

When flavor guides motor control: an effector independence study

Valentina Parma · Roberto Roverato ·
Deborah Ghirardello · Maria Bulgheroni ·
Roberto Tirindelli · Umberto Castiello

Received: 21 March 2011 / Accepted: 12 May 2011 / Published online: 27 May 2011
© Springer-Verlag 2011

Abstract Research on multisensory integration during natural tasks has revealed how chemical senses contribute to plan and control movements. An aspect which has yet to be investigated regards whether the motor representations evoked by chemosensory stimuli, once established for a particular movement, can be used to control different effectors. Here, we investigate this issue by asking participants to drink a sip of flavored solution, grasp with the hand a visual target, and then bring it to the mouth, miming the action of biting. Results show that hand and lip apertures were scaled according to the size of the object evoked by the flavor. Maximum hand and lip apertures were greater when the action toward a small visual target (e.g., strawberry) was preceded by a sip of a “large” (e.g., orange) than a “small” (e.g., almond) flavor solution. Conversely, maximum hand and lip apertures were smaller when the action toward a large visual target (e.g., apple) was preceded by the presentation of a “small” (e.g., strawberry) rather than a “large” flavor solution. These findings support previous evidence on the presence of a unique motor plan underlying the act of grasping with-the-hand and with-the-mouth, extending the knowledge of chemosensorimotor transformations to motor equivalence.

Keywords Chemical senses · Cross-modal interactions · Hand kinematics · Mouth kinematics

Introduction

The way we perceive the external world has been a matter of interest long before the advent of formal science (Aristotle 1986). Although most of the researches in this area have followed a unisensory processing perspective, accumulating evidence suggests that real-world behaviors are guided by the integrated information from more than one sensory source at a time (Ghazanfar and Schroeder 2006). In this respect, the majority of the studies conducted in humans on cross-modal integration have typically focused on perceptual integration and have involved an arbitrary response, such as reaction time, to a sensory stimulus (e.g., Driver and Spence 2000).

More recently, however, research on multisensory processing has been extended to motor control (Castiello et al. 2006, 2010; Gentilucci et al. 1998; Patchay et al. 2003; Tubaldi et al. 2008a, b). In this series of experiments, participants were asked to reach and grasp a visually presented object (i.e., target), following the presentation of a task-irrelevant sensory stimulus (i.e., distractor). Distractors could have been a tactile (Gentilucci et al. 1998; Patchay et al. 2003, 2006), an auditory (Castiello et al. 2010), an olfactory (Castiello et al. 2006; Tubaldi et al. 2008a, b), or a flavor (Parma et al. 2011) stimulus. As an example, participants were asked to drink a sip of strawberry juice and then reach and grasp an orange positioned in front of them. Thus, the object elicited by the flavored solution was a strawberry, a fruit which needs a precision grip (i.e., the opposition of the thumb to the index finger) in order to be grasped. Whereas the visual target was an orange, a fruit which requires a whole-hand grip (i.e., opposition of the thumb to all the other fingers) in order to be grasped. The results indicated either interference or facilitation effects on kinematic parameters such as the

V. Parma · R. Roverato · D. Ghirardello · M. Bulgheroni ·
U. Castiello (✉)
Department of General Psychology, University of Padova,
Via Venezia, 8, 35131 Padova, Italy
e-mail: umberto.castiello@unipd.it

R. Tirindelli
Department of Neuroscience, University of Parma, Parma, Italy

maximum hand aperture. In the first instance, maximum hand aperture was significantly smaller when the orange was grasped preceded by a size-incongruent (e.g., strawberry flavored solution) than when it was grasped preceded by a size-congruent (e.g., apple flavored solution) stimulation or water (i.e., control condition). In the second instance, maximum hand aperture was more size attuned when the orange was grasped preceded by a size-congruent stimulation (e.g., orange flavored solution) than when it was grasped preceded by a size-incongruent (e.g., strawberry flavored solution) or water stimulation (Parma et al. 2011). Therefore, the grasp plan evoked by the flavor of a strawberry (i.e., precision grip) influenced the performance of the whole-hand grip necessary to grasp the orange and successfully accomplish the task.

As can be noticed, research on the cross-modal links in motor control has been chiefly conducted by considering the reach to grasp movement performed by the hand as an experimental window. This is because it is one of the most common actions we execute every day, and in order to be performed, it requires that different sensory modalities act in concert.

Available literature, however, clearly indicated that the action of grasping with the hand shares many similarities with the action of grasping with the mouth. As an example, histological and histochemical investigations showed that a portion of neurons in the *Macaca fascicularis*' brain discharges both when a grasping action is performed by means of the hand or the mouth (Rizzolatti et al. 1988). This common activation does not seem to be caused by a synergism between hand and mouth movements, given that a double dissociation between the presence of neuronal discharge when grasping with the mouth and with the hand has been reported (Rizzolatti et al. 1987). Rather, it appears that, independently from the anatomical effector used to perform the grasping action, these neurons code for the aim of the action itself (Rizzolatti 1987). This viewpoint has also been supported by a few behavioral kinematic (Castiello 1997; Gentilucci et al. 2001) and neuroimaging (Castiello et al. 2000) studies, which provided evidence of the presence of a unique motor plan underlying the parameterization of grasping both with the hand and with the mouth.

Altogether, the above-mentioned findings support the generalized motor program hypothesis (Keele 1968; Hugues and Abbs 1976). In these terms, a generalized motor program consists of an abstract memory structure apt to specify a class of non-specific instructions used to guide a broad range of movements (e.g., “grasp,” “bite”). As demonstrated by investigating handwriting (Merton 1972; Wright 1990; Castiello and Stelmach 1993), these shared higher-order specifications are believed to allow for effector independence and motor equivalence, that is, “the

capacity of the motor system to achieve the same end product with considerable variation in the individual components that contribute to them” (Hugues and Abbs 1976).

Although a number of studies, using a variety of tasks, have assessed the issue of effector independence in terms of a parallelism between mouth and hand movements (Calvert et al. 1999; Gentilucci and Cattaneo 2005; Sato et al. 2010; Castiello 1997; Gentilucci et al. 2001); to our knowledge, no previous research has examined the issue of effector independence within a chemosensory cross-modal context. Therefore, here, we aim at investigating the effects that chemosensory stimuli might have on the kinematics of hand and mouth movements during the performance of a prehensile movement by the hand and a bite action. In terms of effector independence, we expect that a flavor stimulus has the ability to modulate both mouth and hand kinematics. In the light of previous evidence, which has investigated how chemosensory and vision stimuli do integrate during solely hand grasping movements (e.g., Castiello et al. 2006; Tubaldi et al. 2008b; Parma et al. 2011), we hypothesize that interference effects should be evident when the visual target and the preceding flavor-evoked stimulus have a different size. Conversely, when the visual target and the preceding flavor evoke a stimulus sharing a similar size, we expect a more stable patterning of maximum hand and lip aperture toward the to-be-grasped-and to-be-bitten visual target.

Materials and methods

Participants

Six women and 4 men (mean age = 24.76 years, SD = 4.3 years) reporting normal or corrected-to-normal vision, normal smell and taste abilities, and no history of smell and taste dysfunction participated in the study. All gave their informed written consent to participate and were naïve as to the purpose of the experiment. The experimental procedures were in accordance with the declaration of Helsinki and were approved by the Institutional Review Board at the University of Padova. The experimental session lasted approximately 30 min.

Stimuli

Four plastic objects grouped on the basis of their natural size were used as visual targets (Fig. 1). These objects were an apple and an orange that were considered as large targets; an almond and a strawberry were considered as small targets. Plastic objects were used in order to maintain consistent visual attributes and sizes throughout the period

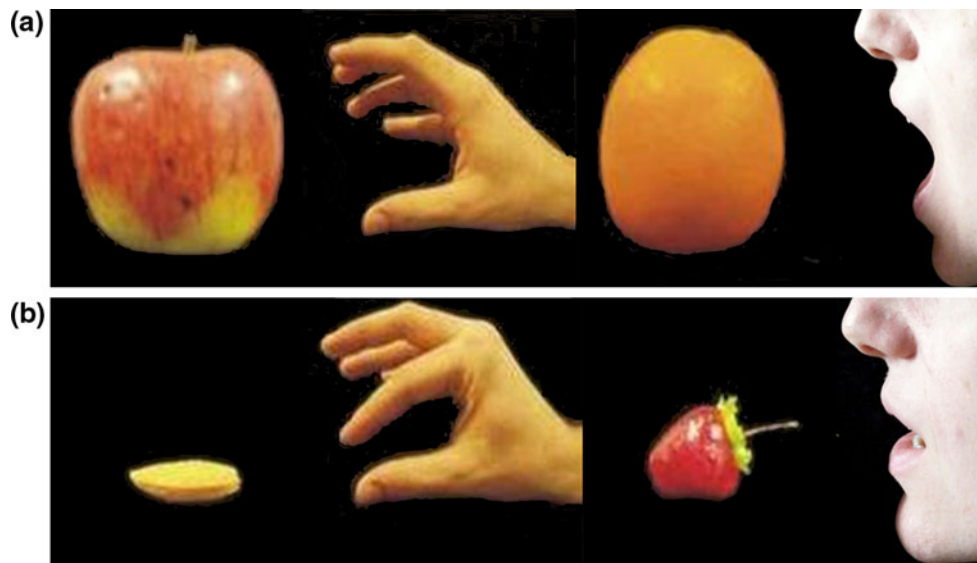


Fig. 1 Panel **a** shows the large visual targets (*apple* and *orange*) and the hand and the mouth apertures naturally used to grasp and bite them. Panel **b** shows the small visual targets (*almond* and *strawberry*) and the hand and the mouth apertures naturally used to grasp and bite them

Table 1 Visual target-flavored solutions combinations for the congruent, incongruent, and control experimental conditions

		Visual target			
		Apple	Orange	Almond	Strawberry
Solutions (flavors)	Apple	LL	LL	LS	LS
	Orange	LL	LL	LS	LS
	Almond	SL	SL	SS	SS
	Strawberry	SL	SL	SS	SS
	Water	CL	CL	CS	CS

LL congruent large, *LS* incongruent large, *SL* incongruent small, *SS* congruent small, *CL* control large, *CS* control small

of experimentation. The flavor stimuli corresponded to the visual targets. Specifically, they consisted of 5 ml of either fruit juice (apple, orange, strawberry, and water-diluted almond syrup) or water. A custom-built apparatus was set to administer flavored solutions from sealed syringes in order to prevent participants to ortho-nasally smell the odors when delivering the flavor stimuli or water. The apparatus consisted in a set of 5 Teflon tubes (0.30 mm diameter). Each of them was connected to a computer-controlled 5-ml-syringe filled-in with the solutions. At the time when the flavor stimulation was delivered, the Teflon tube, providing the to-be-administered solution, was drawn up to the participant's mouth in order to favor the sipping.

Procedure

The target was positioned at the center of a black table surface, at a 33-cm distance from the participant's hand starting position. At the beginning of each trial, participants were asked to eat a piece of water table cracker (1.5 g) to

rinse the mouth from lingering taste and, subsequently, to drink 10 ml of water to remove food residuals. Then, a 5-ml flavored solution was administered. After the sipping, participants were asked to close their eyes and keep them closed till the presentation of an auditory tone (frequency: 800 Hz; 500-ms duration). The auditory tone indicated participants to reach toward, grasp and bring the target object to the mouth, miming the action of biting the fruit. The experimenter visually monitored each trial to ensure subject's compliance to these requirements. A breach of instructions caused the trial to be excluded from the final analyses. A pretest, carried out before the experimental session, evidenced that participants naturally grasped the small objects between the thumb and the index finger (i.e., precision grip) and the large objects opposing the thumb with all the other fingers (i.e., whole-hand grip). There were six experimental conditions (Table 1): (1) congruent large (LL), in which both the flavor and the visual stimulus evoked a large object (e.g., orange-apple); (2) congruent small (SS), in which both the flavor and the visual stimulus

evoked a small object (e.g., strawberry-almond); (3) incongruent large (LS), in which the flavored solution evoked a large object but the visual stimulus evoked a small object (e.g., orange-almond); (4) incongruent small (SL), in which the flavored solution evoked a small object and the visual stimulus evoked a large object (e.g., strawberry-apple); (5) control large (CL), in which the flavor stimulus was water and the visual stimulus evoked a large object (e.g., water-orange); and (6) control small (CS), in which the flavor stimulus was water and the visual stimulus evoked a small object (e.g., water-strawberry). Participants performed 6 trials for each experimental condition for a total of 36 trials. Trials were presented in randomized order within three 12-trial blocks interleaved by a 5-min pause.

Apparatus

A three-dimensional motion analysis system (SMART-D, BTS) equipped with six infrared cameras (frequency, 140 Hz) was used to record movements. The infrared cameras picked up the reflectance of seven passive markers (diameter = 0.25 cm) placed on (a) the wrist, (b) the tip of the index finger, (c) the tip of the thumb of the right-hand (d) the center of the upper lip, (e) the center of the lower lip, (f) the left condylar process, and (g) the right condylar process, respectively. Markers were fastened using marker-sized double-sided tape. Co-ordinates of the markers were reconstructed with an accuracy of 0.2 mm over the field of view. The standard deviation of the reconstruction error was 0.2 mm for the vertical (Y) axis and 0.3 mm for the two horizontal (X and Z) axes. Data were reconstructed, filtered (10 Hz), and analyzed with the SMART-D analyzer software.

Dependent measures and statistical analyses

Kinematic analysis was confined to the amplitude of maximum hand and lip apertures, which are measures that can be equated with each other. To date, this measure appears to be the most effective in revealing how the planning and control of hand movements are affected by irrelevant information presented in a different sensory modality (e.g., Patchay et al. 2005, 2006; Castiello et al. 2006). Maximum hand aperture was calculated as the maximum distance in millimeters between the tip of index finger and the tip of the thumb. Maximum lip aperture was calculated as the distance between the center of the upper and the lower lip. Because the orange and the almond were presented with their skin, and it is not customary to bite them unpeeled, we performed a preliminary analysis on maximum lip aperture comparing trials in which the apple and the strawberry (i.e., bite

appropriate targets) were bitten with trials in which the orange and the almond (i.e., bite inappropriate targets) were bitten. Such analysis did not reveal any significant difference (bite appropriate vs. bite inappropriate targets, $P > .05$). Therefore, data were collapsed in terms of size across fruits. Two 3×2 repeated-measures ANOVAs with “condition” (congruent, incongruent, control) and “target size” (large, small) as within-subjects factors were performed to analyze the amplitude of maximum hand and lip aperture. Bonferroni corrections ($P < .05$) were applied when necessary.

Results

Maximum hand aperture

Results from the ANOVA revealed that the main effect of “target size” [$F(1,9) = 13,257$, $P < .005$, $\eta_p^2 = .60$] and the interaction “condition by target size” [$F(2,18) = 16.71$, $P < .001$, $\eta_p^2 = .65$] were significant.

The size of the visual target affected maximum hand aperture

This is an important aspect of the present study because in order to ascertain the effects of flavor information in terms of “size” on maximum hand aperture, it is necessary to demonstrate that the size of the visual target does affect hand aperture. In this respect, significantly different kinematic patterns of hand shaping for the small and the large targets were found. As witnessed by the significance of the main effect of “target size,” maximum hand aperture was significantly greater for the larger than for the smaller targets (99 mm vs. 71 mm).

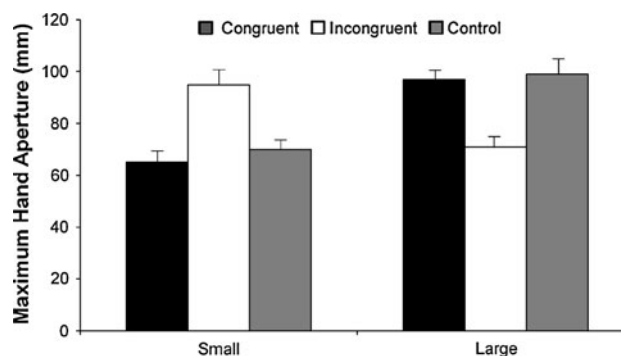


Fig. 2 Schematic representation of the “condition” by “target size” interaction when considering maximum hand aperture. *Black* refers to congruent conditions, *white* to incongruent conditions, and *gray* to control conditions. The object sizes are represented on the X axis. *Bars* represent the standard error of means

The effects of congruent and control flavor–visual information upon maximum hand aperture

As represented in Fig. 2, post hoc contrasts revealed that maximum hand aperture was similar when grasping was preceded by a sip of either “large” flavored solution or water (97 mm vs. 99 mm, $P > .05$). Similarly, maximum hand aperture was not significantly different when the action of grasping the small target was preceded by a “small” flavored solution or by water (65 mm vs. 70 mm, $P > .05$).

The effects of incongruent flavor–visual information upon maximum hand aperture

Figure 2 shows that maximum hand aperture was smaller when the action toward the large target was preceded by a sip of “small” rather than a “large” fruit juice or water (71, 96, 99 mm, respectively; $P_s < .01$). Conversely, when grasping a small target following the delivery of a sip of “large” fruit juice, maximum hand aperture was greater than when the same target was grasped following a sip of “small” fruit juice or water (95, 65, 70 mm, respectively; $P_s < .05$).

Maximum lip aperture

The main effect of “target size” [$F(1,9) = 5.547$, $P < .05$, $\eta_p^2 = .38$] and the “condition by target size” interaction [$F(2,18) = 19.946$, $P < .0001$, $\eta_p^2 = .69$] were significant.

The size of the visual target affected maximum lip aperture

When the visual target was bitten in the absence of preceding flavor information, maximum lip aperture was significantly greater for the larger than for the smaller targets (51.4 mm vs. 49.6 mm). The fact that the size of the visual target influenced maximum lip aperture, as found for maximum hand aperture, is a pivotal finding, given that the aim of the present study is to investigate an effector-independent effect of flavor stimulation upon hand and mouth motor behavior.

The effects of congruent and control flavor–visual information upon maximum lip aperture

As shown in Fig. 3, post hoc contrasts revealed that maximum lip aperture was accurately adjusted to target size when biting a large target preceded by a sip of either “large” flavored solution or water (52 mm vs. 53 mm, $P > .05$). In a similar vein, maximum lip aperture was accurately adjusted to target size when the small target was preceded by either a “small” flavored solution or water (48 mm vs. 48 mm, $P > .05$).

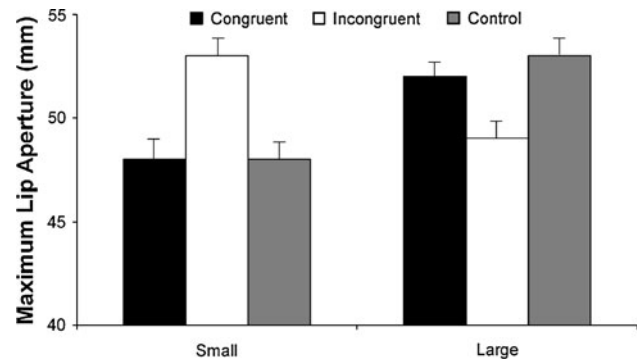


Fig. 3 Schematic representation of the “condition” by “target size” interaction when considering the maximum lip aperture. *Black* refers to congruent conditions, *white* to incongruent conditions, and *gray* to control conditions. The object sizes are represented on the X axis. *Bars* represent the standard error of means

Incongruent flavor–visual information in maximum lip aperture

As depicted in Fig. 3, when grasping a large target following the delivery of a sip of “small” fruit juice, maximum lip aperture was smaller than when the same target was bitten following a sip of either “large” fruit juice or water (49, 52, 53 mm, respectively $P_s < .01$). When the action toward the small target started following a sip of “large” rather than a “small” fruit juice, there was a significant increment in maximum lip aperture (53 mm vs. 48 mm; $P < .05$). Similarly, a significant difference in the amplitude of maximum lip aperture was found when a small target was bitten preceded by a sip of “large” fruit juice or water (53 vs. 48 mm; $P < .001$).

Discussion

The present study aimed at investigating whether hand and mouth kinematics could be affected by the presentation of preceding flavor stimulation. The results indicate that the kinematic patterning of a prehensile movement performed by either the hand or the lips was influenced in a similar vein by the “size” of a flavor. Of relevance, the motor plan evoked by the flavor appears to be surprisingly fine-grained and when elicited can modulate hand and mouth apertures.

In purely motor terms, it was found that the organization of the grasp-with-the-hand motor plan was similar to that characterizing the grasping-with-the-mouth action (Castello 1997; Gentilucci et al. 2001). Specifically, the results for the control conditions indicated that both maximum hand and lip apertures were affected by the size of the to-be-grasped visual target. That is, the large targets induced maximum hand and lip apertures that were significantly greater than those elicited by small targets. These results

confirm the notion of motor equivalence, suggesting that no substantial differences could be retrieved when comparing the kinematics of the act of grasping with the hand or the lips (Castiello 1997; Gentilucci et al. 2001). Naturally, such “equivalence” should consider the reduced absolute opening of the mouth when compared to the hand. These absolute differences in excursion reflect the biomechanical constraints imposed by the anatomy of the hand and the temporomandibular joint, which permits greater and smaller maximum apertures, respectively. This can be considered a classic example of effector-dependent characteristics that, according to Arbib’s hypothesis, are mapped into a dissociable level of the action plan with respect to the general effector-independent information underlying the act of grasping (Arbib 1990).

The central advance of the present study is that the concept of motor equivalence might be extended to cross-modal context involving the chemical senses. The fact that both the hand and the mouth scaled in accordance with the size of the flavor reflects the transformation of flavor-elicited information in motor commands. The motor plan elicited by the flavor stimulus is not totally overridden by the motor plan triggered, at a later time, by the visual target. That is, some aspects of the motor plan elicited by a “size” incongruent flavor stimulus persist in the motor plan executed for grasping the visual target. This effect was evident when comparing the incongruent flavor with the respective flavorless conditions. Put simply, the motor plan elicited by the “size” of the flavor leaked into the motor plan specifically tailored for grasping the visual target. This phenomenon led to interference effects, which were evident in both hand and mouth kinematics. From a perceptual perspective, the representation evoked by flavor seems to contain highly detailed information about the flavor stimulus (i.e., structural features). If flavor had provided a blurred and holistic object’s representation (i.e., a low spatial-resolution of the object’s image), then flavor would not have affected the aperture of the hand and the mouth. Second, from a motor perspective, the flavor representation seems to be mapped into the action vocabulary with a certain degree of reliability. The elicited motor plan embodies specific and selective commands for handling the “tasted” object, and it is fully manageable by the motor system.

At this stage, the natural question is how can this effect be explained? Our preferred ideas are that during initial perceptual analysis, a limited number of objects potentially relevant to action are processed in parallel. This initial perceptual processing flows continuously into areas of the brain that represent and subsequently initiate action. Such perceptual inputs are capable of automatically activating their associated responses without subjects’ intentions to act (Tipper et al. 1998; Castiello 1999). Due to this highly

efficient and automatic conversion of perceptual inputs into actions, different sensory inputs can evoke actions in parallel. As soon as the object evoked by the flavor is identified, an appropriate hand or mouth motor plan is initialized, which then competes with the motor plan triggered by the visual target; this conflict is played out in the kinematics of hand and mouth apertures. Thus, according to this model, the difference between the grasp plans activated by the flavor stimulus and by the visual target is essential for hand/mouth aperture interference effects to be observed. Indeed, when a flavor of a similar “size” as the visual target is presented, hand and mouth apertures are not altered with respect to when no-flavor is presented. A range of alternative explanations might be advanced to explain this finding. First, the information on the to-be-grasped object conveyed by the first modality (e.g., flavor) might be good enough to perform an accurate grasping that the information provided by a second modality (e.g., vision) would not have had any influence on the grasping kinematics. Second, when the “size” of the flavor and the size of the visual target match, the integration of the two modalities carrying similar information about the to-be-grasped object might support the presence of a more stable action. Third, the temporal delay occurring between the delivery of the flavor stimulation and the grasping-with-the-mouth action might have hidden the facilitation effect. Although participants exposed to different stimuli (e.g., olfactory and gustatory), presented at the same time and in the same space, (e.g., flavor), report facilitation effects in terms of both reaction times and accuracy (Gottfried and Dolan 2003; Spence et al. 2000, 2001), this happens only when the task is performed immediately following the chemosensory stimulation. In the present experiment, the start of the grasping-with-the-mouth action was slightly delayed with respect to the delivery of the flavor stimulation. Therefore, facilitation, if any, should have emerged, at the very least, for grasping-with-the-hand action. Having said that, in order to fully disentangle this issue, further research is needed, for example, considering the manipulation of the temporal delay between the hand and the mouth motor plan.

The present findings might allow some speculations on the neural mechanisms underlying the reported effects. The appealing hypothesis is an effector-independent activation of the motor system triggered by a flavor stimulation/processing, a concept that still lacks direct evidence in humans, but plausible if one considers that auditory, olfactory, and visual inputs are indeed able to activate motor brain areas (Ferrari et al. 2005; Cheng et al. 2007; Tubaldi et al. 2011). The starting point comes from comparative literature that provides some evidence for neural networks connecting the orbitofrontal cortex (OFC), which contains multisensory integration sites, with motor regions

(Cavada et al. 2000). Of particular interest for our study is the presence of direct connections between OFC and motor areas such as the ventral premotor area F5. An area that contains classes of neurons that become active when the monkey makes a specific action with its hand or mouth (Rizzolatti et al. 1988). In this connection, we are tempted to suggest that the cortico-cortical connections between OFC and F5 influencing motor output in non-human primates (Bates and Goldman-Rakic 1993) might also exist in humans and account for the influence of multisensory information on motor behavior and, in the present circumstances, in an effector-independent fashion. If this view is accepted, then we might have demonstrated that flavor information might have the potential to trigger activity within the neural networks subtending the control of the hand and mouth.

As a final point, it might be interesting to interpret the present results from an evolutionary perspective. Eating is a high approach-motivated behavior, generally connected to positive feelings. Recent research has revealed that individuals reduce the breadth of their attentional focus, shutting out irrelevant information, while they approach a positive high-motivating target (Gable and Harmon-Jones 2008). This perspective seems to be consistent with the above-mentioned selection for action theory (Allport 1987). Allport (1987), by means of the well-known example of the bowl of fruit, suggested that specific selective attentional mechanisms would focus on a target fruit we particularly desire. Therefore, the attentional focus preferentially narrows down to one object only, resulting in a privileged specification of action parameterization for that object and in the rejection of action parameterization for the irrelevant distractors (e.g., other fruits present in the bowl).

To conclude, the present findings extend current literature on chemosensorimotor transformations while grasping by suggesting the existence of effector-independent motor representations elicited by flavor. This seems to provide further fuel to the notion that acting in a selective manner is a multisensory process that also involves the chemical senses.

References

- Allport DA (1987) Selection for action: some behavioral and neurophysiological considerations of attention and action. In: Heuer H, Sanders F (eds) Perspectives on perception and action. Erlbaum, Hillsdale, pp 395–419
- Arbib MA (1990) Programs, schemas, and neural networks for control of hand movements: beyond the RS framework. In: Jeannerod M (ed) Attention and performance XIII: motor representation and control. Erlbaum, Hillsdale, pp 111–138
- Aristotle (1986) *De Anima* (On the soul, trans: Lawson-Tancred TBH). Penguin Books, London
- Bates JF, Goldman-Rakic PS (1993) Prefrontal connections of medial motor areas in the rhesus monkey. *J Comp Neurol* 256:211–228
- Calvert G, Brammer M, Bullmore E, Campbell R, Iversen S, David A (1999) Response amplification in sensory-specific cortices during crossmodal binding. *Neuroreport* 10:2619–2623
- Castiello U (1997) Arm and mouth coordination during the eating action in humans: a kinematic analysis. *Exp Brain Res* 115:552–556
- Castiello U (1999) Mechanisms of selection for the control of hand action. *Trends Cogn Sci* 3:264–271
- Castiello U, Stelmach G (1993) Generalized representation of handwriting: evidence of effector independence. *Acta Psychol* 82:53–68
- Castiello U, Bennett KMB, Egan GE, Tochon-Danguy HJ, Kritikos A, Dunai J (2000) Human inferior parietal cortex ‘programs’ the action class of grasping. *Cogn Syst Res* 1:89–97
- Castiello U, Zucco GM, Parma V, Ansuini C, Tirindelli R (2006) Cross-modal interactions between olfaction and vision when grasping. *Chem Senses* 31:665–671
- Castiello U, Giordano BL, Begliomini C, Ansuini C, Grassi M, Gilbert S (2010) When ears drive hands: the influence of contact sound on reaching to grasp. *PLoS ONE* 5:887–891. doi: 10.1371/journal.pone.0012240
- Cavada C, Company T, Tejedor J, Cruz-Rizzolo RJ, Reinoso-Suarez F (2000) The anatomical connections of the macaque monkey orbitofrontal cortex. *A Rev Cereb Cortex* 10:220–242
- Cheng Y, Meltzoff AN, Decety J (2007) Motivation modulates the activity of the human mirror-neuron system. *Cereb Cortex* 17:1979–1986
- Driver J, Spence C (2000) Multisensory perception: beyond modularity and convergence. *Curr Biol* 10:R731–R735
- Ferrari PF, Maiolini C, Addressi E, Fogassi L, Visalberghi E (2005) The observation and hearing of eating actions activates motor programs related to eating in macaque monkeys. *Behav Brain Res* 161:95–101
- Gable PA, Harmon-Jones E (2008) Approach-motivated positive affect reduces breadth of attention. *Psychol Sci* 19:476–482
- Gentilucci M, Cattaneo L (2005) Automatic audiovisual integration in speech perception. *Exp Brain Res* 167:66–75
- Gentilucci M, Daprati E, Gangitano M (1998) Haptic information differentially interferes with visual analysis in reaching-grasping control and in perceptual processes. *Neuroreport* 9:887–891
- Gentilucci M, Benuzzi F, Gangitano M, Grimaldi S (2001) Grasp with hand and mouth: a kinematic study on healthy subjects. *J Neurophysiol* 86:1685–1699
- Ghazanfar AA, Schroeder CE (2006) Is neocortex essentially multisensory? *Trends Cogn Sci* 10:278–285
- Gottfried JA, Dolan RJ (2003) The nose smells what the eye sees: crossmodal visual facilitation of human olfactory perception. *Neuron* 39:375–386
- Hugues O, Abbs J (1976) Labial-mandibular coordination in the production of speech: implication for the operation of motor equivalence. *Phonetica* 44:199–221
- Keele S (1968) Movement control in skilled motor performance. *Psychol Bull* 70:387–403
- Merton P (1972) How we control the contraction of our muscles. *Sci Am* 226:30–37
- Parma V, Ghirardello D, Tirindelli R, Castiello U (2011) Grasping a fruit: hands do what flavor says. *Appetite* 56:249–254
- Patchay S, Castiello U, Haggard P (2003) A cross-modal interference effect in grasping objects. *Psychon B Rev* 10:924–931
- Patchay S, Haggard P, Castiello U (2005) Cross-modal links in action: evidence for an object-centred reference frame for control of grasping. *Exp Brain Res* 23:1–11

- Patchay S, Haggard P, Castiello U (2006) An object-centred reference frame for control of grasping: effects of grasping a distractor object on visuomotor control. *Exp Brain Res* 170:532–542
- Rizzolatti G (1987) Functional organization of inferior area 6. Motor area of the cerebral cortex. (Ciba Foundation symposium 132). Wiley, Chichester, pp 171–186
- Rizzolatti G, Gentilucci M, Fogassi L, Luppino G, Matelli M (1987) Neurons related to goal-directed motor acts in inferior area 6 of the macaque monkey. *Exp Brain Res* 67:220–224
- Rizzolatti G, Camarda R, Fogassi L, Gentilucci M, Luppino G, Matelli M (1988) 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
- Sato M, Buccino G, Gentilucci M, Cattaneo L (2010) On the tip of the tongue: modulation of the primary motor cortex during audio-visual speech perception. *Speech Commun* 52:533–541
- Spence C, Kettenmann B, Kobal G, McGlone FP (2000) Selective attention to the chemosensory modality. *Percept Psychophys* 62:1265–1271
- Spence C, McGlone FP, Kettenmann B, Kobal G (2001) Attention to olfaction. A psychophysical investigation. *Exp Brain Res* 138:432–437
- Tipper SP, Howard AL, Houghton G (1998) Action-based mechanisms of attention. *Philos Trans R Soc Lond B* 353:1385–1393
- Tubaldi F, Ansuini C, Dematté ML, Tirindelli R, Castiello U (2008a) Effects of olfactory stimuli on arm-reaching duration. *Chem Senses* 33:433–440
- Tubaldi F, Ansuini C, Tirindelli R, Castiello U (2008b) The grasping side of odours. *PLoS ONE* 3:e1795. doi:10.1371/journal.pone.0001795
- Tubaldi F, Turella L, Pierno A, Grodd W, Tirindelli R, Castiello U (2011) Smelling odors, understanding actions. *Soc Neurosci* 6:31–47
- Wright C (1990) Generalised motor programs: reexamining claims of effector independence in writing. In: Jeannerod M (ed) *Attention and performance XIII: motor representation and control*. Erlbaum, Hillsdale, pp 94–319