

the column. At the concentration present in the eluate, no protein could be detected in the active peak by absorbance at 280 nm, suggesting that extensive purification of the enzyme had been achieved. Although we have not yet completely purified the rat enzyme, cochromatography of ^{75}Se with GSH peroxidase activity through two highly effective purification steps suggests that Se is an integral and necessary part of the enzyme. In our laboratory the enzyme from ovine blood has been purified, yielding a preparation containing at least 2 gram-atom of Se per mole of enzyme (8).

Flohé (9) reported that bovine erythrocyte GSH peroxidase contains no non-protein prosthetic group; however, a Se moiety would probably not be detected by the spectrophotometric methods used by Flohé. Selenite (10) or Se-amino acids (11) enhance the reducing ability of GSH in model systems, and SH groups in GSH peroxidase appear to change their redox state during the catalytic process (9). Whether Se in the enzyme participates in these redox reactions or has some other function is not known.

Several groups of investigators (3) have emphasized the role of GSH peroxidase as the primary mechanism for degrading low levels of H_2O_2 in cells. Since GSH peroxidase also acts on hydroperoxides of unsaturated fatty acids (4), the enzyme plays an important role in protecting membrane lipids, and thus the cell membranes, from oxidative disintegration. Failure of peroxide destruction can explain the hemolysis in vitro and oxidative damage to hemoglobin and possibly the wide variety of degenerative conditions that occur in Se deficiency. A role for Se in GSH peroxidase may also account for the apparent "antioxidant" effects of dietary Se observed by previous workers (12).

Our work offers new insight into the interactions of Se, vitamin E, and the sulfur-containing amino acids in preventing some of the same nutritional diseases. If vitamin E prevents fatty acid hydroperoxide formation, and the sulfur amino acids (as precursors of GSH) and Se are involved in peroxide destruction, these nutrients would produce a similar biochemical result—that is, lowering of the concentration of peroxides or peroxide-induced products in the tissues. Protection against oxidative damage to susceptible nonmembrane proteins by dietary Se but not by vitamin E (2) might explain why some

nutritional diseases respond to Se but not to vitamin E (1). On the other hand, certain tissues or subcellular components may not be adequately protected from oxidant damage because they are inherently low in GSH peroxidase even with adequate dietary Se. Damage to such tissues would be expected to be aggravated by diets high in unsaturated fatty acids and to respond adequately to vitamin E but not to Se.

Measurement of GSH peroxidase may provide a useful means for defining Se requirements and for identifying Se deficiency in animals and humans. With purified GSH peroxidase it should be possible to identify the active form of Se and further clarify its role.

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13. For ascorbate-induced oxidations, the incubation mixture contained: 0.5 mg of hemoglobin per milliliter, 0.5 mM GSH (when added), 3.5 mM ascorbate [prepared as described by Mills (6)] and 1 mM sodium azide. Incubations were carried out at 37°C for 60 minutes; choleglobin formation, expressed as percentage of the total hemoglobin, was determined immediately, as described by Mills (6). For H_2O_2 -induced oxidations, the incubation mixture contained: 0.5 mg hemoglobin per milliliter, 0.5 mM GSH (when added), 0.1 mM H_2O_2 and 1 mM sodium azide. Incubations were carried out at 37°C for 10 minutes. Increase in optical density at 627 nm measured hemoglobin oxidation (6). The data in the table represent the respective hemolyzates from one Se-deficient and one Se-supplemented rat; however, the effect has been confirmed repeatedly by visual observation of hemoglobin discoloration as well as by quantitation of GSH peroxidase activity as presented in the text.
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Haptic Illusion: Apparent Elongation of a Disk Rotated between the Fingers

Abstract. *A disk (coin) turned end over end between thumb and forefinger feels longer to the turning hand. The illusion grows rapidly for 30 seconds but does not become asymptotic within 60 seconds. The illusion increases with coin size and turning rate, and is independent of holding pressure. It appears to involve illusory mechanisms in both hands.*

This report describes an illusion which I first observed while idly turning a penny end over end between my thumbs and forefingers, using two hands. The coin was held on edge so that the balls of the thumb and forefinger of the holding hand were separated by its diameter. This diameter served as the axis about which the same digits of the other hand turned

the coin. The thumb of the turning hand pushed on one rim and the forefinger pulled the opposite rim around. As the fingers came together, the thumb slid back so that it could engage the other rim while the index finger moved forward to catch the edge released by the thumb. This operation was repeated over and over, turning the coin end over end. The coin seemed to stretch

out so that the diameter felt longer to the turning fingers than to the holding fingers. At the same time the curvature of the edge of the coin as felt by the thumb and finger of the hand doing the holding appeared to decrease so that the coin seemed oval in shape. Finally, the illusion disappeared, or at least decreased dramatically, when the coin was looked at or stopped.

To determine whether this illusion is experienced by others without suggesting its nature, I tested 12 college students individually, giving each a penny and telling him to turn it as described above. The subject was instructed to close his eyes and report anything unusual or different as he turned the coin. Care was taken not to suggest any particular change. If no illusion was reported after 60 seconds the subject was asked to attend to the shape of the coin, and after 30 seconds more he was asked whether the diameter felt longer to one hand than to the other. After the trial the subject estimated the ratio of the longer diameter to the shorter.

No subject was aware of the illusion before the experiment. Ten subjects reported the illusion within 60 seconds, the eleventh after being told to attend to the shape of the coin, and the twelfth when asked directly about differences in the felt diameter. All reported that the diameter for the turning hand appeared to increase. For four subjects the diameter for the holding hand appeared to decrease. Estimates of the ratio of the longer to the shorter diameter ranged from 1.2 to 1.8 (mean, 1.43). Four subjects reported that the edge of the coin felt by the holding hand seemed to flatten; for two the curvature appeared to reverse so that the coin seemed pinched into a dumb-bell shape. The illusion was not an idiosyncratic effect and seemed of sufficient general interest for further study. A series of experiments testing the effects of several variables on the illusion is described below.

For all experiments the following general conditions applied. For each experiment, both male and female college students were employed, and from 60 to 100 percent had never experienced the illusion before. All were tested individually, seated at a small table across from the experimenter in a small cubicle. In front of the subject was a shield 60 cm wide by 30 cm high under which he placed his hand during the trials. The shield was tilted toward the subject and a series of draw-

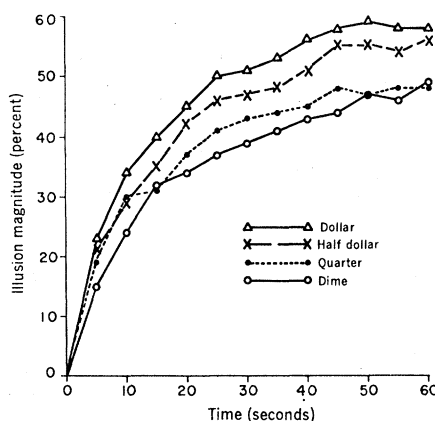


Fig. 1. Growth of the illusion of coin length for four coin sizes. Illusion magnitude is the percentage by which one diameter of a coin appears to exceed the other diameter ($N = 24$).

ings was arranged on it. These ranged, in steps of 2.54 mm, from a circle 2.54 cm in diameter to an oblong figure 2.54 cm high and 7.11 cm long. The oblongs were numbered 0 (circle) to 18. Both ends of all the figures were semicircular. Various disks and other stimulus objects were used: a dime (18 mm in diameter), a nickel (21 mm), a quarter (24 mm), a half dollar (30 mm), a dollar (39 mm), a poker chip (37 mm), and a Ping-Pong ball (37 mm). Other stimuli are described where appropriate below.

The nature of the illusion and the way to obtain it were described to the subject, who then tried it using a nickel. In the entire series of experiments, which included 97 subjects, only one subject failed to obtain the illusion within the 30-second test trial and was excused. The subject was told to hold the coin with his nonpreferred hand, to begin turning it with his preferred hand on command, and after he detected the illusion to call out every few seconds the number of the oblong on the shield corresponding most closely to the felt shape of the coin. After a 30-second practice trial the subject was given a 2-minute rest period, during which specific instructions for the experiment were explained.

To measure the effect of coin size, 24 subjects and four coins were used (dime, quarter, half dollar, and dollar). Each subject used all four coins and was given five 1-minute trials. The order of coins was counterbalanced across the subjects, with each coin being used first, second, and so forth, an equal number of times. On the fifth trial, whichever coin had been used first was used again. Throughout each

trial the experimenter recorded continuously the magnitude of the illusion by noting the highest number reported by the subject during successive 5-second intervals. A 2-minute rest was given between trials. The value of each judgment of the magnitude of the illusion was multiplied by 10, thus making each score represent the percentage by which the length appeared to exceed the height. The results for the first four trials are illustrated in Fig. 1. The effects of coin size on the maximum illusion reported were significant [$F(3, 23) = 3.13$, $P < .05$]. A comparison of the maximum illusion for the first and fifth trials indicated no fatigue or series effects [$F(1, 23) = 1.6$, $P > .2$] (1).

The final illusion magnitude for the dime and quarter of approximately 48 percent is not greatly different from the ratio of 43 percent estimated for the first experiment, in which a penny was used. This correspondence is considered important, for there was some concern that the drawings presented on the shield would be suggestive and tend to inflate the reported illusion magnitudes. Apparently this did not occur to any large extent.

The growth curves presented in Fig. 1 are similar to the growth data for visual figural aftereffects presented by Hammer (2) and to those for kinesthetic figural aftereffects (KFAE) presented by Singer and Day (3). In each case, rapid growth during the initial 15 to 30 seconds is followed by a more gradual increase. This similarity leads to the speculation that similar processes are involved. Two hypotheses are suggested. First, it may be that the apparent flattening of the curved edge felt by the holding fingers results from adaptation to the continual pressure and twisting on the finger tips. This flattening, in turn, may lead to an apparent reduction in the width of the coin. The turning fingers hold the rim a smaller proportion of the time and for them the rim is not twisted into the tips, so less flattening would be expected. This difference in stimulation could lead to the experienced disparity in diameters.

A second possibility is that as the turning fingers turn the coin, they come together for a significant fraction of the time and are separated by no more than the thickness of the coin, while at their widest separation they are only a little farther apart than the diameter of the coin. The holding fingers are always separated by the diameter of the coin. Thus, the turning fingers be-

come adapted to a narrower average separation than the holding fingers. This differential adaptation may lead to the difference in apparent length for the two hands.

In an attempt to isolate the factors involved in the two explanations offered above, the illusion was measured for four stimulus objects. A disk (poker chip) was used to obtain a base measure of the illusion. A sphere (Ping-Pong ball) was used because in rotating it the subjects do not bring the turning fingers together as much as they do in turning a disk, and it does not provide the sharp curved edges of a disk to the holding fingers. Two additional objects were used, intersecting disks (two poker chips intersecting along their diameters at right angles) and a capped disk (a poker chip with 23-mm sections of a Ping-Pong ball glued at opposite ends).

The subjects were told to hold one of the intersecting disks so that the other disk was centered and oriented perpendicular to the axis between thumb and forefinger. The turning fingers could thus ride around the rim of the disk located between the digits of the holding hand. This simulated the sphere for the turning hand and the disk for the holding hand. The subjects were instructed to hold the capped disk with the thumb and finger of the holding hand on the caps and otherwise to turn the disk in the normal fashion, thereby simulating the disk for the turning hand and the sphere for the holding hand. Twenty-four subjects were given four 1-minute trials, complete counterbalancing of the stimulus order was utilized, and there was a 2-minute rest between trials. The maximum illusion magnitudes averaged for 24 subjects were: for the disk, 73.3 percent; for the intersecting disks, 56.7 percent; for the capped disk, 49.6 percent; and for the sphere, 28.3 percent. These differences are significant [$F(3, 23) = 16.14, P < .001$].

The dramatic reduction in the illusion for the sphere does not contradict either explanation. The intermediate effects for the intersecting disks and the capped disk might indicate either that both factors are involved, or that these stimuli failed to isolate the variables adequately. If it is assumed that the factors were isolated and that the sphere affects holding and turning hands equally, then the contribution of the holding hand for a disk (intersecting disk minus sphere) is approximately 29 percent, while the corresponding contribution of the turning

hand (capped disk minus sphere) is approximately 22 percent. These increments do not summate, for the disk exceeds the sphere by only 45 percent instead of 51 percent (29 percent + 22 percent). Thus, either the effects are not perceptually additive, or the initial assumptions are erroneous. Further complications arise when the data on disk size are considered. For larger disks, the turning fingers move through greater ranges of separations and thus should show greater adaptation and hence greater illusory effects. On the other hand, the edges of larger disks have less curvature and therefore should produce less adaptation and smaller illusory effects for the holding fingers. Since the illusion does grow with increased disk size, either the contributions from the two hands do not change equally with changes in disk size or an intricate interaction between the hands is occurring. Alternatively, it may be that the illusion is not separable into components generated individually by the two hands (4).

Two parameters in the manipulation of disks that were observed to vary among subjects were turning speed and holding pressure. Increased grip tension can lead to greater constant errors in haptic judgments of width (5), and this is similar to holding pressure in the experiment reported here. No comparable data are available on speed of exploration. Marginally related is the finding that under some conditions passive stimulation produces greater KFAE than active exploratory stimulation (6). To test the effect of turning rate, 40 subjects were given three trials with a poker chip as the stimulus object. During a 30-second practice trial, the experimenter recorded the rate at which the subject turned the coin. The subject was then instructed that on subsequent trials he would be asked to pace his turning speed in time to a metronome, and was given an additional 30-second practice trial during which he attempted to do so. Two paced speeds were used (50 and 20 rev/min). The remaining trial was unpaced. The order of the three conditions was randomized across the subjects, and 2-minute rest periods separated the trials. The mean turning rates for the self-paced trial and for the 30-second practice trial were the same, 34.1 rev/min. The mean illusion magnitude for 50 rev/min was 62 percent; for self-paced turning, 59 percent; and for 20 rev/min, 49 percent. The effect of turning speed was significant [$F(2,39) = 5.8, P < .01$].

Although this finding is not inconsistent with a KFAE type explanation, the relationship between speed and activity is tenuous.

The effects of holding pressure were tested by giving 20 subjects three 1-minute trials with a poker chip as the stimulus object. On one trial the subject held the coin as lightly as he could without dropping it. For another trial the subject exerted extreme pressure, holding it as tightly as he could, commensurate with his ability to turn it. On a final trial the subject held it with his normal comfortable pressure. After each trial the subject indicated his holding pressure by squeezing a simple spring scale with the same pressure that he exerted during the trial. The order of the three trials was randomized across subjects. The mean pressure recorded for light pressure was 146 g; for normal pressure, 331 g; and for heavy pressure, 735 g. These differences were significant [$F(2,19) = 64.2, P < .01$]. The mean illusion magnitude for light pressure was 45 percent; for normal pressure, 51 percent; and for heavy pressure, 48 percent. These differences were not significant [$F(2,19) = 1.16, P > .2$]. This finding is inconsistent with the results showing a relation between grip tension and constant error in haptic judgments of width.

While this series of experiments has not led to a clear explanation of the illusion, it has introduced the effect, shown its generality, and suggested explanatory mechanisms. The general findings are that larger disks and higher turning rates lead to greater effects. A sphere gives a much smaller effect, and holding pressure appears to be irrelevant. Although the illusion shares general growth characteristics with some forms of KFAE, other data suggest a more complex interaction of adaptation or habituation effects in both hands.

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