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CHOIRS OF PRAISE: SOME ASPECTS OF ACTION UNDERSTANDING IN FIFTEENTH-CENTURY PAINTING AND SCULPTURE

Before I begin, I want to say how much I owe to Marilyn's work on Piero, on the Barberini Inventories, and on *The Place of Narrative* at various critical points in my career.

Did Jan van Eyck go to Italy? This is an old question about Van Eyck, and raises a number of important issues about his art. I do not intend to settle it here. Rather, I ask it because it casts into high relief a central issue in the ways we think about responses to art, and, more specifically, about the relations between observation and action imitation.

Over a century after Van Eyck died, the Ghent chronicler Marcus van Vaernewyck recorded that Jan went to Italy.¹ We know that he made at least four "distant and secret journeys" between 1426 and 1430 in the course of accompanying diplomatic missions of Philip the Good, including two to the Iberian peninsula in 1427 and 1428/29.² Scholars have frequently made a comparison between the revolutionary life-like representations of Adam and Eve on the outer panels of the Ghent Altarpiece and the famous figures in the *Expulsion* scene in the Brancacci Chapel.³ They have suggested that the slightly

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2. Often discussed, with the data well summarized in Elizabeth Dhanens, *Hubert and Jan van Eyck* (New York: Alpine, 1980), 47–50. Her summary is based on the documents in Weale, *Hubert and John van Eyck*.
di sotto in su viewpoint of Van Eyck’s Adam may be derived from Masaccio’s Trinity in Santa Maria Novella.⁴ They have noted the similarity between the figure of God the Father in the niche above Saint George on Or San Michele and some of the prophets looking down from their lunettes on the Ghent Altarpiece, especially Micah and Zachariah.⁵ Recently Penny Howell Jolly commented on the relationship between Jan’s Annunciation and the miraculous image of Santissima Annunziata, and suggested that he may have been in Florence in 1426 or 1428.⁶ Charles Sterling insisted that Jan traveled to Italy in 1426, and pointed to similarities with the work of Gentile da Fabriano.⁷ The greatest Belgian scholar of the altarpiece, Elizabeth Dhanens, thought that the cypresses, palms, and bushy orange trees in the lower register of the altarpiece might be explained by such a journey.⁸ Millard Meiss, in a famous article, attempted the same explanation for the alpine landscape on the Just Soldiers panel.⁹ But are all these alleged borrowings — valid or not — sufficiently direct to argue for a trip to Italy? One has only to consider, for example, the similarity between the figure of God the Father on the Ghent Altarpiece and that of Andrea del Castagno’s similar figure in San Zaccaria in Venice, which could certainly be used as an argument in favor of an Italian journey, to realize once more the difficulty of drawing conclusions for artistic derivation on the grounds of putative visual similarity.

But there is one important set of visual parallels that has never been adequately addressed — even though teachers in the two fields concerned have no doubt often mentioned it. These are the parallels between two of the most beautiful choirs of praise in the history of art.

The first I want to address is the choir (or, more precisely, the choir and musicians) on the panels that flank the Virgin and John the Baptist on the front of the Ghent Altarpiece (Fig. 1). Whether these panels originally occupied the position they now do we do not know. They may originally have served as organ shutters,¹⁰ as has sometimes been suggested,¹¹ but proof is lacking.

⁴ Cf., for example, Dhanens, Van Eyck: The Ghent Altarpiece, 106.
⁵ Ibid., 108–9.
⁸ Her proposal, however, was a little ambiguous, suggesting that the presence of this vegetation “need not necessarily be explained solely in terms of Jan van Eyck’s journey to Spain and Portugal of 1429,” Dhanens, Van Eyck: The Ghent Altarpiece, 105.
¹⁰ For the iconography of organ shutters, see George Servières, La décoration artistique des buffets d’orgues (Paris and Brussels: G. van Oest, 1928). For music-making angels, see, inter alia, plates III and XXVII.
My concern, however, is with the facial expressions and physical actions of the members of these choirs of praise, not with the nettlesome question of the origins and constitution of the Ghent Altarpiece.

On the left are the singers, about whom I shall have the most to say; beneath them runs the inscription "Melos Deo, Laus Perennis, Gratiarum Actio" (A song to the Lord, Perpetual Praise, and the Giving of Thanks). On the right are the instrumentalists who praise God on the harp, organ, and strings: "Laus eum in cordis et organo" (Praise him on strings and with the organ) reads the inscription, fittingly taken from Psalm 150.

The leading chorister on the left, who raises his one hand to beat time and the other to move the lectern to a better position, is clad in the most sumptuous of the brocades in his group, while an equally resplendent ermine-trimmed cope is worn by the diademed figure playing the organ on the right panel. The figures on these panels cannot really be called angels, since they have no wings; but it is worth noting that they wear albs, copes, and dalmatics, and other liturgical garments, just as in the case of the unforgettable angels who attend the Nativity of Christ in the much later Portinari altar of Hugo van der Goes. If not angels, the Eyckian figures are certainly heavenly choirs, and they sing and play with extraordinary concentration. As Elisabeth Dhanens has suggested, they may well allude to the liturgical choir that sings both in the mass of the Church and in the eternal mass of Christ referred to by Rupert of Deutz. But this is not my present concern; rather, it is with action representation.

While the figures on the right panel play their instruments with a kind of sweet and humble concentration, those on the left command much more of our attention. Already in 1586 Lucas de Heere commented on the fact that their expressions — and in particular their mouth movements — were so clear that beholders could easily tell in what register they were singing. Combining the notion of movement with that of expression, Karel van Mander wrote in 1604 that "one can easily tell from their movements — actien — who is singing soprano, who alto, who tenor and who bass." They sing with such open-mouthed enthusiasm and concentration, abandoning themselves to their songs of praise, that it is hard not to want to imitate them, even to wrinkle one's own brows with the apparent difficulty of singing whatever it is they are singing. Indeed, the appearance of difficulty has so struck scholars (and other spectators as well) that it has even been suggested that the high

concentration, furrowed brows, and occasional frown is a direct expressive consequence of the difficulty of the music they are singing. And this is not the least of the kinds of imitative sensations that one may begin to feel in looking at these panels, for anyone who looks more than passingly is pretty much bound to want to strum their fingers rather as the harpist does on the shoulder of the viol player on the right. I shall return to such feels later on.

In the meantime let us turn directly to the kinship between the two works that form the core of this paper: Jan van Eyck's choristers and musicians, and Luca della Robbia's cantoria in Florence (Fig. 2). While a few scholars have commented on the broad similarities, it is remarkable how little they have been discussed, let alone analyzed in detail. In her recent article suggesting that Jan may have visited Florence (either in 1426 or 1428), Penny Jolly does not even mention them. In his magnum opus, Panofsky noted in passing that "the musical 'angels' in the Ghent Altarpiece, it seems, were originally conceived as the northern cousins of Luca della Robbia's glorified choristers on the cantoria of Florence Cathedral." And he left it at that.

Indeed, the few scholars who have actually commented on the matter have been content to note the parallels — which may indeed be all they are. Baldass, for example, remarked that there was "something similar" in the lifelike reliefs of Luca's sculptures — and left it at that. Roberto Salvini was frank about his perplexity in his otherwise perceptive comment that in Luca's cantoria "il freddo formalismo appreso da Michelozzo si riscalda, a contatto probabilmente con gli angeli cantori di van Eyck — indirettamente conosciuti, non possiamo indovinare per quale via — si disgela." Panofsky's statement that Van Eyck's choristers "were originally conceived of as northern cousins" of della Robbia's is also rather evasive. Who, if anyone, borrowed from whom? This is a real crux — for these two works are almost exactly contemporary.

The Ghent Altarpiece was completed in 1432, according to the chronogram that runs along the frames at the base of the lower panels of the closed work, while in all probability, Luca della Robbia received his commission for the cantoria some time before 1431 and continued working on the reliefs through

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17. Many scholars (e.g., Panofsky, Early Netherlandish Painting, 1:227; Baldass, Van Eyck, 48; Dhanens, Van Eyck: The Ghent Altarpiece, 117) have suggested that the design of these panels is Hubert's, while the execution is by Jan, though no convincing proof is ever offered. Cf. the following note.
18. Panofsky, Early Netherlandish Painting, 1:221. The statement, however, is a perplexing one, in the light of Panofsky's claim that the angels were actually conceived by Hubert; see ibid., 227 ("probably designed by Hubert").
21. Dhanens, Hubert and Jan van Eyck, 81.
Luca's work was probably intended to go beside one of the great new organs adjacent to the north and south sacristies in Florence Cathedral, just as Jan's panels may themselves have been conceived as organ shutters. Even the inscription, "Praise him on strings and with the organ" (Laudate eum in cordis et organo), comes from the same psalm (150) that is inscribed in full along the base of the reliefs of Luca's cantoria, and which Luca brilliantly broke down into each of its elements, particularly emphasizing not just the different instruments played, but also the singing and — perhaps most significantly of all for the matter of action representation and imitation — the dancing.

If anything, Luca must have been designing his cantoria in the very years that Jan was at home working on the Ghent Altarpiece. So a number of possibilities present themselves: either Jan van Eyck paid a visit to Italy pretty much at the time of the production of the cantoria; or Luca made a quick trip to the north (which seems less likely); or this is yet one more of those instances in the history of art where apparently very close similarities are attributable to chance and not to direct influence.

But perhaps they are attributable to something else. Both artists clearly made a very close study of human beings singing (and in Luca's case dancing too). Perhaps each artist's remarkable ability to display muscle movements with such precision, as Lucas de Heere already suggested, is sufficient in and of itself to explain the similarities. It was precisely in the section on actien in his didactic poem on the art of painting, the Grondt, that Van Mander gave as an example of good imitation of nature the rapid movements of the hands and fingers on lutes and harps. No wonder that he specifically praised Van Eyck's panels for the way in which the movements — the actien — of the singing angels conveyed the actual sounds of their respective voices. But while for Lucas de Heere too the marvel was that Jan van Eyck's accurate representation of mouth and eye movements enabled one to distinguish between each of the voices, in Luca della Robbia it is the extraordinary representation not just of mouth movements but of the whole body that is likely to seem — and always to have seemed — so compelling.

Psalm 150 only mentions dance once, but it is impossible not to notice the dancing infants in the first and last of the panels on the upper register of Luca's

23. On these see Giovanni Poggi, ed., Il Duomo di Firenze (Florence: Kunsthistorisches Institut in Florenz, 1909), ca.-xxvii. Pope-Hennessy, Della Robbia, 19, notes that Luca's cantoria was substantially complete by 1438 when the authority was given to insert the consoles over the entrance to the north sacristy on which it rested.
25. "In wieckende bootsen salmen met scherpen/ Natuer opmercken, de leden doen slaven/Tzy handen, vinghres, op Luyten oft Herpen"; Van Mander, fol. 14r, par. 32.
26. Ibid., fol. 200r.
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cantoria, and the first and the last of the panels below. It is as if the sculptor realized that the music-making required dance (indeed, Donatello’s cantoria also in Florence Cathedral, like its important predecessor, the pulpit in Prato, would show only dancing infants, that common ancient token of peace and prosperity, and do away with the musicians altogether). To stand in front of Luca’s work, and to look patiently at the figures he sculpted is to have a sense, still never adequately defined, of the kinds of corporeal involvement with representation of which the great nineteenth- and early twentieth-century empathy theorists spoke, from Lotze and Vischer through Lipps, Volkelt, and Aby Warburg and then found a different form of articulation in the phenomenological approaches to art of Merleau Ponty. Already in 1890, William James asserted that “every mental representation of a movement awakens to some degree the actual movement which is its object,” while more recently a considerable amount of research in cognitive psychology and the cognitive neurosciences has been dedicated to the


31. The key text was Warburg’s doctoral dissertation on Botticelli, published as Aby Warburg, Sandro Botticelli’s Geburt der Venus und Frühling: Eine Untersuchung über die Vorstellungen von der Antike in den italienischen Frührenaissance (Hamburg: Leopold Voss, 1893). This is now available, along with the other relevant texts, in Aby Warburg, The Renewal of Pagan Antiquity: Contributions to the Cultural History of the European Renaissance, Texts & Documents (Los Angeles, CA: Getty Research Institute for the History of Art and the Humanities, 1999).


ways in which observing, imagining, or representing actions can excite the motor programs actually used to execute those same actions.  

To gaze at Luca’s nude and half-clothed and clothed infants, some with draperies clinging transparently to their bodies, some with draperies flying, is to have a sense of imminent and endogenous movement, a sense of desiring to move, in ways that seem to emulate with some precision the movements of the figures, as if one were oneself beginning to stretch out one’s hands, to point, to clasp the hands of others, even to open one’s mouth and join the sculpted orchestra and choir in music and jubilation.

But what is really entailed by that “as if,” that frequent associate of vision by which body is joined to sight and felt movement joined to movement observed?

In the first of Luca’s panels, the trumpeters blow their long trumpets across the top of the scene, their cheeks swelling comfortably without effort. Beneath them three children dance, childishly of course, and yet not entirely with grace. Their movements seem a little awkward, and yet, somehow, one’s own body feels stirred too, as if in a certain muscular sympathy with precisely those movements. But is it possible to be more precise about that “somehow,” more than the usual Merleau-Pontyan phenomenology of response to works of art would allow? Perhaps the claim for an empathetic sense of movement is little more than purely psychological, that is, that it is predicated on a psychic response to the fact that the apparent enthusiasm of these musicians and dancers is infectious (whatever we may really mean by the term “infectious”); or perhaps it is some innate sense of what constitutes graceful or decorous or harmonious movement that causes us, as if by some contrary sense, to be thus stirred, as if we, or our bodies, were naturally resistant to such clumsiness.

But then one notices the trumpeters again: could it be that one feels one’s cheeks swell too, at least incipiently, as if in sympathy with theirs? And when, in moving on to the next panel showing the players on the psaltery, one scans the series of mouths opening in praise to the Lord, does one not sense one’s mouth beginning to open more or less in exactly these ways too? One may not see oneself in a mirror, but the sense of imitation seems exact enough.

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But how to calibrate such responses? It is impossible, in asking such questions, to pose them in anything except in terms of first-person responses to third-person actions. To do otherwise would be to prevaricate. Current art history resists the claims of the first person, particularly in the plural; but in claims about automaticity and precognitive corporeal reactions, it is impossible to avoid the generality implicit in all of them. To speak of our responses, or of how we react is not to disallow further pressures on general first-person claims, nor is it to insist on similarity of response when difference might be more plausible, or even appropriate. It is to acknowledge the fundamental heuristics of a procedure that yokes the findings of the contemporary cognitive neurosciences to the understanding of the place of works of art in an inhabited world. It is not to exclude the possibility of different reactions.

Other features of Luca's second panel possess even greater capacity to engender imitative behaviors. When looking at the figure with the thrown-back head on the right, the observer may feel her own head tilt backward too. Reviewing the scene from the beginning, she might feel the same effect in looking at the less strenuous singer on the left. It is at this point that one is likely to notice the hand of the young singer at the extreme left resting his hand on the shoulder of his companion. The movement seems so comfortable, so familiar, so natural, that the desire for some form of emulation may well up within the observer too. The question of the locus and neural substrate of such feels begins to impose itself forcefully.

So it is with the next panel as well. As one's eyes encounter the thrown-back head of the figure who sings in accompaniment to her cithara on the right, one almost has to stop oneself from tilting back one's own head too. Then one may notice, here again, the tender gestures of the silent figures resting their hands on the shoulders of their singing companions; or the eager girl who moves in from the left, just opening her mouth in song; or the gesture — so understandable and so emulable — of the girl rushing in from the left to wrap her fingers around one of those of the awkward child in the front of the first panel; or the two children pointing upward, excitedly, indexically, to the singing figures above them in the third panel; or the two children in the second, who have sat themselves down to play on their junior psalteries. In seeing them, especially the first child on the left, it is all too easy to imagine sinking down to sit and sing in the manner he does. In this same panel, just as in the case of Jan's choristers, it is almost as if one's mouth silently opens again, to join that choir — and perhaps even to emulate the actions of their joined hands. Luca's art is so remarkable that it seems to encourage its beholders, somehow or another, to participate in the movements he so vividly depicts.

But how, more precisely? Thanks to the new cognitive neurosciences it is possible to be more precise about the kinds of felt participatory movements I have attempted to suggest in the preceding paragraphs. These are the kinds
of felt movement that also engaged the attention of the nineteenth-century empathy theorists, whose ideas also lay, I believe, at the basis of Berenson’s theory about the “life-enhancing” qualities of Renaissance art. This was the theory (if it can be called that) that viewing the actions portrayed in the painting and sculpture of the High Renaissance actually enhances one’s sense of one’s own muscular capacities.36

Imitation is an old topic in the history of art. For the most part it has been understood in terms of artistic imitation of a model, whether in real life or in art. It has not been much considered in terms of the imitation of the representation of movement in works of art — or, to put it still more precisely, in terms of the felt imitation of the representation of movement and action in a work of art, or in images more generally. Despite the obvious relevance of such a topic for the history of art, and despite the now vast neuroscientific literature on just this subject, it has been ignored by art historians. For the sake of clarity it should be noted that by “action representation” neuroscientists mean the representation of actions in the brain. I confine myself here to perhaps the most important area of research in this whole domain of the understanding of the neural bases of action imitation.37 In one of the most important neuroscientific discoveries of the last decade, a group of scientists working in Parma under Giacomo Rizzolatti discovered mirror neurons in the ventral premotor region (area F5) of the brain of the macaque monkey.38

A few years after Rizzolatti and colleagues’ initial discoveries, mirror circuits

36. See n. 62 below.
were also discovered in the human brain, in the inferior parietal lobule to which the premotor cortex is connected, and in the posterior area of the infero-frontal gyrus (Brodmann’s area 44), the functional equivalent of F5 in monkeys that in humans overlaps with Broca’s area, a fact of some significance that I hope to deal with in later papers.39

Mirror neurons are a specific class of visuomotor neurons that have been found to fire both when we perform an action and when we observe a similar action performed by another.40 The implications of this are clear. During observation of an action both by a macaque monkey and a human, there is a recruitment of the very same neural structures that would normally be involved in the actual execution of the observed action. In other words, we may suppose that when we see an action in a picture, the same parts of the brain (chiefly in the premotor cortex and the inferior parietal lobule) fire that would do so if we were engaged in those same actions ourselves.41 It thus becomes possible to begin to understand that frequent sense of physical empathy with depicted actions that observers feel when they look at pictures, and to give an account of the neural bases for the much-discussed sense of bodily involvement with particular actions and movements within pictures. Obviously there are questions of attention that enter into consideration here; but at last, as the biological bases of empathy and emotion become clearer, one can stop talking as vaguely as art historians and critics habitually do about our corporeal involvement with paintings and sculptures. The neural substrates of the empathetic feels we have in our muscles when we see some particularly striking movement in a picture, or even in our skin when we see the puncturing, wounding, or mutilation of body and flesh in a painting, are now evident.42

The majority of mirror-neuron experiments have found the “as if” effect — response to the sight of the movements of others as if one were executing the same movement oneself — in the case of transitive actions, like reaching for food or gripping an object.43 In monkeys, mirror-neuron discharge was not found

40. Rizzolatti, Fogassi, and Gallese, “Neurophysiological Mechanisms” (as in n. 37), 661.
41. Several of the mirror-neuron experiments were done on the basis of the observation of actions shown in photographs, but none in works of art.
43. As was made clear at the outset, e.g., Gallese et al., “Action Recognition”; and Rizzolatti et al.,
in the case of non-goal directed actions; similarly, when a mirror system was first detected in humans, it seemed only to be activated upon observation of goal-directed actions, like grasping for food or reaching for the hand or finger of another (as in the case of the little dancers in the first of Luca's panels). But it has now become clear that the mirror system is activated in the imitation of non-goal directed actions too. Mirror neurons also fire in the case of holding, manipulating, tearing, and ripping — basically all object-related hand movements. But clearly this is still less than art historians might like. What of the neural substrate of other matching mechanisms? What, for example, are the neural bases of other imitative feels, of non-goal directed movements, such as dancing and buccal movements — the movements of the mouth, and other forms of zygomatic movement, such as smiles, frowns, and so on? There is some evidence of matching systems for these as well. Before returning to the subject of dancing figures, however, let us stay with the issue of buccal movements, a topic that has not by any means been exhausted in the literature and is, of course, central to the issue with which this paper began.

By now a great deal is known about responses to facial expressions. The art-historical literature has always been rich in this area. Exactly as Giovanni Battista della Porta and Charles Le Brun might have predicted, neuroscientists have now identified a region of the brain that selectively fires in response to the sight of faces. This is the fusiform face area (FFA) located on the part of the temporal lobe known as the fusiform gyrus. When fearful faces are seen, for example, signals are sent directly from the FFA to the amygdala, which projects backward to the visual cortex and forward to the prefrontal cortices for processing. We thus not only instantly recognize a sad face, but

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44. Much is now available. For a good overview with particular reference to the critical work of Charles Le Brun, see especially Jennifer Montagu, The Expression of the Passions: The Origin and Influence of Charles Le Brun's Conférence sur l'expression générale et particulière (New Haven and London: Yale University Press, 1994). But see also the useful work by Jean-Jacques Courtine and Claudine Haroche, Histoire du visage: Exprimer et taire ses émotions, XVIe-début XIXe siècle (Paris: Rivages, 1988). While the whole physiognomic tradition from Giovanni Battista della Porta on has been well-studied, there still remain a number of historical figures who deserve much more attention than they have received so far in this context, notably the prolific writer on the expression and recognition of the passions, Marin Cureau de la Chambre (1595–1669).


also, because of the engagement of the amygdala in cases of fear, and the anterior insula in cases of disgust, are likely to feel similar emotions ourselves.

In the case of less emotionally-laden movements like those produced by singing, the literature is sparser, but rich and relevant enough to our choirs of praise. It begins with Melzoff and Moore’s famous experiments of almost thirty years ago. They demonstrated that, contrary to Piaget’s estimate that infants learned to imitate facial gestures of adults between 8 and 12 months of age, infants as young as 12 to 21 days old imitate gestures such as lip protrusion, mouth opening, tongue protrusion, and sequential finger movements. And the illustrations to their pioneering article of 1977 (Fig. 3) provide a remarkable parallel to the mouths of the singing choristers of the Ghent Altarpiece and of the cantoria, especially in the opening of the mouths to sing. (Figs. 4-6)

Of course, all that this parallel may demonstrate is what is already obvious, namely that both Van Eyck and della Robbia were exceptionally gifted imitators of living models. Indeed, it is not a matter of what Salvini called a fusion of “vivido naturalismo — nelle bocche con tanta franchezza aperta al canto — e di suprema idealità”; it is “vivido naturalismo.” But Melzoff and Moore’s work take us much further than this. In 1983 they demonstrated that imitation of buccal movements in particular could be pushed back to newborns from less than one hour to three days old. The clear implication of their articles — and these illustrations — is that imitative buccal movements are not only the consequence of learning and experience but also indicate a more basic imitative capacity. Melzoff and Moore thought that this cross-modal function might explain what seems to be an automatic ability to link visual stimuli with muscular responses. In a later article, significantly entitled “Molyneux’s babies” (after the famous thought-experiment by the eighteenth-century philosopher Molyneux about whether a newly-sighted man could immediately identify shapes as squares, spheres, cubes, and so on), Melzoff went still further. He did a series of experiments showing that by eighteen weeks of age, infants recognize that /a/ sounds, for example, go with mouths that are open wide, /i/ sounds with mouths that have retracted lips, and /u/ sounds with mouths whose lips are protruded and pursed. We now have a reasonably secure — and very

48. Ibid., 75.
49. Salvini, “Banchieri fiorentini,” 87. The naturalism, the extreme lifelikeness of the figures on the Ghent Altarpiece had been long commented upon. For the comments of Hieronymus Münzer in 1495 (“videntur omnia esse viva”) and van Vaemewyck in 1566, see Dhanens, Hubert and Jan van Eyck, 108–11.
suggestive — scientific context for the old claims by Van Mander that one could see who sang high, middle and low, and the more recent, perfectly intuitive claim by Baldass that the pitch of the voices of the singing angels on the Ghent Altarpiece was revealed by the shape which Van Eyck gave to their mouths.52

But Meltzoff and Moore's cross-modal explanation never seemed an entirely sufficient explanation for the imitation of buccal movements such as these. Once mirror neurons were discovered that underlay action representation in the brain, it seemed clear that it would not be long before similar neurons would also be found to code specific mouth movements. In 2001 Buccino and others wrote an important article in which they demonstrated that the mirror system is not restricted to goal-directed hand actions but applies to a rich repertoire of body actions as well, thus providing, as they put it, "a neural substrate for a matching mechanism."53 They showed that somatotopic activation occurred in the premotor cortex during the observation of all actions (actions, it must be noted, rather than just simple movement, exactly as Van Mander intended with the actien, expressive movements that painters were expected to master fully). Two years later, Ferrari and his colleagues discovered mouth mirror neurons that motorically code mouth actions as well.54 One should remember that when one observes an action, mirror neurons fire even if one does not actually move the relevant muscles themselves. This may account for the extraordinary feeling of imitation that one may have in looking, for example, at the singing figures on the Ghent Altarpiece or on Luca della Robbia's cantoria. Just as the neuronal responses discovered by Rizzolatti and his colleagues occurred in response to the observation of object-related and goal-directed movements, so too a large portion of the mouth mirror neurons found by Ferrari and colleagues relate to ingestive functions, such as grasping, sucking, or breaking food. But Meltzoff's

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52. Baldass, Jan van Eyck, 40.
53. "The effector-related somatotopic activation pattern in the premotor cortex during the mere observation of actions proves that in humans the mirror system is not restricted to hand actions, but includes a rich repertoire of body actions. It therefore constitutes a neural substrate for a matching mechanism....","; G. Buccino et al., "Action Observation Activates Premotor and Parietal Areas in a Somatotopic Manner: An fMRI Study," European Journal of Neuroscience 13.2 (2001): 403.
experimental work on Molyneux's problem suggests an imitative process when it comes to non-goal-directed mouth actions as well. Indeed, Ferrari and colleagues noted that the most effective visual stimuli for triggering mirror neurons are in fact communicative mouth gestures.  

In 2003 Watkins and his colleagues pushed these discoveries towards their larger and, in my view, still more significant conclusions. They showed how visual observation of speech-related lip movements both in monkeys and in humans enhanced the excitability of the motor units underlying speech production, particularly those in the left hemisphere: the hemisphere, as is well known, that plays a large role in language production.  

While Watkins and colleagues noted that the changes in motor resonance during perception was located in the primary motor cortex, where there are no mirror neurons, Rizzolatti and his colleagues insisted that such changes are mediated by the mirror-neuron system in the premotor cortex. In other words, the increase in motor excitability during both visual and auditory perception of speech are likely to be largely due to inputs from the premotor areas. None of this, however, diminishes the central relevance of the discovery of a mirror system for its role in the imitative feels we have in the case both of goal-directed actions of the limbs and of communicative buccal ones as well.

There is more. As in the case of the observation of the other movements, the mirror-neuron research has demonstrated that observation of buccal movements actually enhances the motor excitability of the relevant somatotopic areas in the brain. This enhancement of motor excitability during visual observation occurs in a wide range of movements, especially goal-directed ones. What now requires further study is the relevance of action understanding for non goal-directed movements, such as dancing. Here too Calvo-Merino and colleagues have made a useful begin-
ning by illuminating the critical relationship between expertise and imitation. Yet anyone who looks more than passingly at the dancing putti of Luca della Robbia's cantoria (or, for that matter, Donatello's cantoria in Florence and the famous outdoor pulpit in Prato) cannot but have some sense of incipient imitative action, one that entails not fear but a feeling of lightness and well-being. Such responses, it is true, are much less well understood than negative emotional responses, like fear, which now have been much studied. Still, the neuroscience of action understanding offers support for Bernard Berenson's often-dismissed views of what he described as the "life-enhancing" qualities that he believed could ensue from looking at figures in movement, especially in superior works of art. As is well-known, he often claimed that the quality of the depiction of figures in action and movement to be seen in the best works of Pollaiuolo, Michelangelo, and other Renaissance artists could provide viewers with an enhanced sense of their own muscular capacities. Little can he have foreseen the discoveries that offer an account of how observers seem to join in the movements of others, and that seem so relevant to the singing angels on the Ghent Altarpiece and to their southern counterparts on Luca's cantoria. It is now possible, I believe, to give new and exact meaning to what we mean when we say that we seem to participate in the dance of Luca's putti and join in the songs of praise sung by his and Jan van Eyck's choristers — just as we do in the case of the choirs of deserved praise that we join in offering to Marilyn Lavin today.

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61. Fear and disgust have been particularly well-studied, with much rich information now available on the role of the amygdala and the insula in these emotions. For a good overview, see now the excellent survey by LeDoux (as in n. 46).
62. For perhaps the most striking passage of this kind, see the heading on "Representation of Movement" in the section on Pollaiuolo (VIII) in Bernhard Berenson, The Florentine Painters of the Renaissance (New York: G.P. Putnam's Sons. 1896), 50–56. The essay was collected in all the editions of The Italian Painters of the Renaissance from 1930 on; it will be found in Bernhard Berenson, The Italian Painters of the Renaissance (London and Glasgow: Collins Fontana, 1962), 76–79.

Fig. 2. Luca della Robbia, Cantoria. Florence, Museo dell’Opera del Duomo.

Fig. 4. Luca della Robbia, Singing Boys. *Cantoria*, Florence, Museo dell'Opera del Duomo.

Fig. 5. Luca della Robbia, Singing Girls. *Cantoria*, Florence, Museo dell'Opera del Duomo.