

Grasp With Hand and Mouth: A Kinematic Study on Healthy Subjects

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Gentilucci, Maurizio, Francesca Benuzzi, Massimo Gangitano, and Silvia Grimaldi. Grasp with hand and mouth: a kinematic study on healthy subjects. *J Neurophysiol* 86: 1685–1699, 2001. Neurons involved in grasp preparation with hand and mouth were previously recorded in the premotor cortex of monkey. The aim of the present kinematic study was to determine whether a unique planning underlies the act of grasping with hand and mouth in humans as well. In a set of four experiments, healthy subjects reached and grasped with the hand an object of different size while opening the mouth (*experiments 1 and 3*), or extending the other forearm (*experiment 4*), or the fingers of the other hand (*experiment 5*). In a subsequent set of three experiments, subjects grasped an object of different size with the mouth, while opening the fingers of the right hand (*experiments 6–8*). The initial kinematics of mouth and finger opening, but not of forearm extension, was affected by the size of the grasped object congruently with the size effect on initial grasp kinematics. This effect was due neither to visual presentation of the object, without the successive grasp motor act (*experiment 2*) nor to synchronism between finger and mouth opening (*experiments 3, 7, and 8*). In *experiment 9* subjects grasped with the right hand an object of different size while pronouncing a syllable printed on the target. Mouth opening and sound production were affected by the grasped object size. The results of the present study are discussed according to the notion that in an action each motor act is prepared before the beginning of the motor sequence. Double grasp preparation can be used for successive motor acts on the same object as, for example, grasping food with the hand and ingesting it after bringing it to the mouth. We speculate that the circuits involved in double grasp preparation might have been the neural substrate where hand motor patterns used as primitive communication signs were transferred to mouth articulation system. This is in accordance with the hypothesis that Broca's area derives phylogenetically from the monkey premotor area where hand movements are controlled.

INTRODUCTION

A previous neurophysiological study (Rizzolatti et al. 1988) discovered in the premotor cortex of monkey (area F5) (Matelli et al. 1985) a class of neurons that fire when the animal grasps an object with both its hands and mouth. Usually, neuron discharge is selective for the type of hand grip. Neuron discharge occurs during hand or mouth movements even if, frequently, it starts when the target-stimulus is visually presented provided that its size is congruent with the type of hand grip coded by the neuron. We interpreted the discharge of these neurons as grasp commands sent to the effectors usually used to accomplish this motor act. They can code the aim of the

motor act that is taking possession of the object (Gentilucci and Rizzolatti 1990; Rizzolatti and Gentilucci 1988). Functionally, this class of neurons can be involved in preparing successive motor acts performed with both the hand and the mouth. Grasping a piece of food with the hand is frequently followed by bringing it to the mouth to be ingested. Grasping a piece of food with the mouth is usually followed by hand grasp movements to placing it correctly in the mouth. Kinematic studies carried out on humans (Gentilucci et al. 1997; Marteniuk et al. 1987) showed that during actions formed by a sequence, each motor act is planned in function of the successive one. Consequently, the grasp command can be sent to different distal effectors to prepare a series of successive motor acts. In the case of grasp, information about the way to appropriately grasp that object can be provided. The first aim of the present kinematic study was to determine whether humans also perform simultaneous preparation of grasp with hands and mouth. We tested this hypothesis by studying the possible interference of grasp preparation on the kinematics of aimless distal and proximal movements. The likely interference of grasping on co-occurring aimless distal movements is further supported by the observation that, frequently, humans perform aimless aperture-closure mouth movements during skilled movements of hand manipulation (Darwin 1998).

Inferior premotor area of humans involved in hand and arm movements is adjacent to Broca's area, which is known to be involved in speech production. However, recent data obtained by neuroimaging studies indicate that Broca's area becomes active also during execution of hand and arm movements (Bonda et al. 1994; Schlaug et al. 1994), during mental imagery of hand grasping movements (Decety et al. 1994; Grafton et al. 1996), and during tasks involving hand mental rotations (Parsons et al. 1995). In addition, neurophysiological studies have shown that the monkey premotor F5 area where preparing-grasp-with-mouth-and-hand neurons were recorded is also involved in recognizing the same action performed by another individual (Gallese et al. 1996). Overall, these data suggest the hypothesis that Broca's area derives phylogenetically from F5 premotor area (Rizzolatti and Arbib 1998). If this hypothesis is correct, we can reliably postulate a relation between grasping objects and speech production. Words are formed by the sequence of syllables, which are considered the units of speech (Levelt and Wheeldom 1994; Tabossi et al. 2000). Similarly,

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action is the sequence of motor acts, as for example reaching and grasping. Motor acts can be considered the units of movement aimed to a target. The second aim of the present study was to determine whether grasp control influences pronunciation of syllables.

EXPERIMENT 1

Methods

Eight right-handed [according to Edinburgh Inventory (Oldfield 1971)] subjects (5 women, 3 men, age 19–23) participated in the present experiment to which they gave informed consent. All of them were naïve as to the purpose of the experiment.

In a dark and soundproof room each subject sat in front of a black table, placing his/her right thumb and index finger, held in the pinch position, on a circle located on the table plane (starting position, SP in Fig. 1). SP was 15 cm distant from table edge. Target object was one of two white parallelepipeds with square base: small object (sides 3×3 cm, height 1 cm), and large object (sides 5×5 cm, height 1 cm). On their visible face either the symbols "XX" (XX configuration) or a configuration of small points randomly scattered in the same area occupied by XX (cloud configuration) could be printed in black. XX was 2 cm wide and 1.5 cm high. The points of the cloud configuration were obtained by decomposing the two XX using a PC software. One parallelepiped was placed on the plane of the table at a distance of 15 cm from SP.

Subjects were required to reach and grasp the target object with their right thumb and index finger and to lift it, independently of the configuration printed on the object (Fig. 1). In addition, when the XX configuration was presented, they were required to open simultaneously their mouth. Mouth opening amplitude was arbitrary. However, subjects were explicitly required to maintain it constant throughout the experimental session. They closed their mouth at the end of the action before moving their hand back to SP. We adopted this experimental paradigm 1) to avoid an automatic and synchronous opening of both the mouth and the hand and 2) in the attempt of eliciting mouth opening independent from the size of the object to be grasped. Illumination of the room (rising time of the lamp, 15 ms) was the signal for the two movements to begin. Subjects were required to reach and grasp the target with the maximal velocity compatible with the accuracy required by the task. Grasp was always accomplished by positioning the fingers on the sides of the object parallel to the



FIG. 1. Schematic representation of the experimental apparatus used in experiment 1. SP, starting position.

subjects' transverse axis (horizontal sides). No instruction about velocity of mouth opening was given.

Each experimental session consisted of 24 trials. In 16 trials, target objects with the XX configuration were presented: in 8 trials the target was large, and in the others it was small. In the other eight trials, target objects with the cloud configuration were presented: in four trials the target was large, and in the others it was small. Target objects were pseudorandomly presented.

Movements of arm and mouth were recorded using the three-dimensional (3D)–optoelectronic ELITE system (B.T.S. Milan, Italy). It consists of two TV cameras detecting infrared reflecting markers at the sampling rate of 50 Hz. Movement reconstruction in 3D coordinates and computation of the kinematic parameters are described in a previous work (Gentilucci et al. 1992).

In the present study five markers were used. The first marker was placed on the styloid process of the radius at the wrist; the second and the third markers were placed on the base of the nail of the thumb and the index finger, respectively. The fourth and the fifth marker were placed on the center of the upper and the lower lip, respectively.

We analyzed 3D displacements, velocities, and accelerations of the markers. The marker placed on the subject's wrist was used to analyze the reach component. We computed the time courses of the modules of the acceleration spatial vector and of the tangential velocity vector. The reach component is constituted by an acceleration and deceleration phase (see, as an example, Fig. 2). We analyzed the acceleration phase and, in particular, the following kinematic parameters: peak acceleration, peak velocity, and time-to-peak velocity. We studied the grasp component by analyzing the time course of the distance between the thumb and the index finger. This is constituted by a finger aperture phase (grip aperture or hand shaping) and a phase of finger closure on the object (see, as an example, Fig. 2). We analyzed the grip aperture phase and measured the following kinematic parameters: peak velocity of grip aperture, maximal grip aperture, and time to maximal grip aperture. We studied the lip aperture by analyzing the time course of the distance between the upper and lower lip. We measured peak velocity of lip aperture, maximal lip aperture, and time to maximal lip aperture. Finally, we calculated the time lag (TL) of mouth-opening beginning with respect to finger-opening beginning. We analyzed initial kinematic parameters of arm and mouth movements because we were interested in studying the effects of the motor preparation rather than those of movement execution control, according to the scopes of the present study. The procedures for calculating beginning and end of hand and lip movements were identical to those previously described (Gentilucci et al. 1994).

The experimental design included two within-subjects factors (target size: small vs. large; lip opening: absent vs. present) for reaching-grasping analysis and one within-subjects factor (grasped target size: small vs. large) for lip aperture and TL analyses. Separate ANOVAs were carried out on mean values of reaching-grasping parameters, lip-aperture parameters, and TL. Newman-Keuls post hoc test was used.

Results

HAND REACHING-GRASPING. *Reaching.* Arm peak acceleration was affected by no factor, whereas arm peak velocity [$F(1,7) = 6.6$, $P < 0.03$, 665.7 vs. 654.0 mm/s] decreased and time to arm peak velocity increased [$F(1,7) = 7.3$, $P < 0.03$, 331.1 vs. 350.5 ms] when reaching the small object.

Grasping. Peak velocity of grip aperture [$F(1,7) = 45.2$, $P < 0.0003$] and maximal grip aperture [$F(1,7) = 306.9$, $P < 0.00001$, Fig. 2] were greater when grasping the large object (Fig. 2). Also time to maximal grip aperture was longer, although not significantly (Fig. 2).

MOUTH OPENING. Peak velocity of lip aperture [$F(1,7) = 5.8$, $P < 0.05$], maximal lip aperture [$F(1,7) = 5.2$, $P < 0.05$], and

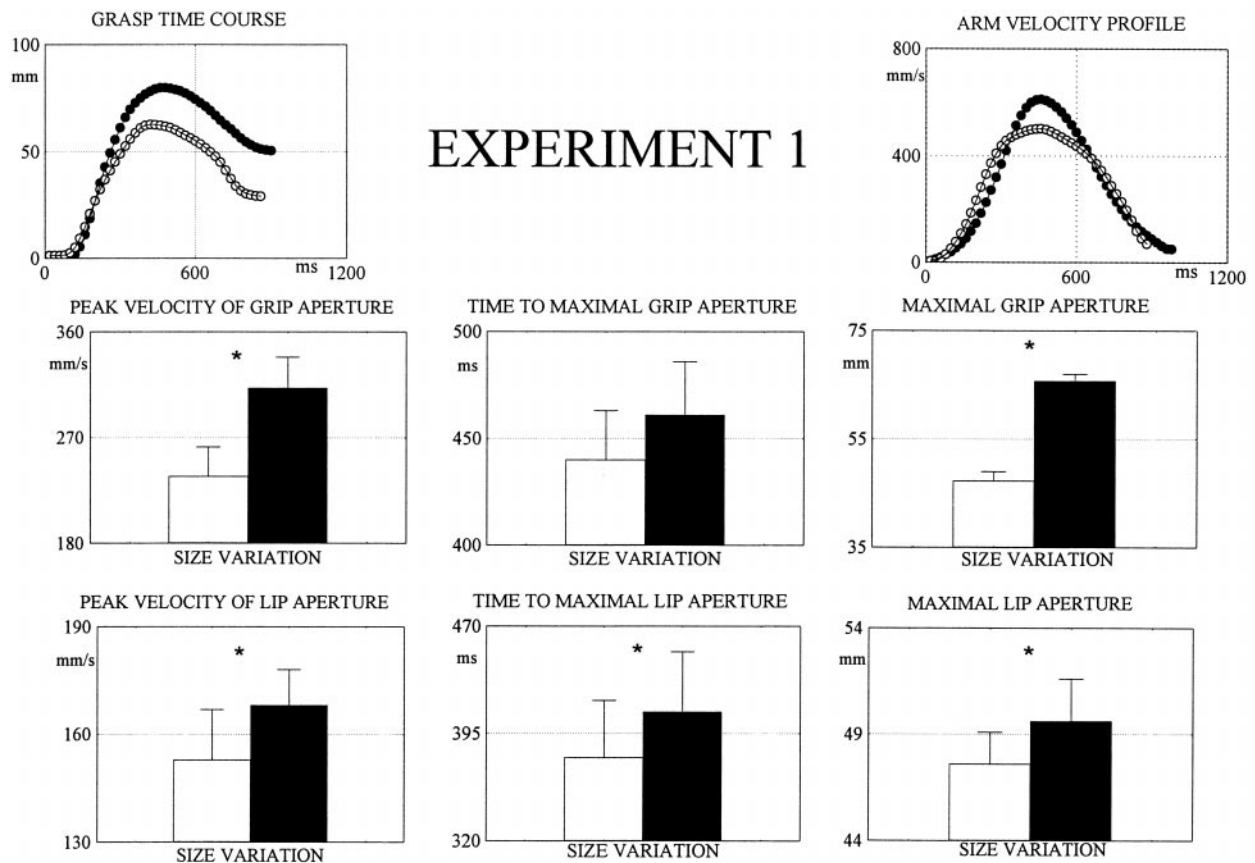


FIG. 2. Reaching-grasping with the right hand and lip aperture executed in *experiment 1*. *Top row*: representative example of grasp time course (*left panel*) and reach velocity profile (*right panel*). Note that grasp is constituted by a finger aperture phase till a maximum (maximal grip aperture) and a finger closure phase. Reach is constituted by an acceleration phase till a maximum (arm peak velocity) and a deceleration phase. *Middle row*: mean values of grasp parameters. *Bottom row*: mean values of lip aperture parameters. □ and ■, movements directed to the small and large target, respectively. Bar markers are SE. * Significance in the ANOVA.

time to maximal lip aperture [$F(1,7) = 5.4$, $P < 0.05$] increased when reaching-grasping was directed to the large object (Fig. 2).

TL was affected by no factor. On average it was 25.3 ms.

Discussion

According to the results of previous experiments (Corradini et al. 1992; Gentilucci et al. 1991; Jakobson and Goodale 1991), both the reach and the grasp components were affected by object size.

Although subjects were required to maintain mouth opening constant throughout the experimental session, lip opening was affected by object size. The first hypothesis is that hand shaping during grasp influenced mouth opening. The finding that the size effect on lip opening was lower than that on hand shaping (see Fig. 2) can be easily explained by the mutual influence between two motor programs simultaneously activated. The first one implemented an equal lip aperture, independently of the presented object, whereas the second one implemented a different aperture according to object size. However, two alternative hypotheses cannot be excluded. First, subjects unconsciously matched the size of the presented object by opening their mouth, independently of grasp. This hypothesis was tested in *experiment 2* in which subjects opened their

mouth in the presence of the same stimuli presented in *experiment 1*, but without grasping them. Second, reach velocity, which varied with object size, influenced mouth opening. This hypothesis was tested in *experiment 3*, in which reaching-grasping and contemporaneous mouth opening were required. Experimental paradigm was manipulated to induce reach velocity to vary, and hand shaping to remain constant. To this purpose we chose to vary target distance. In an alternative experimental paradigm we could require subjects to reach and grasp an object placed at the same location by using different velocities. However, one of the two velocities would not be appropriate for reaching-grasping that object, and, consequently, accuracy requirement during reach should vary. This could affect hand shaping during grasp as previously Wing et al. (1986) observed using this experimental paradigm. In contrast, subjects would use two natural velocities to reach and grasp an object located at two distances, and the probability of variation in accuracy requirement during reach could be lower.

EXPERIMENT 2

Methods

A new sample of eight naive right-handed [according to Edinburgh Inventory (Oldfield 1971)] subjects (5 women, 3 men, age 20–24) participated in the present experiment to which they gave informed consent.

Apparatus and stimuli were the same as in *experiment 1*. When the XX configuration was presented, subjects were required to open their mouth by an arbitrary amplitude, but to keep it constant throughout the experimental session. Objects were never grasped. Experimental session consisted of 24 trials as in *experiment 1*. Data recording and analysis were the same as in *experiment 1*. Two markers were used. They were placed at the center of the upper and the lower lip. The lip aperture was studied by analyzing the time course of the distance between upper and lower lip. The measured lip aperture kinematic parameters were peak velocity of lip aperture, maximal lip aperture, and time to maximal lip aperture. The experimental design included one within-subjects factor (stimulus size: small vs. large). Separate ANOVAs were carried out on mean values of lip aperture parameters.

Results

Peak velocity of lip aperture, maximal lip aperture, and time to maximal lip aperture were not affected by stimulus size (Fig. 3).

EXPERIMENT 3

Methods

A new sample of eight naïve right-handed [according to Edinburgh Inventory (Oldfield 1971)] subjects (3 women, 5 men, age 23–30) participated in the present experiment to which they gave informed consent.

Apparatus was the same as in *experiment 1*. The target objects were the two large parallelepipeds used in *experiment 1*. A target could be placed on the plane of the table at a distance of either 14 or 28 cm from SP. As in *experiment 1*, subjects were required to reach and grasp the object, and to open simultaneously their mouth by a constant amplitude, but only in presence of the XX configuration.

Data recording and analysis were the same as in *experiment 1*. The experimental design included two within-subjects factors (target distance: near vs. far; lip opening: absent vs. present) for reaching-grasping analysis and one within-subjects factor (stimulus distance: near vs. far) for lip aperture and TL analyses. Separate ANOVAs were carried out on mean values of reaching-grasping parameters, lip aperture parameters, and TL. Newman-Keuls post hoc test was used.

Results

HAND REACHING-GRASPING. Reaching. Arm peak acceleration [$F(1,7) = 45.2, P < 0.0003$], arm peak velocity [$F(1,7) = 106.9, P < 0.00001$], and time to arm peak velocity [$F(1,7) = 12.9, P < 0.009$] increased with distance (Fig. 4). Arm peak acceleration and arm peak velocity decreased also when reaching the far object and opening the mouth [interaction between target distance and lip opening; peak acceleration, $F(1,7) = 22.7, P < 0.002, 4,712.5$ vs. $4,320.3$ mm/s², peak velocity, $F(1,7) = 31.4, P < 0.0008, 817.6$ vs. 778.6 mm/s].

Grasping. Maximal grip aperture was not affected by target distance, whereas peak velocity of grip aperture [$F(1,7) = 5.7, P = 0.05, 348.2$ vs. 304.3 mm/s] decreased and time to maximal grip aperture [$F(1,7) = 4.6, P < 0.0003, 534.0$ vs. 600.0 ms] increased with target distance.

MOUTH OPENING. Peak velocity of lip aperture, maximal lip aperture, and time to maximal lip aperture were not affected by stimulus distance (Fig. 4).

No factor affected TL. On average it was 8 ms.

Discussion

The results of *experiment 3* confirm that target distance affects initial reach kinematics (Gentilucci et al. 1991, 1994; Jeannerod 1988). Nevertheless, these effects did not influence lip opening. Taken together, these results rule out that reach velocity exerts an effect on mouth opening. According to previous results (Chieffi and Gentilucci 1993; Gentilucci et al. 1994) target distance influenced initial grasp. The lack of an effect on mouth opening could be due to the contemporaneous decrease in finger velocity and increase in time to maximal grip aperture with distance. Indeed, the variation in the two parameters produced the same maximal grip aperture, such as they induced the same maximal lip aperture. That is, mouth opening could be related to the global grasp motor act, but not to variation in single kinematic parameters. In fact, neither peak velocity of lip aperture, nor time to maximal lip aperture followed the variation in the corresponding grasp parameters.

Reaching far target slowed down when mouth opening occurred simultaneously. This result can be explained by the increase in task difficulty when subjects both reached the far target (Fitts 1954) and performed two actions contemporaneously (reaching-grasping and mouth opening).

The results of *experiments 2* and *3* confirm that grasping an object influences mouth opening. Can hand grasp influence movements of other body effectors, and, in particular, movements of proximal effectors? We tested this hypothesis in *experiment 4* during which subjects reached and grasped an object with their right hand while extending their left forearm.

EXPERIMENT 4

Methods

A new sample of eight naïve right-handed [according to Edinburgh Inventory (Oldfield 1971)] subjects (5 women, 3 men, age 20–24) participated in the present experiment to which they gave informed consent.

EXPERIMENT 2

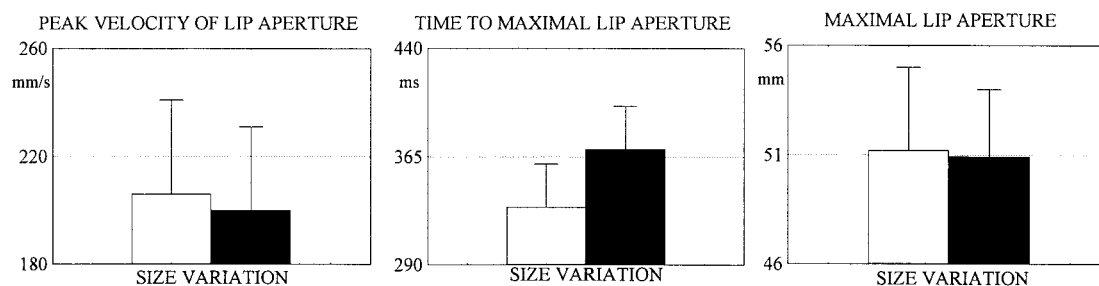


FIG. 3. Mean values of lip aperture parameters collected in *experiment 2*. Other conventions as in Fig. 2.

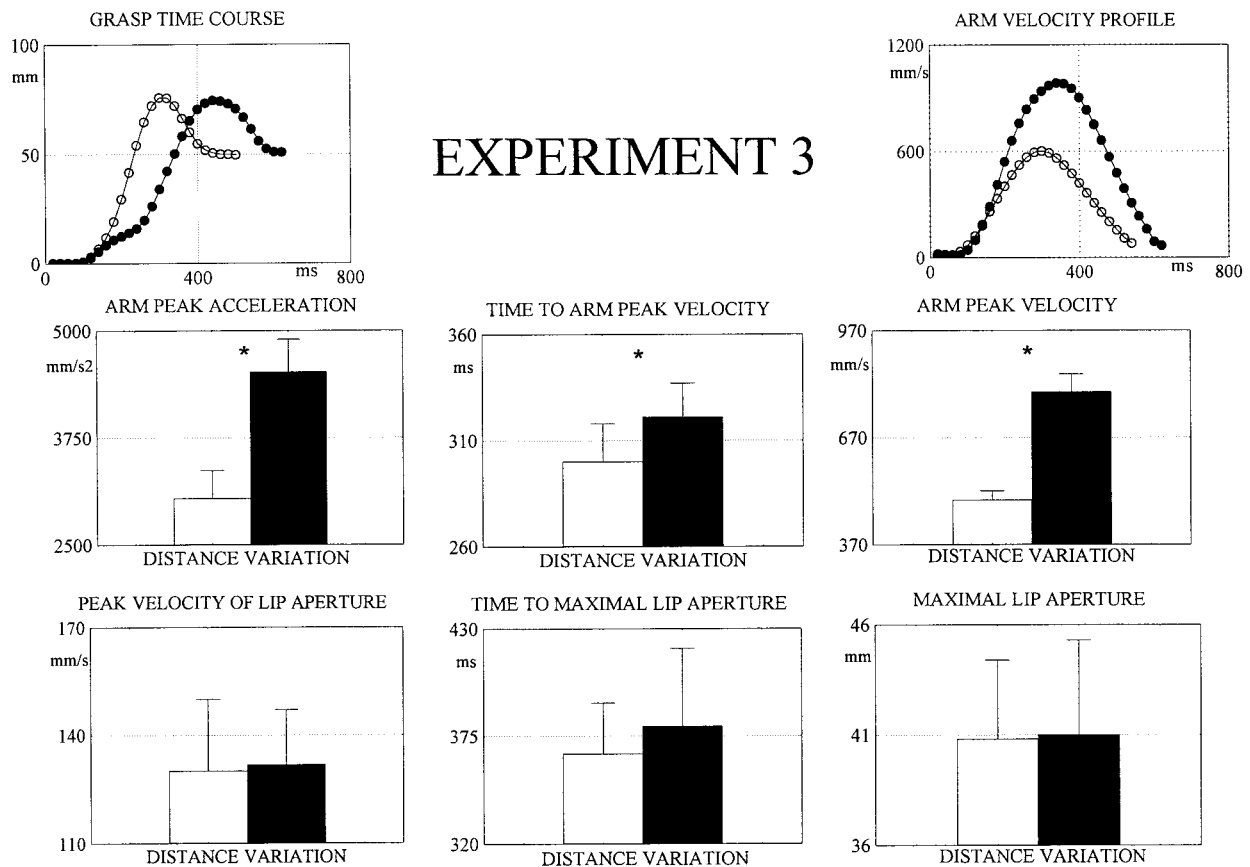


FIG. 4. Reaching-grasping with the right hand and lip aperture executed in *experiment 3*. □ and ■, movements directed to the near and far target, respectively. Other conventions as in Fig. 2.

Apparatus and stimuli were the same as in *experiment 1*. Also procedure was the same except that subjects were required to extend their left forearm by a constant and arbitrary amplitude, while they reached and grasped, with the right hand, the target with the XX configuration. The mouth was not opened.

Data recording followed the same procedure as in *experiment 1*. In the present experiment, five markers were used. Three markers were used to study reaching-grasping, as in *experiments 1* and *3*. The fourth and the fifth marker were placed on the shoulder and on the wrist of the left arm to study forearm extension at elbow. The measured reaching-grasping parameters were the same as in *experiment 1*. The forearm extension was studied by measuring the time course of the distance between wrist and shoulder. The kinematic parameters were the following: peak velocity of forearm extension, maximal forearm extension, and time to maximal forearm extension. TL was the time lag of elbow-extension beginning with respect to grasp beginning. Data analyses were the same as in *experiment 1*.

Results

HAND REACHING-GRASPING. Reaching. Arm peak acceleration [$F(1,7) = 7.4, P < 0.03, 3,323.0$ vs. $3,117.6$ mm/s²] and arm peak velocity [$F(1,7) = 13.2, P < 0.008, 595.9$ vs. 573.4 mm/s] decreased when reaching the small object, whereas time to arm peak velocity was affected by no factor. Arm peak acceleration [$F(1,7) = 24.5, P < 0.002, 3,496.6$ vs. $2,943.8$ mm/s²] and arm peak velocity [$F(1,7) = 27.3, P < 0.001, 610.2$ vs. 558.0 mm/s] decreased when left forearm was extended.

Grasping. Peak velocity of grip aperture [$F(1,7) = 51.8, P < 0.0002$], and maximal grip aperture [$F(1,7) = 248.4, P < 0.00001$] were greater when grasping the large object (Fig. 5). Time to maximal grip aperture was also longer, although not significantly (Fig. 5).

FOREARM EXTENSION. Peak velocity of forearm extension, maximal forearm extension, and time to maximal forearm extension were affected by no factor (Fig. 5).

TL (mean value 13 ms) was affected by no factor.

Discussion

Grasping objects of different size with the hand did not affect a movement performed with a proximal effector. In contrast, right reach was slowed down by left forearm extension. An explanation of this result is the possibility of reciprocal interference between movements of proximal effectors. In addition, greater trunk stabilization probably occurred when the two arms moved simultaneously. This could slow down reach since it is known that arm and trunk movements are strictly coordinated during reaching-grasping actions (Wang and Stelmach 1998).

Grasping with the right hand appears to have an effect on mouth opening. Consequently, it is possible to postulate the existence of a reciprocal influence only among movements of distal effectors. In particular, grasping with the right hand can affect hand movements executed with the left hand and vice versa. In support of this hypothesis stand previous neurophys-

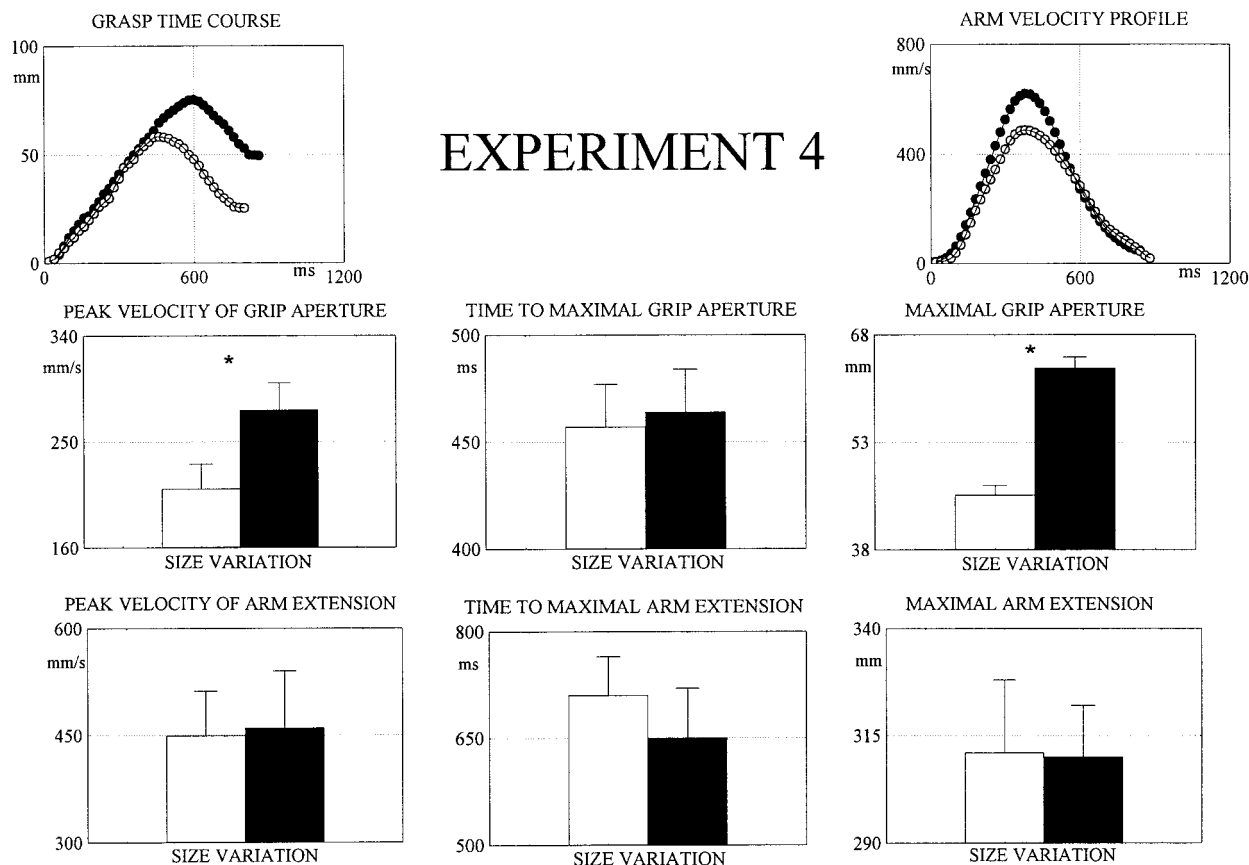


FIG. 5. Reaching-grasping with the right hand and left arm extension executed in *experiment 4*. *Top row*: representative example of grasp time course (*left panel*) and reach velocity profile (*right panel*). *Middle row*: mean values of grasp parameters. *Bottom row*: mean values of forearm extension parameters. Other conventions as in Fig. 2.

iological data recorded from the monkey premotor cortex (Rizzolatti et al. 1988); these findings show a class of neurons firing when grasping an object independently of whether the right or the left hand was used. In *experiment 5* we tested the influence of hand grasp on finger aperture with the other hand.

EXPERIMENT 5

Methods

A new sample of eight naïve right-handed [according to Edinburgh Inventory (Oldfield 1971)] subjects (6 women, 2 men, age 20–24) participated in the present experiment to which they gave informed consent.

Apparatus and stimuli were the same as in *experiment 1*. Subject's thumb and index finger of both the right and the left hand, held in the pinch position, were placed on the table plane. The grasping hand was located on SP. Subjects were required to reach and grasp the object with their thumb and index finger and to lift it. When "XX" was printed on the object, they were required to open contemporaneously the thumb and the index finger of the other hand by an arbitrary amplitude, constant throughout the experimental session.

Each experimental session consisted of 48 trials. Four subjects reached and grasped the target with their right hand and opened their left fingers in the 1st 24 trials, whereas they reached and grasped the target with their left hand and opened their right fingers in the successive trials. The other four subjects reversed the order of hand use.

Movement recording was the same as in the previous experiments. In the present experiment, five markers were used. Three markers

were used to study reaching-grasping as in *experiments 1, 3, and 4*, and the other two markers placed on thumb and index finger tips of the other hand were used to study finger aperture. The finger aperture was studied by analyzing the time course of the distance between the thumb and index finger. The measured finger aperture kinematic parameters were peak velocity of finger aperture, maximal finger aperture, and time to maximal finger aperture. TL was the time lag of finger-opening beginning with respect to grasp beginning. The experimental design included three within-subjects factors (hand: right vs. left, target size: small vs. large; finger opening: absent vs. present) for reaching-grasping analysis and two within-subjects factors (hand: right vs. left, grasped target size: small vs. large) for finger aperture and TL analyses. Separate ANOVAs were carried out on mean values of reaching-grasping parameters, finger aperture parameters, and TL.

Results

HAND REACHING-GRASPING. *Reaching.* Arm peak acceleration was affected by no factor, whereas arm peak velocity [$F(1,7) = 29.9, P < 0.0009, 888.6$ vs. 863.7 mm/s] decreased and time to arm peak velocity [$F(1,7) = 5.6, P = 0.05, 331.1$ vs. 350.5 ms] increased when reaching the small object.

Grasping. Peak velocity of grip aperture [$F(1,7) = 47.0, P < 0.00002$] and maximal grip aperture [$F(1,7) = 307.5, P < 0.00001$] were greater when grasping the large object (Fig. 6). Also time to maximal grip aperture was longer, although not significantly (Fig. 6).

FINGER OPENING. Maximal finger aperture [$F(1,7) = 5.8, P < 0.05$], and time to maximal finger aperture [$F(1,7) = 5.6, P =$

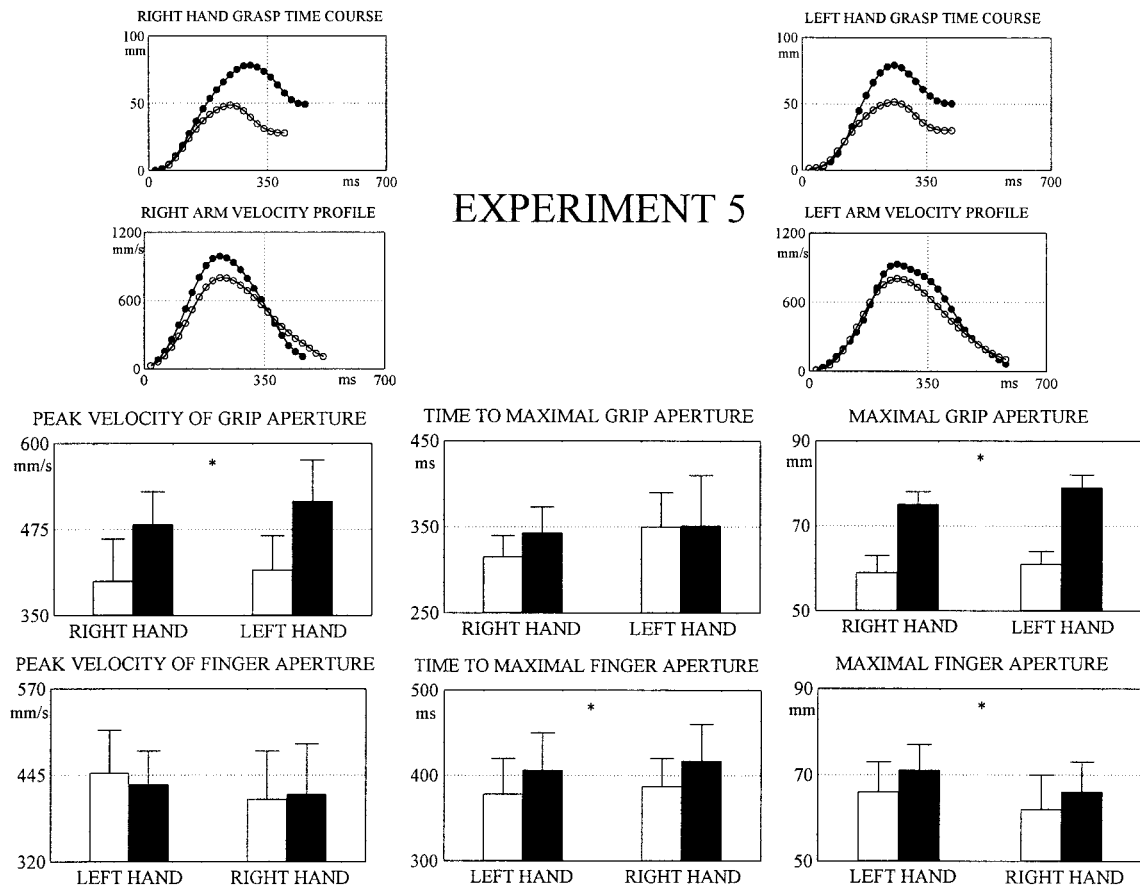


FIG. 6. Reaching-grasping and finger aperture executed in *experiment 5*. From top to down: 1st row: representative examples of time course of grasp executed with the right hand (*left panel*) and with the left hand (*right panel*); 2nd row: representative examples of velocity profiles of the right hand (*left panel*) and of the left hand (*right panel*) reaches; 3rd row: mean values of grasp-with-the-right-hand parameters and grasp-with-the-left-hand parameters; 4th row: mean values of right-fingers-aperture parameters and left-fingers-aperture parameters. Other conventions as in Fig. 2.

0.05] increased when reaching-grasping was directed to the large object (Fig. 6). Peak velocity of right finger aperture showed the same trend, although this was not significant (Fig. 6).

Mean TL was -65 ms, that is finger opening preceded grasp beginning, independently of the hand. In fact, TL was not affected by any factor.

Discussion

Grasping with the right hand influenced left finger opening, and grasping with the left hand influenced right finger opening. The effect was the same for both the two hands. Indeed, the shaping of the two grasping hands varied with target size in the same way. Correspondingly, the variation in finger aperture of the two hands was the same. In addition, finger aperture was of the same order of magnitude as maximal grip aperture (Fig. 6). Overall, these data suggest that the movements of the two hands were related to each other, both depending on object size analysis. This supports our hypothesis that the grasp command is sent to the distal effectors commonly used to perform this motor act.

In a previous study (Gentilucci et al. 1998) we observed an interference effect of the right hand on the left hand greater than the reverse, according to the notion that the left hemisphere controls both hands (Beisteiner et al. 1995; Kim et al.

1993). Consequently, the effect of right hand grasping on left hand opening might be stronger than the reverse. This discrepancy can be explained by the fact that, differently from the movements tested in our previous study (Gentilucci et al. 1998), finger aperture was an aimless internally driven movement, and probably it was easily influenced by the grasp program also when executed with the left hand.

Kinematics did not differ between reaching-grasping with the right and the left hand. The target was placed at an easily reachable distance, and the two target sizes did not require great accuracy during reaching-grasping. Consequently, movement could be easily executed also by the less skilled (left) hand.

In *experiments 1–3* we studied the influence of the grasping hand on mouth opening. Can the reverse be possible, that is an influence of the grasping mouth on finger opening? We tested this hypothesis in *experiment 6*.

EXPERIMENT 6

Methods

A new sample of eight naïve right-handed [according to Edinburgh Inventory (Oldfield 1971)] subjects (5 women, 3 men, age 19–23) participated in the present experiment to which they gave informed consent.

In a dark and soundproof room each subject sat in front of a black table, as in *experiment 1* (Fig. 7). His/her right thumb and index finger, held in the pinch position, were placed on the plane of the table. Target objects to be grasped with the mouth were two bread cubes: a small object (sides $1 \times 1 \times 1$ cm), and a large object (sides $3 \times 3 \times 3$ cm). Objects smaller than those presented in *experiment 1* were chosen according to the smaller maximal mouth opening with respect to the maximal finger opening. They were placed on a support on the visible face of which a red disk could be placed (RD in Fig. 7). The support was placed on the table plane at a distance of 20 cm from the edge of the table. Subjects were required to reach the object by flexing their trunk, to grasp it with their mouth and to come back to the starting position (Fig. 7). When the red disk was presented, they were required to open contemporaneously their right thumb and index finger by an amplitude independent of the presented object. Although opening was arbitrary, subjects were required to maintain it constantly throughout the experimental session. Illumination of the room was the signal for starting the movements. Subjects were required to reach and grasp the bread cube with the maximal velocity compatible with the accuracy required by the task. No instruction about finger opening velocity was given.

Each experimental session consisted of 24 trials. In 16 trials the red disk was presented: in 8 trials the object was large, in the others it was small. In one-half of the remaining eight trials the object was large; in the others it was small. Objects were randomly presented.

Movement recording was the same as in the previous experiments. In the present study four markers were used. Two markers were placed on the center of the upper and the lower lip, respectively, and the other two markers were placed on the base of the nail of the right thumb and index finger, respectively. The grasp component was studied by analyzing the time course of the distance between the upper and lower lip. The measured grasp kinematic parameters were the following: peak velocity of lip aperture, maximal lip aperture, and time to maximal lip aperture. The finger aperture was studied by analyzing the time course of the distance between the thumb and index finger. The measured finger aperture kinematic parameters were the following: peak velocity of finger aperture, maximal finger aperture, and time to maximal finger aperture. Time lag (TL) of finger-opening beginning with respect to mouth-opening beginning was calculated.

The experimental design included two within-subjects factors (target size: small vs. large; finger opening: absent vs. present) for mouth grasping analysis and one within-subjects factor (grasped target size:

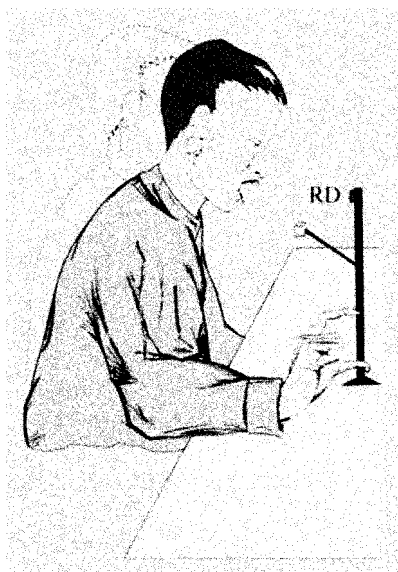


FIG. 7. Schematic representation of the experimental apparatus used in *experiment 6*. RD, red disk.

small vs. large) for finger aperture and TL analyses. The same analyses as in the previous experiments were carried out.

Results

MOUTH GRASPING. Grasp-with-the-mouth time course was similar to grasp-with-the-hand time course (compare Fig. 8 with Fig. 2). Peak velocity of lip aperture [$F(1,7) = 53.7, P < 0.0002$], maximal lip aperture [$F(1,7) = 29.6, P < 0.001$] and time to maximal lip aperture [$F(1,7) = 27.6, P < 0.001$] were greater for the large object (Fig. 8). Maximal lip aperture [$F(1,7) = 10.9, P < 0.001, 27.1$ vs. 29.1 mm] and time to maximal lip aperture [$F(1,7) = 10.8, P < 0.001, 543.8$ vs. 583.0 ms] increased when fingers were opened.

FINGER OPENING. Maximal finger aperture [$F(1,7) = 9.9, P < 0.001$], and time to maximal finger aperture [$F(1,7) = 12.0, P < 0.001$] increased when grasp with the mouth was directed to the large object (Fig. 8). Peak velocity of finger aperture was poorly affected by grasped object size.

Mean TL was -53 ms, that is beginning of mouth opening followed beginning of finger opening. No factor influenced it.

Discussion

Grasping with the mouth influenced finger opening, as well as in *experiment 1*, where grasping with the hand influenced mouth opening. The variation in finger aperture with object size was of the same order of magnitude as the variation in finger aperture recorded in *experiment 5* (compare Fig. 8 with Fig. 6). In other words, variation in finger aperture was independent of the variation in amplitude of the grasping effector, that is the left and right hands in *experiment 5* and the mouth in the present experiment, but seemed to be related to the variation in object size. In fact, in the present experiment the variation in maximal aperture of the grasping mouth was approximately 30% lower than the variation in maximal aperture of the grasping hand recorded in *experiments 1* and *5* (compare Fig. 8 with Figs. 2 and 6). This also explains why the variation in lip aperture with object size in *experiment 1* was lower than the variation in finger aperture recorded in *experiments 5* and *6*. Briefly, the aperture of the effector seemed to pantomime its shaping during grasp.

Unlike *experiment 1*, grasp beginning followed finger-opening beginning. This result may be explained by yaw inertia greater than finger inertia, which might delay mouth movement beginning. If inertia played a role, we should have observed a similar effect in *experiment 4* when we compared forearm extension with hand grasping. This was not the case. Another possibility is that the command to start the movement is primarily sent to the hand, which guides the other distal movements.

The finding that mouth shaping increased when fingers opened can be due to the difficulty of performing two tasks contemporaneously. Difficulty could increase also because reaching with the trunk an object to be grasped with the mouth is an unusual movement.

In the present experiment finger opening resembled a grasp movement. That is, subjects could unconsciously pantomime a grasp motor act. Our hypothesis, also according to previous neurophysiological data (Rizzolatti et al. 1988), is that multiple grasp commands can be sent to distal effectors, whose succes-

EXPERIMENT 6

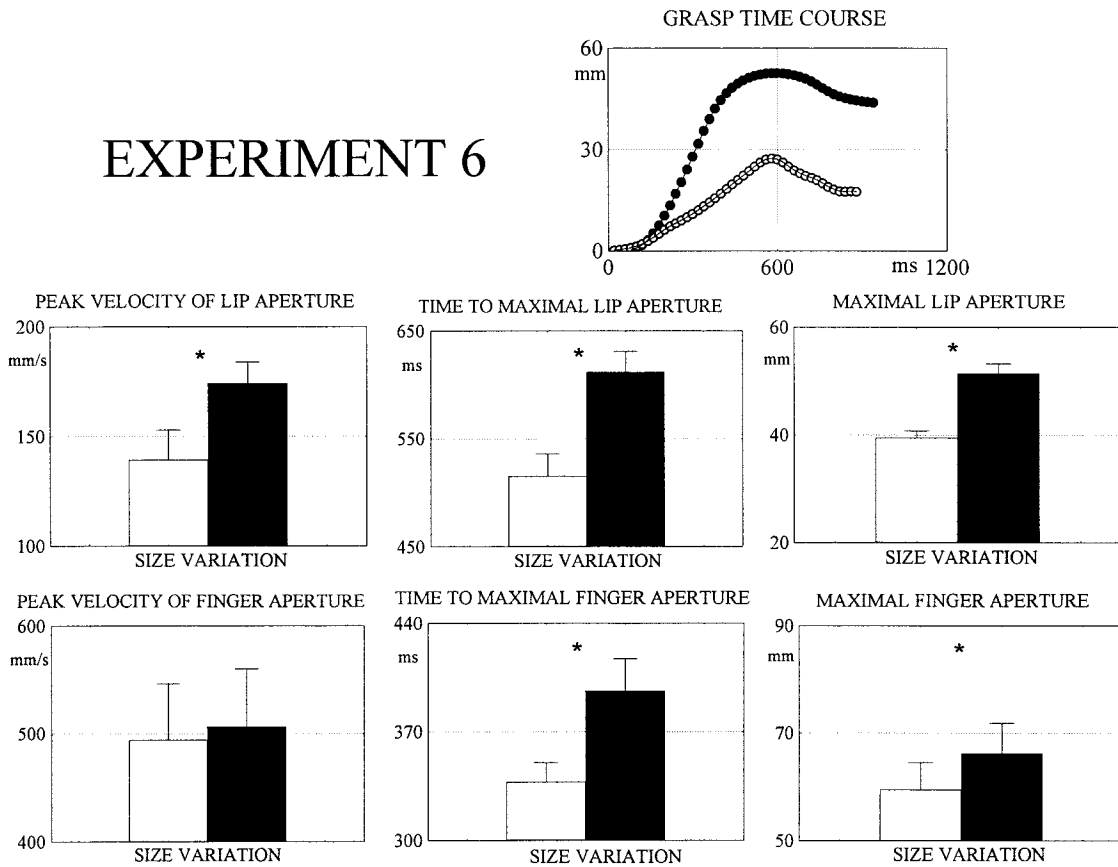


FIG. 8. Grasping with the mouth and right finger aperture executed in *experiment 6*. *Top panel*: representative example of grasp time course. *Middle row*: mean values of grasp parameters. *Bottom row*: mean values of finger aperture parameters. Other conventions as in Fig. 2.

sive motor pattern resembles the grasp motor act. Consequently, finger motor patterns unrelated to the grasp pattern should not be influenced by preparation of grasp with the mouth. We tested this hypothesis in *experiment 7*.

EXPERIMENT 7

Methods

A new sample of eight naïve right-handed [according to Edinburgh Inventory (Oldfield 1971)] subjects (3 women, 5 men, age 20–25) participated in the present experiment to which they gave informed consent.

Apparatus and stimuli were the same as in *experiment 6*. Subjects were required to reach a piece of bread by flexing their trunk, to grasp it with their mouth, and to come back to the starting position. When the red disk was presented, they were required to abduct their right index and middle fingers by an arbitrary and constant amplitude (Fig. 9). The required finger movement is a typical gesture pantomiming scissors cutting. The procedure was the same as in *experiment 6*.

Movement recording was the same as in the previous experiments. In the present study, four markers were used. Two markers were placed on the center of the upper and the lower lip, respectively, and two markers were placed on the base of the nail of the index and middle fingers, respectively. The grasp component was studied by analyzing the time course of the distance between the upper and lower lip, as in *experiment 6*. The finger aperture was studied by analyzing the time course of the distance between the index and middle finger. The measured finger aperture kinematic parameters were peak velocity of finger aperture, maximal finger aperture, and time to maximal

finger aperture. TL was measured as in *experiment 6*. Data analyses were the same as in *experiment 6*.

Results

MOUTH GRASPING. Peak velocity of lip aperture [$F(1,7) = 36.0$, $P < 0.0005$], maximal lip aperture [$F(1,7) = 35.6$, $P < 0.006$], and time to maximal lip aperture [$F(1,7) = 6.7$, $P < 0.04$] were greater for the large object (Fig. 10). Peak velocity of lip aperture [$F(1,7) = 5.7$, $P < 0.05$, 137.1 vs. 146.4 mm/s]

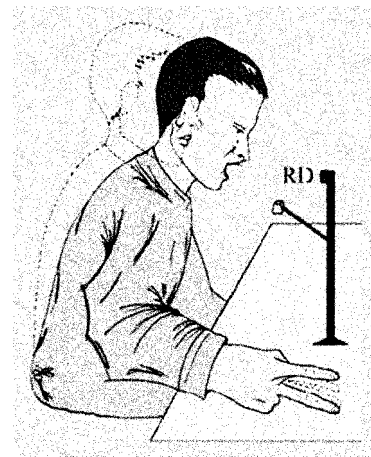


FIG. 9. Schematic representation of the experimental apparatus used in *experiment 7*.

EXPERIMENT 7

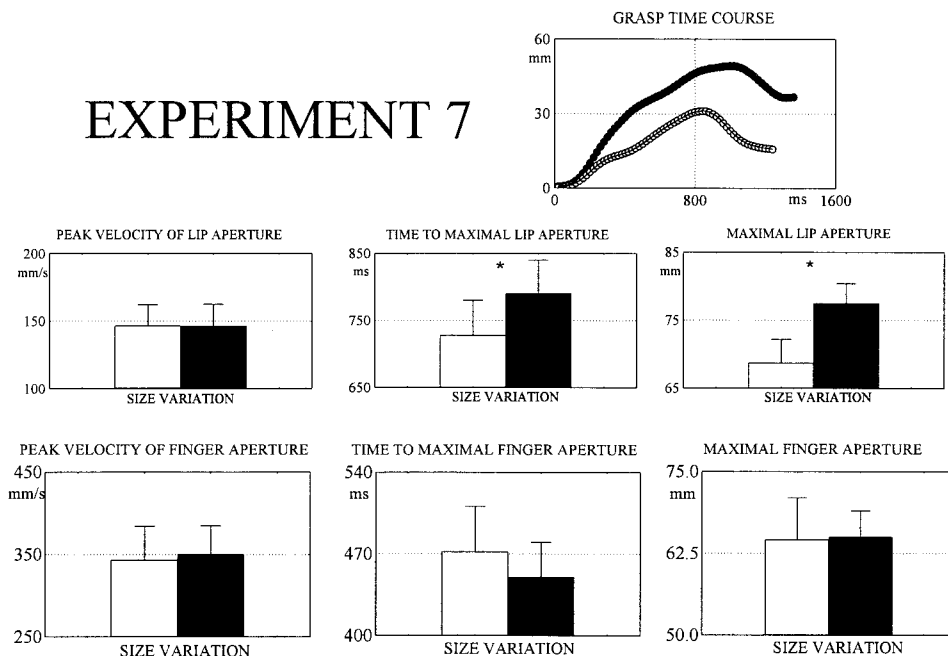


FIG. 10. Grasping with the mouth and right finger aperture executed in *experiment 7*. Other conventions as in Fig. 8.

and maximal lip aperture [$F(1,7) = 5.1$, $P = 0.05$, 73.1 vs. 70.3 mm] increased when fingers were opened.

FINGER OPENING. Peak velocity of finger aperture, time to maximal finger aperture, and maximal finger aperture were not affected by grasped object size (Fig. 10).

TL (mean value -20 ms) was affected by no factor.

Discussion

Grasping with the mouth did not affect finger opening. Values of maximal finger aperture recorded in the present experiment were comparable with those recorded in *experiment 6* (compare Fig. 10 with Fig. 8). Consequently, should an effect of the grasped object size on finger opening be present in the present experiment, it could not be masked by a smaller finger aperture.

Two not mutually exclusive hypotheses can explain the results of *experiments 6* and *7*. The first one is that the command to grasp with the mouth is directly sent to muscles whose contraction controls opposition of the thumb to the other fingers. The second one is that the command is sent to an intermediate circuit, which implements opposition of thumb to the other fingers. By assuming that the second hypothesis is correct, the grasp command could be inhibited when hand position was incompatible with grasping the presented object. This was tested in *experiment 8*.

EXPERIMENT 8

Methods

A new sample of eight naïve right-handed [according to Edinburgh Inventory (Oldfield 1971)] subjects (3 women, 5 men, age 21–24) participated in the present experiment to which they gave informed consent.

Apparatus and stimuli were the same as in *experiment 6*. During the experimental session subjects placed their right hand on their back (Fig. 11) instead of placing it on the plane of the table. Procedure,

movement recording, and data analyses were the same as in *experiment 6*.

Results

MOUTH GRASPING. Peak velocity of lip aperture [$F(1,7) = 49.4$, $P < 0.002$], maximal lip aperture [$F(1,7) = 81.0$, $P < 0.00001$], and time to maximal lip aperture [$F(1,7) = 36.5$, $P < 0.0005$] were greater when grasping the large object (Fig. 12). Time to maximal lip aperture [$F(1,7) = 11.4$, $P < 0.01$, 427.0 vs. 499.6 ms] and maximal lip aperture [$F(1,7) = 6.8$, $P < 0.04$, 66.1 vs. 67.8 mm] increased when fingers were opened.

FINGER OPENING. Peak velocity of finger aperture, time to maximal finger aperture, and maximal finger aperture were not statistically affected by grasped object size (Fig. 12). However, note in Fig. 12 a small but not significant effect of grasped object size on maximal finger aperture.

TL (mean value 24 ms) was affected by no factor.



FIG. 11. Schematic representation of the experimental apparatus used in *experiment 8*.

EXPERIMENT 8

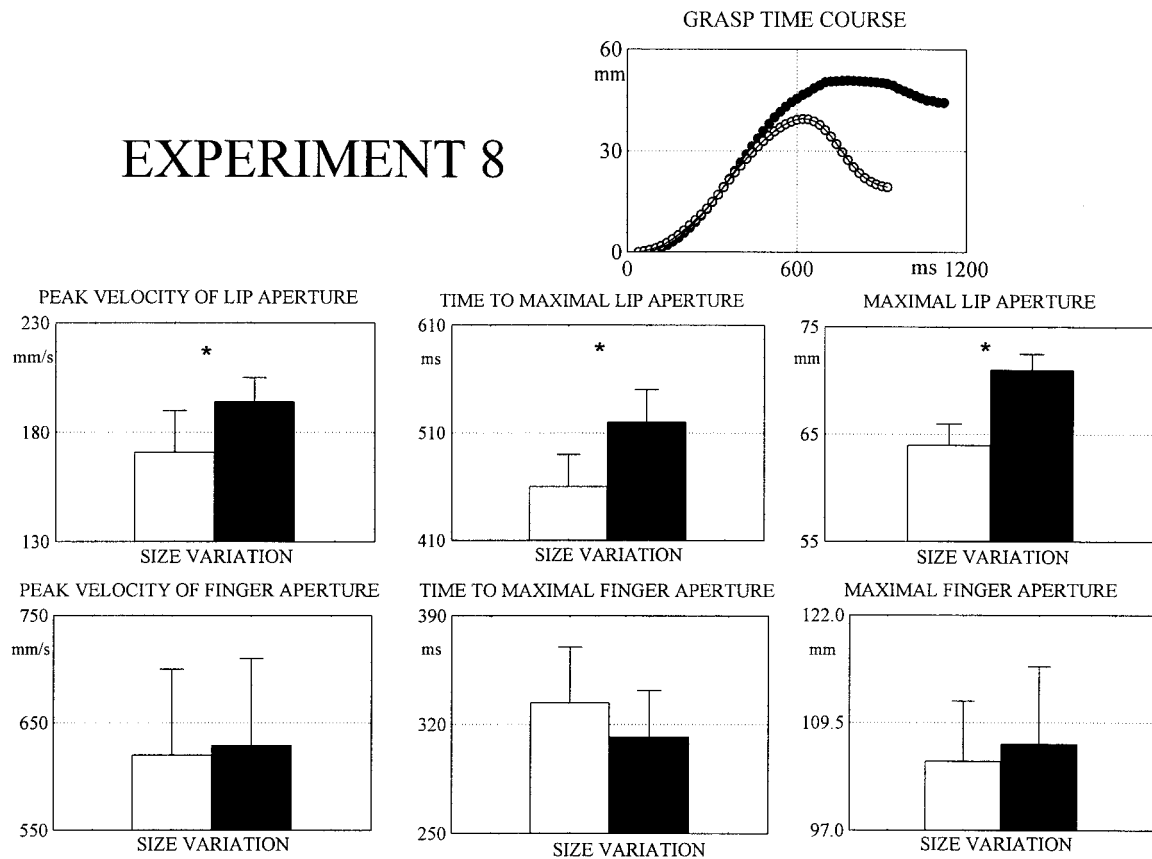


FIG. 12. Grasping with the mouth and right finger aperture executed in *experiment 8*. Other conventions as in Fig. 8.

Discussion

Finger aperture was poorly influenced by grasped object size. This finding can be due to hand position incompatible with object grasping. However, also preclusion of hand vision could increase finger variability, masking a grasp effect. Against this explanation there are the following arguments. 1) A lack of an effect was also found on initial finger opening parameters as well; these are poorly affected by visual control of the relationships between finger aperture and target size during movement. 2) In *experiments 6* and *7* subjects probably controlled fingers with peripheral vision, since they foveated the reaching-grasping target (Jeannerod 1988; Paillard 1982). Consequently, the inaccuracy in finger control was probably the same as when in *experiment 8* vision of the hand was precluded.

Taken together, the results of the previous experiments suggest that the reciprocal influence between hands and mouth movements is not due to a command directly sent to hand and mouth muscles. Conversely, we hypothesize the existence of intermediate circuits where hand and mouth muscle contractions are implemented. We previously (Gentilucci and Rizzolatti 1990; Rizzolatti and Gentilucci 1988) hypothesized that monkey premotor areas are involved in hand-and-mouth grasp preparation. We suggest that human premotor areas are likely to be involved in preparing the grasp act independently of the used effector. However, up to now there are no neuroimaging data showing that areas, where grasp with the mouth and grasp with the hand are prepared and/or imagined, partially overlap with each other.

In the previous experiments we compared a movement directed to a target, that is grasping an object with hand or mouth, with an aimless, internally driven, movement, that is lip or finger opening. Consequently, subjects could unconsciously pantomime a grasp movement. We chose to study the mutual influence between hand grasp movements and mouth movements driven by a visual stimulus, that is pronouncing read syllables because (see INTRODUCTION) we hypothesized that the two movements are related to each other. This is based on the hypothesis that Broca's area seems to derive phylogenetically from F5 premotor area of monkey where neurons involved in commanding grasp with hands and mouth and in recognizing grasp motor acts were recorded (Rizzolatti and Arbib 1998).

EXPERIMENT 9

Methods

A new sample of eight naïve right-handed [according to Edinburgh Inventory (Oldfield 1971)] subjects (5 women, 3 men, age 21–24) participated in the present experiment to which they gave informed consent.

Apparatus was the same as in the previous experiments. Objects to be reached and grasped were the small (sides 3 × 3 cm, height 1 cm) and the large object (sides 5 × 5 cm, height 1 cm) used in *experiment 1*. On their visible face either a syllable or a cloud configuration could be printed. The syllables could be the following: “GU” (/gu/), “GA” (/gʌ/), “PU” (/pu/), “PA” (/pʌ/). That is, either velar or labial consonants were presented. The syllable was 2 cm wide and 1.5 cm high. We chose to present the syllables printed on the target face to induce a simultaneous analysis of object size and syllable, and, consequently, a simultaneous implementation of two motor programs, which more

likely could influence each other. A different location of syllable could induce successive visual-motor integration and reduce the probability of reciprocal interference. One parallelepiped was placed on the plane of the table at a distance of 15 cm from SP.

Subjects were required to reach and grasp the object with their right thumb and index finger and to lift it. In addition, they were required to pronounce the presented syllable contemporaneously to reaching-grasping. They were required to use the same acoustic volume as during normal conversation. Procedure was the same as in the previous experiments.

Each experimental session consisted of 70 trials. Each syllable was presented in 14 trials: in 7 trials it was presented on the large target object; in the others it was presented on the small target object. In 14 trials, target objects with the cloud configuration were presented: in one-half of the trials they were large; in the others they were small. Target objects were pseudorandomly presented.

Movements of arm and mouth were recorded as in *experiment 1*. The following reach and grasp parameters were analyzed: arm peak acceleration, arm peak velocity, time to arm peak velocity, peak velocity of grip aperture, maximal grip aperture, and time to maximal grip aperture. The following lip aperture kinematic parameters during syllable pronouncing were analyzed: peak velocity of lip aperture, maximal lip aperture, and time to maximal lip aperture. Time lag (TL) of lip-opening beginning with respect to finger-opening beginning was calculated.

We recorded the voice emitted by six subjects during syllable pronouncing. A microphone (Studio Electret Microphone, 20–20,000 Hz, 500 Ω, 5 mV/Pa/1 kHz) was placed on the table at the distance of

50 cm from the subject's frontal plane. A microphone was connected to a PC for sound recording by a card device (16 PCI Sound Blaster). Mean spectrograms of each syllable were computed by using a fast Fourier transform (FFT) during the conditions of grasping the small and the large object. New plots were constructed by means of mean spectrograms. Abscissa was frequency, and ordinate was the sum of the power levels recorded for each frequency. Maximal power level value and corresponding frequency were measured.

On reaching-grasping parameters, two series of ANOVAs were carried out. In the first series we compared the effects of pronunciation of each syllable on arm and mouth kinematics. The experimental design included three within-subjects factors (consonant: G vs. P; vowel: U vs. A; object size: small vs. large). In the second series we compared the effect of syllable pronouncing on arm and mouth kinematics. The condition of pronouncing each syllable was compared with the "silent" condition. In the ANOVAs the within-subjects factors were the following two: syllable pronouncing (present vs. absent) and object size (small vs. large). On lip aperture parameters, TL, and sound parameters, one series of ANOVAs was carried out. The experimental design included the three following within-subjects factors: consonant (G vs. P), vowel (U vs. A), and object size (small vs. large). In all analyses Newman-Keuls post hoc test was used.

Results

HAND REACHING-GRASPING. Reaching. Arm peak acceleration and time to arm peak velocity were affected by no factor,

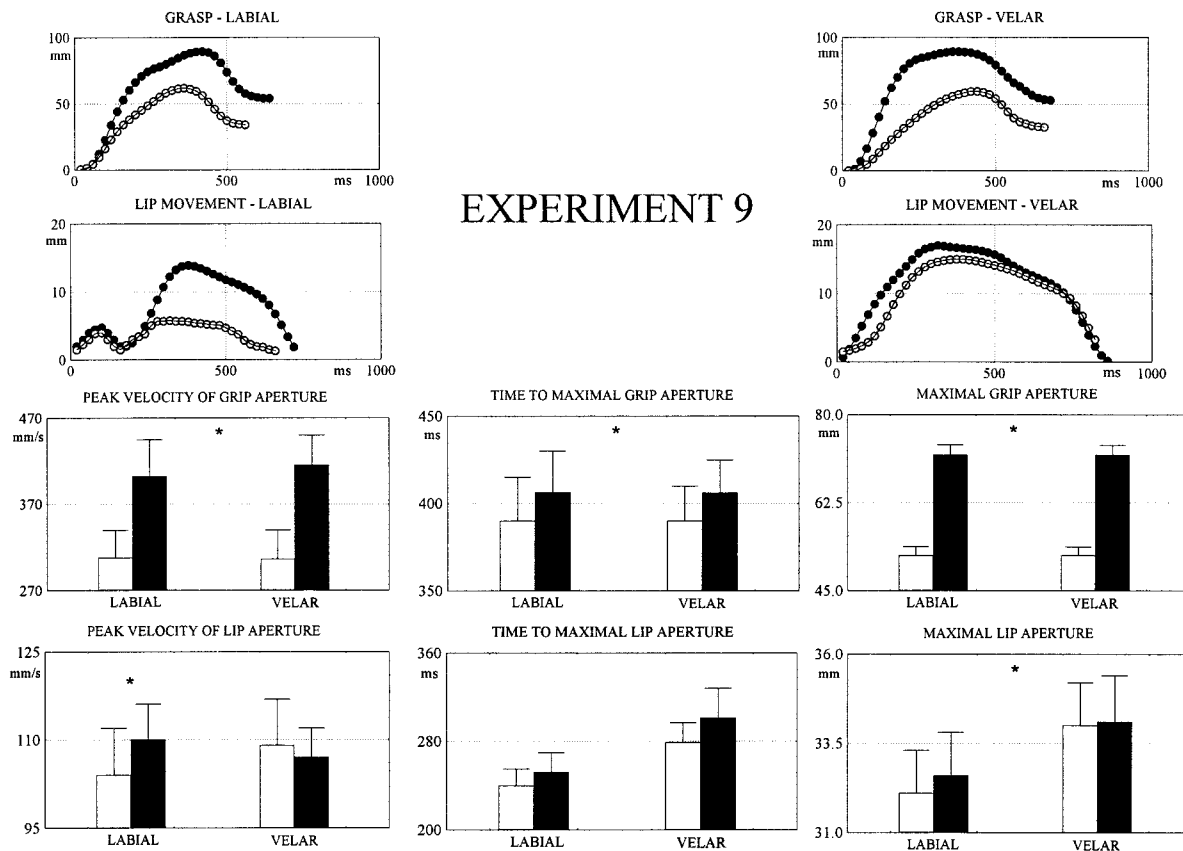


FIG. 13. Reaching-grasping with the right hand and syllable pronouncing executed in *experiment 9*. From top to down: 1st row: representative examples of grasp time course while pronouncing a labial (left panel) and a velar (right panel); 2nd row: lip aperture-closure time course while pronouncing a labial (left panel) and a velar (right panel). Frequently, pronouncing a labial was constituted by a double lip aperture-closure. The 1st maximal lip aperture was always much smaller than the 2nd one. 3rd row: mean values of grasp parameters. 4th row: mean values of lip aperture parameters. Other conventions as in Fig. 2.

whereas arm peak velocity [$F(1,7) = 16.0$, $P < 0.005$, 815.4 vs. 796.5 mm/s] decreased when reaching the small object.

Grasping. Peak velocity of grip aperture [$F(1,7) = 26.4$, $P < 0.001$], time to maximal grip aperture [$F(1,7) = 5.5$, $P = 0.05$], and maximal grip aperture [$F(1,7) = 573.8$, $P < 0.00001$] were greater when grasping the large object (Fig. 13).

SYLLABLE PRONOUNCING. Peak velocity of lip aperture was affected by vowel [$F(1,7) = 12.6$, $P < 0.009$] and by the interaction between vowel and consonant [$F(1,7) = 23.6$, $P < 0.002$]. Peak velocity of lip aperture did not significantly vary when pronouncing GU (112.1 mm/s) and GA (104.7 mm/s), whereas it was greater when pronouncing PA (128.4 mm/s) with respect to PU (86.0 mm/s, $P < 0.01$). The interaction between consonant and object size was significant [$F(1,7) = 7.3$, $P < 0.03$]. Peak velocity of lip aperture increased when pronouncing the labial (P) and grasping the large object (Fig. 13). Maximal lip aperture increased when pronouncing G with respect to P [$F(1,7) = 11.5$, $P < 0.01$, Fig. 13]. It was larger when grasping the large object [$F(1,7) = 11.8$, $P < 0.01$, Fig. 13]. Time to maximal lip aperture increased when grasping the large object, although not significantly (Fig. 13).

Maximal power level was significantly greater when pronouncing A than U [$F(1,5) = 33.3$, $P < 0.002$; Fig. 14]. It was higher also when grasping the large object [$F(1,5) = 6.5$, $P = 0.05$, Fig. 14]. Frequency was affected only by vowel [$F(1,5) = 92.1$, $P < 0.0002$, Fig. 14].

TL was affected by consonant [$F(1,7) = 15.2$, $P < 0.005$; P, 72.0 ms; G, -9.6 ms], vowel [$F(1,7) = 11.6$, $P < 0.01$; U, 18.2 ms; A, 44.6 ms], and object size [$F(1,7) = 7.2$, $P < 0.03$; large object, 37.8 ms; small object, 25.0 ms].

Discussion

Grasping an object influenced pronouncing a syllable. Lip opening was affected by grasped object size especially when a

labial was pronounced. This effect did not depend on a larger lip excursion (see Fig. 13), but probably on a greater control on motor lip pattern, which was the specific effector used to pronounce a labial. In addition, voice was affected by grasped object size, and a different temporal coupling was observed between hand and mouth movement beginning, according to the pronounced syllable and object size. Probably, different inner or outer parts of mouth were specifically used to pronounce each syllable (Ladefoged 1975; Perkel and Nelson 1982). Movements of these parts were specifically influenced by the grasping hand. Summing up, grasping with the hand influenced not only mouth aperture, but also the complex articulation system used for syllable pronunciation.

Pronouncing a syllable did not influence grasp. Theoretically, an effect was possible. In fact, both mouth opening and sound production varied with pronunciation of different syllables. Sound production (at least the parameters measured in the present experiment) was influenced only by vowel (Young and Sachs 1979), whereas lip opening was affected by both vowel, consonant, and by their interaction (Ladefoged 1975; Perkel and Nelson 1982). All these variations were comparable with variation in grasp parameters with object size (see Fig. 13). It is possible that in a different experimental paradigm, in which pronunciation of the same syllable was required, although with different acoustic volumes, an effect on grasp might be found. However, this paradigm is inappropriate for the scope of the present experiment, because we were poorly interested in studying the possible synchronism between hand and mouth movements.

The finding that grasp influenced speech production, but speech production did not influence grasp control, can be due to the fact that the control of shaping of the grasping hand depends more on visual analysis of object properties (i.e., size and shape) than the control of mouth motor pattern on vision of a printed syllable. Consequently, a motor implementation based on analysis of real physical features of the target has probably easier access to a more abstract motor implementation in which the correspondence between mouth pattern and syllable features is more arbitrary. The hypothesis of the strict relation between intrinsic object properties and grasping hand control is in accordance with the results of our previous studies (Gentilucci and Gangitano 1998; Gentilucci et al. 2000). Indeed, we observed an effect even of the automatic reading of words related to intrinsic and extrinsic target properties on the control of grasp and reach parameters.

GENERAL DISCUSSION

The results of the present study suggest that grasping with the hand or with the mouth can affect movements of other distal effectors (*experiments 1 and 3–6*). Variation in hand-or-mouth shaping (initial grasp kinematics more related to planning), as a function of intrinsic object properties influenced other distal movements. This effect was consequent neither to vision of the object without grasping it (*experiment 2*) nor to synchronism between finger and mouth opening. Indeed, grasp parameters, which changed as a consequence of changes in extrinsic object properties (*experiment 3*), did not influence movement of other distal effectors. In sum, the transformation of visual intrinsic object properties in a grasp motor pattern is the necessary prerequisite for an influence of grasp on the

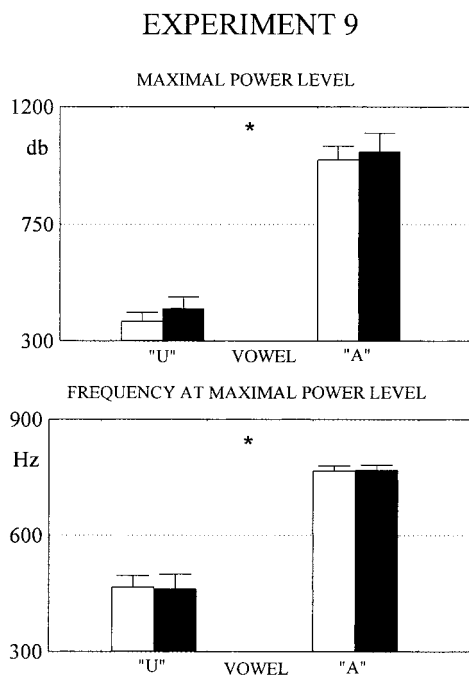


FIG. 14. Mean values of sound parameters collected in *experiment 9* during syllable pronunciation. Other conventions as in Fig. 2.

movement of other distal effectors. Conversely, grasp control did not influence movement of a distal effector not resembling grasp (*experiment 7*), and it poorly influenced resembling-grasp movement of a distal effector placed in a position incompatible with grasping the object (*experiment 8*). Taken together, these results are in favor of our initial hypothesis that the grasp command can be sent to the circuits controlling movements of distal effectors. It provides information on how to appropriately grasp the object. Their function can be related to preparing motor acts in succession when a complex action is performed (Gentilucci et al. 1997), as, for example, reaching and grasping a food with the hand and ingesting it after bringing it to the mouth. Our data suggest also that the grasp signal is effective when effector position is appropriate for the grasp motor act.

The second hypothesis of the present study was that grasp control influenced mouth control during syllable pronouncing. Indeed, this was observed. Grasping with the hand affected not only aperture of the mouth, but selectively affected movement of inner or outer parts of the mouth according to pronunciation of the syllable. Indeed, synchronization between hand and mouth movement beginning varied according to the syllable, and sound power level varied according to object size. It has been proposed that Broca's area derives phylogenetically from premotor areas where arm and hand movements are controlled (Rizzolatti and Arbib 1998). In support of this hypothesis, Broca's area is activated also when hand movement is imagined (Decety et al. 1994; Grafton et al. 1996). Moreover, we found that automatic reading of words related to target properties affected the control of reaching-grasping movements according to their meaning (Gentilucci and Gangitano 1998; Gentilucci et al. 2000). If the hypothesis of a strict relation between speech control and hand control is correct, it raises a problem about their functional relationship. Although speculative, a possible explanation is that during evolution an initial form of communication used hand gestures. Successively, hand gestures were probably transformed into speech by means of the use of multiple motor commands to hands and mouth (Armstrong et al. 1995). Premotor neurons involved in generating multiple grasp signals to hands and mouth might be used to transfer motor patterns from hand to mouth. The hypothesis of a common substrate used for hand gesture and speech production is supported by a research showing that deaf children, when learning American Sign Language, go through a "hand-babbling" stage, in which they manipulate sublexical elements of signs, much like the babbling stage of hearing infants (Petitto and Marentette 1991).

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REFERENCES

- ARMSTRONG DF, STOKOE WC, AND WILCOX SE. *Gesture and the Nature of Language*. Cambridge, UK: Cambridge Univ. Press, 1995.
- BEISTEINER R, HOLLINGER P, LINDINGER G, LANG W, AND BERTHOZ A. Mental representations of movements. Brain potentials associated with imagination of hand movements. *Electroencephalogr Clin Neurophysiol* 96: 183–193, 1995.
- BONDA E, PETRIDES M, FREY S, AND EVANS AC. Frontal cortex involvement in organized sequence of hand movements: evidence from positron emission tomography study. *Soc Neurosci Abstr* 20: 353, 1994.
- CHIEFFI S AND GENTILUCCI M. Coordination between the transport and the grasp components during prehension movements. *Exp Brain Res* 94: 471–477, 1993.
- CORRADINI L, GENTILUCCI M, LEO T, AND RIZZOLATTI G. Motor control of voluntary movements. Kinematic and modelling study. *Biol Cybern* 67: 347–360, 1992.
- DARWIN C. *The Expression of the Emotions in Man and Animals* (3rd ed.). London: Harper Collins, 1998.
- DECETY J, PERANI D, JEANNEROD M, BETTINARDI V, TADARY B, WOODS R, MAZZOTTA JC, AND FAZIO F. Mapping motor representations with positron emission tomography. *Nature* 371: 600–602, 1994.
- FITTS PM. The information capacity of the human motor system in controlling the amplitude of movement. *J Exp Psychol* 47: 381–391, 1954.
- GALLESE V, FADIGA L, FOGASSI L, AND RIZZOLATTI G. Action recognition in the premotor cortex. *Brain* 119: 593–609, 1996.
- GENTILUCCI M, BENUZZI F, BERTOLANI L, DAPRATI E, AND GANGITANO M. Language and motor control. *Exp Brain Res* 133: 468–490, 2000.
- GENTILUCCI M, CASTIELLO U, CORRADINI ML, SCARPA M, UMILTÀ C, AND RIZZOLATTI G. Influence of different types of grasping on the transport component of prehension movements. *Neuropsychologia* 5: 361–378, 1991.
- GENTILUCCI M, CHIEFFI S, SCARPA M, AND CASTIELLO U. Temporal coupling between transport and grasp components during prehension movements: effects of visual perturbation. *Behav Brain Res* 47: 71–82, 1992.
- GENTILUCCI M, DAPRATI E, AND GANGITANO M. Haptic information differentially interferes with visual analysis in reaching-grasping control and in perceptual processes. *Neuroreport* 9: 887–891, 1998.
- GENTILUCCI M AND GANGITANO M. Influence of automatic word reading on motor control. *Eur J Neurosci* 10: 752–756, 1998.
- GENTILUCCI M, NEGROTTI A, AND GANGITANO M. Planning an action. *Exp Brain Res* 115: 116–128, 1997.
- GENTILUCCI M AND RIZZOLATTI G. Cortical motor control of arm and hand movements. In: *Vision and Action: The Control of Grasping*, edited by Goodale MA. Norwood, NJ: Ablex, 1990, p. 147–162.
- GENTILUCCI M, TONI I, CHIEFFI S, AND PAVESI G. The role of proprioception in the control of prehension movements: a kinematic study in a peripherally deafferented patient and in normal subjects. *Exp Brain Res* 102: 483–494, 1994.
- GRAFTON ST, ARBIB MA, FADIGA L, AND RIZZOLATTI G. Localization of grasp representation in humans by positron emission tomography. 2. Observation compared with imagination. *Exp Brain Res* 112: 103–111, 1996.
- JAKOBSON LS AND GOODALE MA. Factors affecting higher-order movement planning: a kinematic analysis of human prehension. *Exp Brain Res* 86: 199–208, 1991.
- JEANNEROD M. *The Neural and Behavioural Organization of Goal-Directed Movements*. Oxford, UK: Oxford Univ. Press, 1988.
- KIM SG, ASHE J, HENDRICH K, ELLERMANN JM, MERKLE H, UGURBIL K, AND GEORGOPOULOS AP. Functional magnetic resonance imaging of motor cortex: hemispheric asymmetry and handedness. *Science* 261: 615–617, 1993.
- LADEFOGED P. *A Course of Phonetics*. Cleveland, OH: Harcourt Brace, 1975.
- LEVELT WJ AND WHEELDOM L. Do speakers have access to a mental syllabary cognition? *Cognition* 50: 239–269, 1994.
- MARTENIUK RG, MACKENZIE CL, JEANNEROD M, ATHENES S, AND DUGAS C. Constraints in human arm movements trajectories. *Can J Psychol* 41: 365–378, 1987.
- MATELLI M, LUPPINO G, AND RIZZOLATTI G. Patterns of cytochrome oxidase activity in the frontal agranular cortex of the macaque monkey. *Behav Brain Res* 18: 125–137, 1985.
- OLDFIELD RC. The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia* 9: 97–113, 1971.
- PAILLARD J. The contribution of peripheral and central vision to visually guided reaching. In: *Analysis of Visual Behavior*, edited by Ingle DJ, Goodale MA, and Mansfield RJW. Cambridge, MA: MIT Press, 1982, p. 367–385.
- PARSONS LM, FOX PT, DOWNS JH, GLASS T, HIRSCH TB, MARTIN CC, JERABEK PA, AND LANCASTER JL. Use of implicit motor imagery for visual shape discrimination as revealed by PET. *Nature* 375: 54–58, 1995.
- PERKEL JS AND NELSON WL. Articulatory targets and speech motor control: a study of vowel production. In: *Speech Motor Control*, edited by Grillner S,

- Lindblom B, Lubker J, and Persson A. Oxford, UK: Pergamon, 1982, p. 187–204.
- PETITTO LA AND MARENTETTE PF. Babbling in the manual mode: evidence for the ontogeny of language. *Science* 251: 1493–1496, 1991.
- RIZZOLATTI G AND ARBIB MA. Language within our grasp. *Trends Neurosci* 21: 188–194, 1998.
- RIZZOLATTI G, CAMARDA R, FOGASSI L, GENTILUCCI M, LUPPINO G, AND MATELLI M. Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Exp Brain Res* 71: 491–507, 1988.
- RIZZOLATTI G AND GENTILUCCI M. Motor and visual-motor functions of the premotor cortex. In: *Neurobiology of Neocortex*, edited by Rakic P and Singer W. New York: Wiley, 1988, p. 269–284.
- SCHLAUG G, KNORR U, AND SEITZ RJ. Inter-subject variability of cerebral activation in acquiring a motor skill: a study with positron emission tomography. *Exp Brain Res* 98: 523–534, 1994.
- TABOSSI P, COLLINA S, MAZZETTI M, AND ZOPPELLO M. Syllables in the processing of spoken Italian. *J Exp Psychol Hum Percept Perform* 26: 758–775, 2000.
- WANG J AND STELMACH GE. Coordination among body segments during reach-to-grasp action involving the trunk. *Exp Brain Res* 123: 346–350, 1998.
- WING AM, TURTON A, AND FRASER C. Grasp size and accuracy of approach in reaching. *J Mot Behav* 18: 245–260, 1986.
- YOUNG ED AND SACHS MB. Representation of steady-state vowel in the temporal aspects of the discharge patterns of populations of auditory nerve fibers. *J Acoust Soc Am* 66: 1381–1403, 1979.