that is, a peck to the side key containing the sample stimulus, activated a food hopper which allowed the bird 1.5-second access to mixed grain (reinforcement); an incorrect response resulted in a 1.5-second blackout. A total of 224 trials (half color and half line orientation) were randomly presented during each daily session and were separated by intertrial intervals of 10 seconds. The data reported below are from the last 192 trials of each session.

After both birds stabilized above 90 percent correct on the "element" matching or nondivided-attention task described above, they were trained on a "compound" or divided-attention task. This training differed from the element matching only in that the sample in a given trial contained three white lines superimposed on a colored background. In half the trials the birds were still required to match on the basis of line orientation, and in half, color. Thus, the compound sample stimuli did not predict which of the two elements would later appear for matching, so that the birds were forced to attend to both stimulus dimensions. Once again both birds stabilized above 90 percent correct.

The experiment was concerned with the stimulus duration required to maintain some level of performance. Accordingly, we adopted a psychophysical technique in which performance was fixed at 80 percent correct and the duration of the sample stimulus was varied to maintain that performance. Our procedure was a modification of Taylor and Creelman's (*5*) PEST (Parameter Estimation by Sequential Testing). In PEST, some value of the independent variable (stimulus duration) is assumed to be just sufficient to maintain a particular performance. During a session the independent variable converges on that threshold value through a series of diminishing "up-and-down" steps; the momentary value changes when a Wald sequential likelihood ratio test (*5*) yields a decision of too many or too few correct responses relative to the expected performance value. Our modification involved using a double PEST during each session in which each bird was treated as two observers; one observer matched on the basis of colors and the other observer matched on the basis of line orientation. Within each pair of days during this phase of the experiment, compound and element matching sessions were randomly scheduled. Within each session, trials involving color and line orientation matching occurred equally often in a random sequence. During each of these sessions, the computer separately and independently "titrated" sample stimulus duration in the color and line orientation trials. Estimates of separate threshold durations were therefore attempted during each session for both line orientation and color trials.

Figure 1 depicts the distributions of sample stimulus durations recorded during the first 50 PEST sessions. The estimates of stimulus duration derived from compound sessions generally exceeded those derived from element sessions. Rank-sum tests (*6*) indicated that compound-element differences were significant for both line orientation ($P < .02$) and color ($P < .001$) matching for both birds.

Assuming that stimulus duration reflects the minimum amount of time necessary to process stimulus input, we view these results as evidence of a central information-processing channel of limited capacity. When channel capacity must be shared between two separate stimulus dimensions, a longer stimulus duration is required in order to process each dimension.

WILLIAM S. MAKI, JR.
TERRY C. LEUIN
Department of Psychology,
University of California,
Berkeley 94720

References and Notes

1. N. S. Sutherland and N. J. Mackintosh, *Mechanisms of Animal Discrimination Learning* (Academic Press, New York, 1970).
2. D. S. Blough, *Science* **166**, 125 (1969).
3. P. H. Lindsay, in *Attention: Contemporary Theory and Analysis*, D. I. Mostofsky, Ed. (Appleton-Century-Crofts, New York, 1970).
4. D. E. Broadbent, in *Current Problems in Animal Behavior*, W. H. Thorpe and O. L. Zangwill, Eds. (Cambridge Univ. Press, London, 1961); D. R. Thomas, F. Freeman, J. G. Svinicki, D. E. S. Burr, J. Lyons, *J. Exp. Psychol. Monogr. 83* (No. 1), part 2 (1970).
5. M. M. Taylor and C. D. Creelman, *J. Acoust. Soc. Amer.* **41**, 782 (1967). The PEST parameters were target percent correct (80), deviation limit for the Wald test (± 1 correct response), and minimum step size (10 msec); other parameters (starting step size, initial level, and maximum step size) were monitored during initial PEST training to obtain the maximum likelihood of a decision, or near decision, during a given session.
6. W. J. Dixon and F. J. Massey, Jr., *Introduction to Statistical Analysis* (McGraw-Hill, New York, ed. 2, 1957). Our analyses included only estimates of sample stimulus duration that resulted from step sizes of 40 msec or less for bird 67 and 80 msec or less for bird 69. Twenty-two percent of the estimates did not meet these criteria. (Our computer simulations of PEST have shown that even under relatively ideal conditions, PEST will sometimes fail to reach decisions in a given number of trials.) Nonparametric rank-sum tests were used as the data did not meet the assumptions underlying parametric tests. However, to guard against possible sources of bias in our analyses, we also performed analyses of variance on log-transformed duration estimates when (i) only criterial pairs of days were included, and (ii) all data were included. These analyses showed that all compound-element comparisons were statistically significant ($P < .01$).
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Splitbrain Monkeys: Cerebral Control of Ipsilateral and Contralateral Arm, Hand, and Finger Movements

Abstract. *The connections of the descending pathways in the monkey suggest that each hemisphere controls independent arm, hand, and finger movements contralaterally, but mainly arm movements ipsilaterally. This difference could be observed in splitbrain monkeys executing a visuomotor task with one eye covered, provided tactile guidance of the movements was largely prevented.*

The descending cortical and brainstem pathways to the spinal cord represent the main instrument by which the brain controls movements. In the rhesus monkey these pathways terminate on cells (i) the dorsal horn, (ii) the motoneuronal cell groups of the ventral horn, and (iii) the intermediate zone (Rexed's laminae VI to VIII in cat) (*1, 2*) which contains the bulk of the spinal interneurons to the motoneurons. The fibers to the dorsal horn modulate mainly sensory transmission while the fibers to the intermediate zone especially influence motoneurons (*3*).

In the rhesus monkey the descending corticospinal fibers from each hemisphere terminate (Fig. 1) in the dorsolateral part of the intermediate zone contralaterally and in its ventromedial part bilaterally. In addition, many corticospinal fibers are distributed directly to contralateral motoneurons of distal extremity muscles (for example, those of wrist and fingers) (*4*). The descending brainstem pathways terminate mainly in the intermediate zone (Fig. 1). On the basis of their termination pattern they may be subdivided into two groups, (i) a lateral brainstem pathway which terminates in the dorsolateral part of the intermediate zone unilaterally and (ii) a ventromedial pathway which terminates in the ventromedial parts, to some degree bilaterally. The former pathway is mainly derived from the contralateral magnocellular red nucleus (*5, 6*). The latter consists of several tracts that are derived from the interstitial nucleus of Cajal, the superior colliculus, the vestibular complex, and the medial bulbar reticular formation (*2, 7*). In addition to its direct corticospinal connections each hemisphere is also connected indirectly with the spinal cord by way of cortical projections to the cells of origin of the descending brainstem pathways. These projections are distributed to the magnocellular red nucleus ipsilaterally and to cell groups of the ventromedial brainstem pathway bilaterally (*6*). Thus, each hemisphere is connected both directly and indirectly with the dorsolateral part of the spinal intermediate zone contralaterally and with its ventromedial parts bilaterally (Fig. 1).

Findings in the cat suggest that the fiber connections of the cells in the two subdivisions of the intermediate zone differ. The fibers from the cells in the dorsolateral part seem to distribute preferentially to motoneurons of distal extremity muscles, while those from cells in the ventromedial parts seem to distribute preferentially to motoneurons of axial and proximal limb muscles (*8*).

If these propriospinal connections in the rhesus monkey are arranged in the same way as they are in the cat, it implies that the pathways to the ventromedial part of the intermediate zone would especially govern axial and proximal limb movements (integrated limb-body movements) while those to the dorsolateral part would especially govern distal extremity movements. These inferences are supported by the findings of Lawrence and Kuypers (*9*). Their findings also indicate that the direct cortical projections to the motoneurons of distal extremity muscles provide the capacity for a high degree of fractionation of movements as exemplified by relatively independent finger movements (*9*). In view of these anatomical and functional findings the differences in the ipsilateral and contralateral distribution of the descending pathways suggest that each hemisphere by way of its descending connections may steer independent arm, hand, and finger movements contralaterally, but mainly arm movements ipsilaterally.

In order to test this hypothesis, the optic chiasm, corpus callosum, anterior and hippocampal commissures, massa intermedia, and dorsal mesencephalic commissures were transected in seven rhesus monkeys. This was done under hypothermia in order to minimize postoperative cerebral edema. The four animals that have been killed so far survived the operation for 4 to 7 months. Histologically, the transection of the commissures was found to be complete with the exception of the most caudal portion of the intercollicular commissure.

The motor performance of the animals was studied with one of their eyes covered, thus restricting the visual imput to one half of the brain. When they picked up pieces of food from either a table top or forceps, their arm, hand, and finger movements ipsilateral or contralateral to the open eye did not differ strikingly, and relatively independent hand and finger movements were executed on either side. However, in the ipsilateral hand these independent movements seemed to occur only after the hand made contact with the food. Such contact would presumably recruit the full motor guidance of the nonseeing hemisphere by way of the somatosensory pathways which decussate below pontine levels and thus are not interfered with by splitbrain surgery.

In order to unmask the possible difference between the motor control of the ipsilateral and the contralateral hand an attempt was made to minimize tactile guidance of the hand movements. For this purpose a special testboard was designed which maintains visual contrast between food morsels and background but minimizes tactile contrast (see Fig. 2). The board is painted black and contains small food wells that just accommodate a small food morsel with its upper surface flush to the board. From each food well two or three radially oriented grooves are cut through which individual fingers can dislodge the morsel from the well.

When the animals, with one eye covered, were presented with a small food morsel in the board, the hand contralateral to the open eye was brought toward the food. The index finger was then placed into one of the grooves with a relatively independent finger movement and the food was dislodged from the well by movements of this finger and of the thumb. The hand and fingers ipsilateral to the open eye behaved quite differently. The hand was brought to the proper place on the board by an accurate reaching movement of the arm. However, the hand and fingers did not pick the food morsel out of the well. Instead, they began to

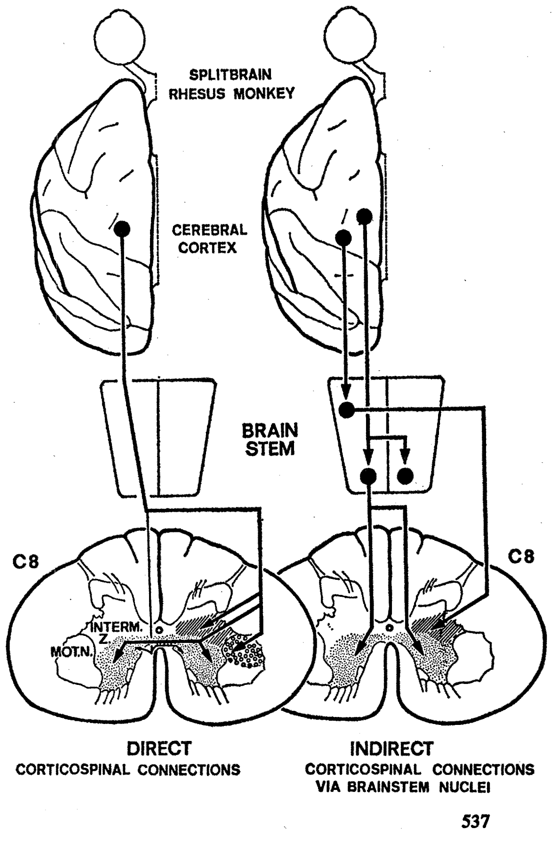

Fig. 1. Diagram of the cortical connections to the spinal cord, both directly (left) and indirectly by way of the brainstem pathways (right) in the rhesus monkey. Ipsilaterally, the direct and indirect connections lead to the ventromedial part of the intermediate zone (stippled). Contralaterally the direct and indirect connections lead to both the dorsolateral (shaded) and the ventromedial (stippled) parts of the intermediate zone. Further, contralaterally many direct connections are established with motoneurons of distal extremity muscles (∘°∘).

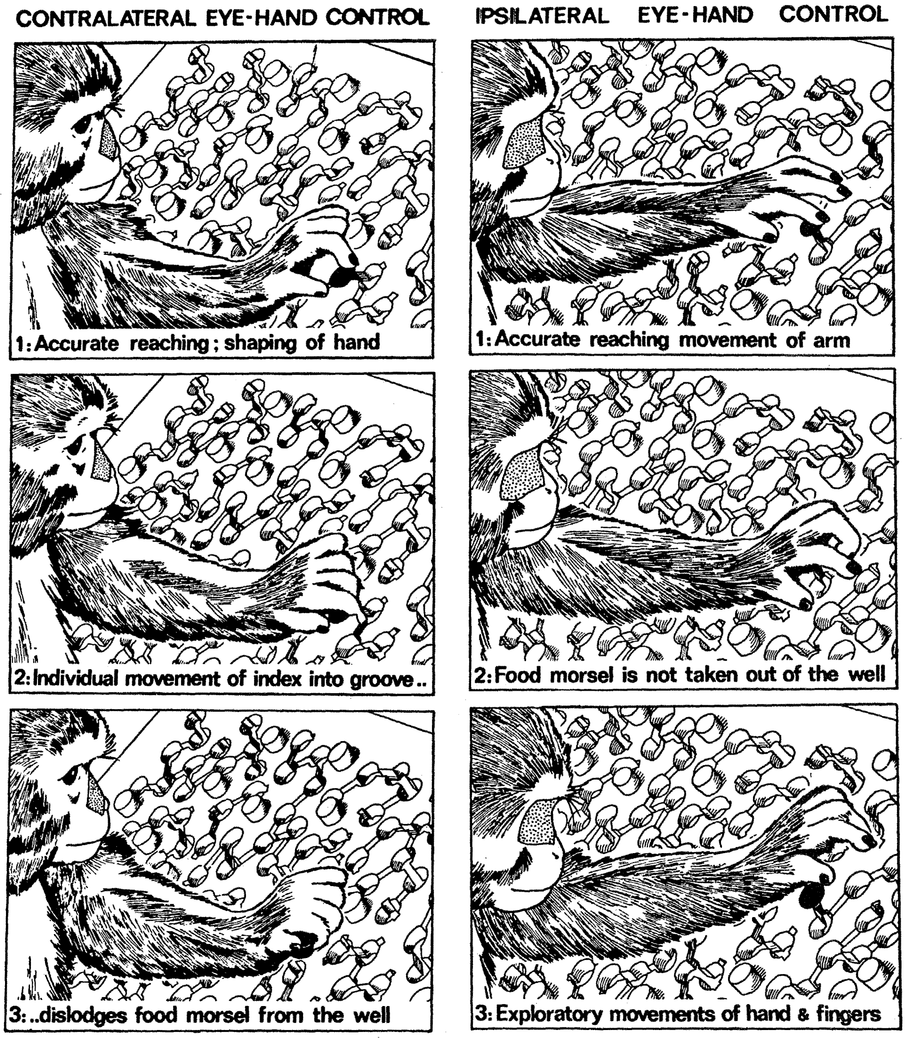

Fig. 2. Drawings from a film showing hand and finger movements of a splitbrain monkey, with one eye covered, taking a food morsel from our testboard which minimizes tactile contrast between a food morsel and background. Under guidance of the contralateral eye (left column) the index finger and thumb dislodge the food morsel from the well. Under guidance of the ipsilateral eye (right column) the hand is brought to the proper place but the food morsel is not taken from the well. Instead, hand and fingers explore the board's surface as if blind.

explore the area tactually as if blind, lacking visual guidance. However, the inability of the ipsilateral hand to retrieve the food morsel was not caused by a defect in vision, since the contralateral hand, when released, immediately picked the food morsel out of the well. The "blind" behavior of hand and fingers when guided by the ipsilateral eye persisted throughout the survival period.

When large food morsels which protruded above the board's surface were used, they were retrieved by either hand. In doing so either hand displayed delicate and relatively independent hand and finger movements. However, in the hand ipsilateral to the open eye, these delicate movements again seemed to occur only after the hand touched the food morsel.

The animals were also presented with small and large food morsels in the board after they were blindfolded. Under these circumstances, hand and fingers explored the board surface and retrieved the large food morsels by means of delicate, relatively independent hand and finger movements. However, they did not retrieve the small food morsels that apparently remained undetected.

These findings led to the following conclusions. For the retrieval of small food morsels visual guidance is essential. Under visual guidance both the contralateral and the ipsilateral hand can be brought to the proper place by means of a proximal arm movement. However, under visual guidance, only the hand contralateral to the open eye appears to receive adequate motor control to execute the individual hand and finger movements necessary for the retrieval of the food morsel. Such distal motor control apparently is not available to the ipsilateral hand and fingers. In fact, the exploratory movements of this hand closely resemble the hand and finger movements of blindfolded animals searching for food on the board. These conclusions support the original hypothesis based on the anatomical and functional findings.

Our findings are in striking agreement with those obtained in human patients (*10*). However, in splitbrain monkeys and chimpanzees ipsilateral eye-hand control is the subject of controversy. Some authors (*11*) have stated that ipsilateral eye-hand control is poor in splitbrain monkeys, while others (*12*) observed that the contralateral and ipsilateral eye-hand combinations were equally proficient in reaching, visual pursuit, and grasping. Further, some authors (*13*) observed abnormal movements in the ipsilateral eye-hand combination, for example, "fanning" of the fingers, which, however, appeared to be transient. Our findings may help to resolve this controversy, first by emphasizing that the limitations of the ipsilateral control mainly pertain to relatively independent distal movements of the extremities [mentioned briefly by other authors (*14*, *15*)] and further by demonstrating that these limitations are easily masked by tactile guidance of the distal extremity movements through the nonseeing hemisphere.

Our behavioral findings seem to support the "simple connectionist's point of view" (*16*) (which still persists) that each half of the brain may steer independent movements of arm, hand, and fingers contralaterally but mainly arm movements ipsilaterally. However, this point of view is tenable only if the proximal arm movements executed under guidance of the ipsilateral eye can still occur independent of the descending pathways from the nonseeing hemisphere.

J. Brinkman
H. G. J. M. Kuypers

*Department of Anatomy,
Rotterdam Medical Faculty,
Rotterdam, Netherlands*

References and Notes

1. H. G. J. M. Kuypers, *Brain* **83**, 161 (1960); W. W. Chambers and C. N. Liu, *J. Comp. Neurol.* **123**, 257 (1965).
2. H. G. J. M. Kuypers, W. R. Fleming, J. W. Farinholt, *J. Comp. Neurol.* **118**, 107 (1962).
3. P. Andersen, J. C. Eccles, T. A. Sears, *J. Neurophysiol.* **27**, 63 (1964); A. R. Morrison and O. Pompeiano, *Arch. Ital. Biol.* **103**, 538 (1965); E. E. Fetz, *J. Neurophysiol.* **31**, 69 (1968).

→ C. G. Phillips, *Proc. Roy. Soc. London Ser. B* **173**, 141 (1969); H. G. J. M. Kuypers and J. Brinkman, *Brain Res.* **24**, 29 (1970).

5. O. Pompeiano and A. Brodal, *J. Comp. Neurol.* **108**, 225 (1957).
6. H. G. J. M. Kuypers and D. G. Lawrence, *Brain Res.* **4**, 151 (1967).
7. R. Nyberg-Hansen, *Ergeb. Anat. Entw. Gesch.* **39**, 6 (1966); J. M. Petras, *Brain Res.* **6**, 275 (1967).
8. P. Sterling and H. G. J. M. Kuypers, *Brain Res.* **7**, 419 (1968); A. Rustioni, H. G. J. M. Kuypers, G. Holstege, *ibid.* **34**, 255 (1971).
9. D. G. Lawrence and H. G. J. M. Kuypers, *Brain* **91**, 1 (1968); *ibid.*, p. 15.
10. R. W. Sperry, M. S. Gazzaniga, J. E. Bogen, *Handbook of Clinical Neurology* (North-Holland, Amsterdam, 1968), vol. 4, pp. 273–291; N. Geschwind, *Modern Trends in Neurology* (Butterworth, London, 1970), vol. 5, pp. 29–40.
11. J. L. de C. Downer, *Brain* **82**, 251 (1959); M. S. Gazzaniga, *Exp. Neurol.* **8**, 14 (1963).
12. R. E. Myers, R. W. Sperry, N. Miner McCurdy, *Arch. Neurol.* **7**, 195 (1962); P. Black and R. E. Myers, *Functions of the Corpus Callosum* (Churchill, London, 1965), pp. 47–59; C. R. Hamilton, *J. Comp. Physiol. Psychol.* **64**, 434 (1968).
13. M. S. Gazzaniga, *Exp. Neurol.* **8**, 14 (1963); J. S. Lund, J. L. de C. Downer, J. S. P. Lumley, *Cortex* **6**, 323 (1970).
14. R. F. Mark and R. W. Sperry, *Exp. Neurol.* **21**, 92 (1968).
15. M. S. Gazzaniga, *ibid.* **23**, 11 (1969).
16. ———, *The Bisected Brain* (Appleton-Century-Crofts, New York, 1970), p. 58.
17. We thank Prof. D. H. G. Keuskamp and Mr. R. Ducardus, Department of Anaesthesiology, Dijkzigt University Hospital, Rotterdam, for their help with the hypothermic procedure and Dr. R. M. Latto for reading the manuscript. This study was supported in part by grant 13-31-12 of the Dutch Organization for Fundamental Research in Medicine (FUNGO) and by a Dutch interdepartmental government grant.

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Eye and Head Turning Indicates Cerebral Lateralization

Abstract. *When solving verbal problems, right-handed people usually turn head and eyes to the right, whereas with numerical and spatial problems, these people look up and left. Left-handed people differ in all these respects. The results suggest that the direction in which people look while thinking reflects the lateralization of the underlying cerebral activity.*

In bisymmetrical animals, each side of the central nervous system programs sensory and motor activity for the contralateral side. Man has acquired, in addition, mental processes that are free of specific spatial reference and are distributed asymmetrically between the cerebral hemispheres. An example of symmetrical facilities are the frontal centers for lateral orientation. They control the turning of head and eyes; when the effects of the two centers are equally balanced, attention is directed straight ahead (*1*). Asymmetry is exemplified by the lateralization of language processes to the left side of the brain and lateralization of spatial and temporal processes to the right side of the brain (*2*). When stimulus is to be processed, it is advantageous to present it to the input channel in such a way that it is contralateral to the hemisphere specialized for this process (*3*). The cerebrum is a highly linked system, and only a few synapses separate any two cortical neurons. This makes the cerebrum vulnerable to interference between two concurrent operations, particularly when both are programmed by the same cerebral hemisphere. Thus, when subjects await a verbal stimulus and must also look centrally, the verbal activation overflows into the left-sided orientation center, driving attentional balance off center and to the right (*4*). Laterality of thought processes in man might therefore be determined by using the direction of orientation as an indicator (*5*). When the two hemispheres are equally active, orientation of the subject should be centered on the median plane. When one hemisphere is primarily involved, head and eyes should turn to the opposite side. Those movements would be secondary to the central activity, rather than in direct response to external stimulation.

We predicted that right-handed subjects would orient themselves to the right during verbal activity and to the left during spatial thought. Left-handed subjects could orient themselves either way in either case. The orientation of subjects thinking about numerical problems could not be predicted.

Forty undergraduate subjects participated, 20 right-handed (RH) and 20 left-handed (LH) as ascertained by questionnaire (*6*). Each subject was seated in a desk chair in a lighted, soundproof room, facing a wall covered by a floor-length black cloth. A camera (Sony Videocorder) was focused on him through a small opening in the cloth. The experimenter sat behind the subject, and the recording apparatus was behind the experimenter.

Three sets of 20 questions each were prepared. A "verbal" set was derived from scales 1 to 3 of the Proverbs Test. A "numerical" set consisted of simple calculations and problems based on the quantitative ability section of the Medical College Admissions Test Study Book and the Graduate Record Examination Study Book. Spatial questions required the subject to visualize and specify spatial relationships of familiar local landmarks and visual arrangements.

The subject was told to concentrate

Table 1. Means and summary of analysis of variance for experiment 1; V, verbal; N, numerical; S, spatial; ns, nonsignificant. Specific contrasts were done following a significant interaction.

	Horizontal			Up			Right		
	V	N	S	V	N	S	V	N	S
				Eye					
RH means	13.4	7.8	8.0	4.4	10.2	9.4	11.5	3.7	1.8
LH means	13.9	13.2	13.3	3.4	4.4	3.7	5.5	6.4	6.0
Hand preference × problem-solving mode		$P < .0001$			$P < .0001$			$P < .0001$	
Specific contrasts	V vs. N	N vs. S	V vs. S	V vs. N	N vs. S	V vs. S	V vs. N	N vs. S	V vs. S
RH: *P*	< .0001	ns	< .0001	< .0001	ns	< .0001	< .0001	ns	< .0001
LH: *P*	ns	ns	ns	ns	ns	ns	ns	ns	ns
				Head					
RH means	8.2	4.0	4.0	5.8	8.6	9.9	7.2	2.6	1.7
LH means	13.0	11.8	11.8	3.6	5.3	4.0	5.8	4.6	6.0
Hand preference × problem-solving mode		$P < .02$			$P < .01$			$P < .0001$	
Specific contrasts	V vs. N	N vs. S	V vs. S	V vs. N	N vs. S	V vs. S	V vs. N	N vs. S	V vs. S
RH: *P*	< .0001	ns	< .0001	< .001	ns	< .0001	< .0001	ns	< .0001
LH: *P*	ns	ns	ns	< .05	ns	ns	ns	< .03	ns