in the opposite direction. The higher weight discrimination threshold in the TVR condition cannot be attributed solely to an occlusion effect of vibration.

Experiment 2 showed that discrimination in both of the static conditions was impaired in comparison with the active condition. Some aspect of the lifting movement aids discrimination. The static raised condition also produced a significantly finer discrimination than the static horizontal condition. This suggests that receptors sensitive to changes in tension or muscular tonus (in this case the Golgi tendon organs in the elbow and wrist flexors) may be responsible in part for our appreciation of weight.

In Experiment 2, the DL rose from 4.93 g with normal active lifting to 6.24 g with a maintained tension, an increase by a factor of 1.27. This is comparable to the increase, by a factor of 1.24, of the TVR lifting over normal active lifting in Experiment 1. The similarity of these ratios in these two conditions may be due to the contribution of afference—possibly that from tension receptors.

Performance was poorer in the static horizontal condition (DL = 7.18 g) than in the active condition (DL = 4.93 g) by a factor of 1.46. However, this figure is considerably less than the factor of about 5 found by previous researchers (e.g., Weber, 1834/1978, and Wundt, 1892/1894). This could have been due to the loss of either the efference or the afference that occurs during normal lifting movements, or both.

In Experiments 1 and 2, subjects were asked to discriminate between the weight of successively lifted objects. This is not the same as asking subjects to concentrate on bodily sensations or the amount of effort needed (which indeed they can do, as McCloskey et al., 1974, demonstrated). In the TVR condition, subjects could not refer to a sense of effort or sensations of innervation as none were present. Evidence of this is provided by Burke, Hagbarth, and Lofstedt (1976a, 1976b), who have shown that efferent signals generated by the TVR contraction do not use the same cortically originating efferent pathways as do ones generated during voluntary contraction.

Where and how efferent and afferent information are combined to give the "weight" of the object is not yet known. It would seem improbable, on the basis of the results obtained, that the weight of lifted objects was based solely upon efference copy with no reference to afferent input. Subjects are able to discriminate reasonably well on the basis of afferent information in conjunction with abnormal efferent information. Gandevia (1982) has shown the influence of afferent signals upon the command signal and discusses their role in fine tuning for the efferent signals. Our experimental results are in keeping with the view that, for weight discrimination at least, both afferent and efferent signals contribute. Possibly, efferent signals calibrate the system to expect a certain range of stimulus intensities (e.g., Gregory, 1968). This, in turn, affects the way afferent signals are interpreted.

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